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유럽 너도밤나무(*Fagus sylvatica* L.)幼苗發達 동안의 한 同位酵素 遺傳子座에서의 生存力選擇*[1]

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Viability Selection at an Allozyme Locus during Development in European Beech (*Fagus sylvatica* L.)*[1]

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The genetic structures at one leucine aminopeptidase locus (LAP-A) of acorns, seedlings raised in greenhouse and forest from the two beech provenances, West Germany and Rumania, were investigated and compared with each other. In many pairwise comparisons significant differences in genotypic structure as well as genic structure were ascertained between different developmental stages. In both the provenances, the allelle A_2 seems to have advantage at both seedling stages raised under two different conditions. Homozygous carriers of A_2 allele survived best in greenhouse, while heterozygous carriers especially with A_2 allelle possessed great viability under more variable environmental conditions. Since a distinct different genetic background was present in two base populations, the identical effect of the allele A_2 confirms the adaptiveness of this locus. With aid of some measures such as viability parameter and genetic distance, the character of occurred viability selection is further explained. The possible significance of this locus at this early stage is discussed in relation to adaptation of this long lived tree species to heterogeneous environment.

서독과 루마니아의 너도밤나무 2개 産地로 부터 얻어진 種子와 그로부터 溫室과 林分內에서 발아된 幼苗의, 서로 다른 3가지 發達時期의 한 leucine aminopeptidase 遺傳子座에서의 遺傳的 構造가 相互間에 비교되었다. 많은 비교에서 서로 다른 發達時期間에 對立遺傳子的 및 遺傳子型的 構造의 차이가 인정되었다. 兩 産地에서 공통으로 對立遺傳子 A_2가 相異한 조건하에서 얻어진 幼苗時期에서 優越性을 보였다. 對立遺傳子 A_2의 同型接合體가 온실내에서의 生存力이 가장 높았으며 보다 異質的 環境條件을 지닌 林分內에서는 異型接合體, 특히 對立遺傳子 A_2의 異型接合體가 월등한 生存力을 보였다.

兩 産地의 種子의 遺傳的 構造가 서로 뚜렷이 相異함에도 불구하고 對立遺傳子 A_2의 同等한 効果는 이 遺傳子座의 適應性을 확인해 준다.

生存力 變數와 遺傳的 間隔등의 비교를 통해, 일어난 生存選擇의 特性과 強度가 설명되었다. 이 遺傳子座의 發達初期에 있어서의 가능한 중요성이 異質的 環境에서 오랜동안 살아가는 林木의 適應과 관련되어 토론되었다.

INTRODUCTION

Recent investigations using isozyme analysis have shown large amounts of genetic variation within and between populations of flowering plants (for review see Nevo, 1978; Brown, 1979; Hamrick et al. 1979). Long lived woody plants seem to contain higher levels of genetic variation than do other species (Hamrick et al. 1979), though investigation of many different enzyme systems is not yet enough to convince it. Gregorius et al. (1979) presented a biological interpretation that the genic diversity of individual is very important for tree plants exposed to temporal and spatial heterogeneous environments during their long life. The environmental situations of one tree could be heterogeneous at each

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developmental stage. The different ecological factors at one stage also exercise different influence over the carriers of certain genes and genotypes at the loci active at this given stage. In order to cope up with these demands, i.e. for survival of these carriers, many of these loci, as much as possible, should be heterogeneous.

In a given environment, the available genetic potentiality of a population determines the direction as well as the speed of adaptation. Adaptation of a population at a distinct stage depends also on the genetic structure at this stage. During ontogenesis natural selection acts continuously on different phenotypic characters. Only the individuals, which adaptecd better to given environments can survive. Therefore, the individuals survived in later ontogenetic stages were possibly strongly selected.

Beech in Europe is mainly naturally regenerated and therefore considered as one species good adapted to given habitat conditions. On the basis of the results of some provenance tests (Burger, 1948; Krahl-Urban, 1958; Hoffmann, 1962), it is assumed that there are relative large differences in genetic constitutions between different beech populations. The poor development of seedlings in natural regeneration can be attributed to many factors, namely, low germination percent of acorns (see Rohmeder, 1972), biotic and abiotic environmental factors during wintering of acorns and development of seedlings, for instance, kind of soil preparation, weather conditions etc. (Burschel et al. 1964). According to these authors, in two stands prepared in different ways the maximal seedling numbers in spring amounted to 8-60% and 2-23% of fallen acorns in preceding autumn. In sommer these numbers were decreaesed further by 4-12% and 1-15%. Under natural conditions, seedling number on unprepared plot amounted only to 4-15% and 1-2% on the two stands.

Since beech is mainly naturally regenerated, and also characterized by drastic reduction of population size from fructification till first few years, this tree species is very interesting with respect of population genetics. Genetic structure of a base population also could change, when such drastic reduction of population size takes place. Besides chance effect, such change in genetic structure can occur only by different viability of different genotypes (viability selection). The present paper describes viability selection at one allozyme locus (leucine aminopeptidase; E. C. 3. 4. 11. 1; LAP-A) during some early developmental stages in two beech populations. The ontogenetic studies and the genetic control of these allozymes are already described in detail (see Kim, 1979, 1980).

MATERIALS AND METHODS

(1) Plant materials and field collection. For the present investigations the acorns of two different provenances were supplied. Since there was no mast in 1978 in West Germany, one came from Rumania (whose detailed information was not available), and the other from southern part of West Germany (Provenance area 81013"Schwäbische Alb and Bayerischer Jura") stored after harvest in 1977.

A random sample of 600 acorns per provenance served as base populations. Cotyledons were used for electrophoresis.

A random sample of 1000 acorns per provenance was stratified for about 3 weeks at 3°C, and raised in greenhouse under normal conditions.

An experimental plot, about 80m² large, sloped slightly (11°) to east-southeast and under relative good sunny conditions, was selected in a about 120-year-old pure beech stand which was under the control of "Klosterforstamt Göttingen". Because of a heavy snow fall in 1978/79 winter, the acorns could be spread on this plot only at the end of Feb. 1979 by the removing about 20cm high snow. A right soil preparation was not possible, because the ground was too wet. Vegetations were removed and the ground was flattened after plowing. After uniformly spreading the acorns, the surface was covered again with snow. For each provenance 20m² large seedbed (300 acorns per m²) was made available. In order to avoid any injury to acorns and seedlings by wild animals, 1m high wire fence was set up and a net was stretched over the entire plot.

In both cases, greenhouse and forest, all seedlings were numerically labelled shortly after germination (here defined as unfolding of cotyledons). A small piece of opened cotyledons was cut off for genetic investigation. it did not affect the following development of seedlings. The samples were stored at −20°C in a deep freezer until use.

(2) Electrophoresis. Starch gel zone-

electrophoresis was performed using a modified discontinuous buffer system as described by Poulik (1957). The extracting and staining procedures as well as other experimental methods are already described in detail (see Kim, 1980).

The genetic structures at Locus LAP-A in three different developmental stages, the acorns lot, the seedligs raised in greenhouse, and in forest, were investigated and compared with each other.

RESULTS

(1) Comparison of genetic structures between the different developmental stages. Table 1 shows the genic and genotypic structures at LAP-A locus of three developmental stages. As is evident in the table there was a distinct difference in genotypic structure between base populations (acorns). The most frequent genotype A_1A_1 in German provenance amounts to 26% but only 5% in Rumanian provenance. Another homozygote A_3A_3 amounts to only 18% in German provenance but is the most frequent genotype in Rumanian provenance (50%). As regards genic structure, the allele A_1 is 37% for German but only 14% Rumanian provenance, and A_3 is 31% and 60% respectively for both provenances.

The genotypic structure of two base populations show large deviations from the Hardy-Weinberg expectations (Table 1). Thus they contained a great excess of homozygotes which is distinguished by comparisons of observed heterozygotes with expected from Hardy-Weinberg equilibrium (Ho/He). This value amounts to 0.54 in German and 0.45 in Rumanian provenance. It means, that the observed portion of heterozygotes in both provenances corresponds about half of the expected.

Comparison of these basic structures with those of seedlings in greenhouse makes evident the parallel increase of homozygote A_2A_2 and decrease of heterozygotes A_1A_2 and A_1A_3 in greenhouse of both provenances (Table 1). With regard to the allele frequency, allele A_1 is decreased evidently for the benefit of allele A_2. Genotypic structures of seedlings of both provenances in greenhouse show yet great deviation from expected Hardy-Weinberg proportion (Table 1).

The change of genetic structure of seedlings in forest shows a different tendency (Table 1). The heterozygotes, especially carriers of allele A_2 increased in forest which means reversed decrease of homozygotes. The decrease of homozygotes amounts to 10% for A_1A_1 and A_2A_2 in German provenance and

Table 1. Genic and genotypic structures at locus LAP-A of the different developmental stages for the two provenances (X^2 tests the fit of genotypic structure at each stage to Hardy-Weinberg proportions.)

Provenance	Develop. stage	Genotype frequency										N	X^2	Allele frequency			
		A_1A_1	A_2A_2	A_3A_3	A_4A_4	A_1A_2	A_1A_3	A_1A_4	A_2A_3	A_2A_4	A_3A_4			A_1	A_2	A_3	A_4
W. Germany	Acorns	.255	.188	.181	.010	.086	.140	.008	.115	.012	.005	592	256.6^{+++}	.372	.294	.311	.023
	Seedlings greenh.	.241	.327	.198	.012	.037	.056	.006	.099	.012	.012	162	154.1^{+++}	.290	.401	.281	.028
	Seedlings forest	.140	.200	.160	.000	.160	.120	.020	.180	.020.	000	50	7.6	.290	.380	.310	.020
Rumania	Acorns	.047	.194	.498	.005	.047	.130	.008	.048	.005	.018	599	368.6^{+++}	.139	.244	.596	.021
	Seedlings greenh.	.034	.241	.508	.013	.024	.071	.007	.068	.003	.031	295	185.7^{+++}	.085	.288	.593	.034
	Seedlings forest	.039	.252	.406	.000	.084	.110	.013	.077	.000	.019	155	74.6^{+++}	.142	.332	.510	.016

Significance levels α : 0.05^{+}, 0.01^{++} and 0.001^{+++}

Table 2. Statistical test for difference in genic and genotypic structrures at locus LAP-A between different developmental stages. (Significance levels were determined for pairwise comparisons by a G-test. First row in each is for genic and second for genotypic structures.)

Provenance	Pairwise comparison			Pooled
	Acorns and Seedl. greenh.	Acorns and Seedl. for.	Seedl. greenh. and Seedl. for.	
W. Germany	14.84^{++}	3.98	0.50	17.20^{++}
	25.46^{++}	6.93	15.69^{++}	32.75^{++}
Rumania	15.87^{++}	10.52^{+}	12.46^{++}	26.21^{+++}
	16.96^{+}	9.52	13.12	25.37^{+}

Significance levels α: 0.05^{+}, 0.01^{++} and 0.001^{+++}

for A_3A_3 in Rumanian provenance. Among the heterozygotes, A_1A_3 and A_2A_3 in German provenance increased double and A_1A_2 increased four times in both provenances. The great deviation of genotype frequency from Hardy-Weinberg proportion at the beginning diminished essentially in Rumanian provenance and is no more significant in German provenance. Despite the great difference in genotype frequency, allele frequency of both seedling stages of German provenance do not show any distinct difference.

If one compares this genetic structure of seedlings in forest with the basic structure, the increase of heterozygotes show almost the same tendency, although the difference is not so large as between base populations and seedlings in greenhouse (Table 1). Table 2 shows the results of G-test between the different genic and genotypic structures.

(2) Comparison of genotypic and genic viability parameter. The interpretation of this observed change of genetic structure by viability selection should be ascertained with a measure, which reflects directly viability difference of certain genotypes or alleles. To this end, the next viability parameter was used. The survival probability (1_{ij}^{S}) of the genotype with alleles A_i and A_j from the beginning till the next stage S is:

$$1_{ij}^{S} = \frac{N_{ij}^{S}}{N_{ij}^{B}}$$

where N_{ij}^{S} is the number of this genotype at stage S and N_{ij}^{B} is the number of this genotype in base population.

The viability parameter (V_{ij}^{S}) of the genotype A_iA_j at the stage S is:

$$V_{ij}^{S} = 1_{ij}^{S}\frac{N^{B}}{N^{S}} = \frac{P_{ij}^{S}}{P_{ij}^{B}}$$

where N^B and N^S are total individual number in base population and at the stage S respectively. N^S/N^B is reduction intensity of population size from beginning to stage S. P_{ij}^{b} and P_{ij}^{S} are the relative frequency of genotype A_iA_j in base population and at stage S respectively.

This parameter of one genotype amounts to 1, when a population at a later stage possesses the same proportion of this genotype as that of base population. This means that the survival rate of this genotype is directly identical to the reduction of total population (selection neutrality). If this parameter exceeds 1, the correspondent genotype has selection advantage and when smaller than 1, the genotype has selection disadvantage. This principal meaning of the viability parameter is also analogous appricable to alleles, where the number of genotypes is replaced by that of alleles.

In the table 3, the genic and genotypic viability parameters in two different seedling stages are given. The allel A_4 and the genotypes with this allele which in most cases amounted to under 3% were left out. In forest as well as in greenhouse the allele A_2 shows the largest value of this parameter in both provenances (Table 3a). The parameters of alleles A_3 and A_1 are smaller than 1 or show neutrality. This advantage of allele A_2 can be directly connected with the genotypic

Table 3. Genic and genotypic viability parameter at locus LAP-A for two seedling stages.
(An allele (A_4) and four genotypes (A_4A_4, A_1A_4, A_2A_4 and A_3A_4 with rare frequency (under 3%) were left out.)

a. Genic viability parameter

Allele	W. Germany		Rumania	
	Seedl. greenh.	Seedl. for.	Seedl. greenh.	Seedl. for.
A_1	0.78	0.78	0.61	1.02
A_2	1.37	1.29	1.18	1.36
A_3	0.90	1.00	1.00	0.86

b. Genotypic viability parameter

Genotype	W. Germany		Rumania	
	Seedl. greenh.	Seedl. for.	Seedl. greenh.	Seedl. for.
A_1A_1	0.94	0.55	0.73	0.83
A_2A_2	1.74	1.07	1.24	1.30
A_3A_3	1.09	0.89	1.02	0.82
A_1A_2	0.43	1.86	0.51	1.79
A_1A_3	0.40	0.86	0.55	0.84
A_2A_3	0.86	1.57	1.40	1.60

viability parameters (Table 3b). Among three homozygotes the parameters of A_2A_2 and A_3A_3 exceed 1, and the selection advantage of A_2A_2 is more distinct. On the contrary the parameters of all heterozygotes in both provenances lie under 1, except of A_2A_3 in Rumanian provenance. This clearly means, that selection acted against heterozygotes during seedling-stage in green house. During seedling stage in forest the genotpyic viability parameters show another tendency. The values of the heterozygotes with the allele A_2 are the largest; 1.86 and 1.79 for A_1A_2 and 1.57 and 1.60 for A_2A_3 respectively in both provenances. Among homozygotes only the parameter for A_2A_2 exceed 1. The other homozygotes were selected against.

These results can be summarized as follows: The allele A_2 has advantage at both seedling stages in green house and in forest. With the exception of the heterozygote A_2A_3 of Rumanian provenance, the homozygotes, especially A_2A_2 has selection advantage in greenhouse. To the contrary, in forest all genotypes with the allele A_2 show the parameter larger than 1. Among these genotypes the two heterozygotes have essentially larger value than that of homozygote A_2A_2.

(3) Comparison of genic and genotypic distance. The extent of change in genetic structure by viability selection can be elucidated with aid of genetic distance parameter. Table 4 represents the estimated genic and genotypic distance by Gregorius (1974) between provenances and developmental stages. For better comparison these estimates are represented geometrically in Fig. 1. In German provenance the

Table 4. Genetic distance between developmental stages in both provenances, and between provenances at each stage.
(first row in each is for genic second for genotypic distance.)

a. Between developmental stages

Prov.	Acorns and Seedl. greenh.	Acorns and Seedl. for.	Seedl. greenh. and Seedl. for.
W. Germany	0.112 0.165	0.086 0.171	0.029 0.290
Rumania	0.057 0.098	0.091 0.130	0.101 0.130

b. Between provenances

Acorns	Seedl. greenh.	Seedl. for.
0.285 0.336	0.318 0.346	0.200 0.317

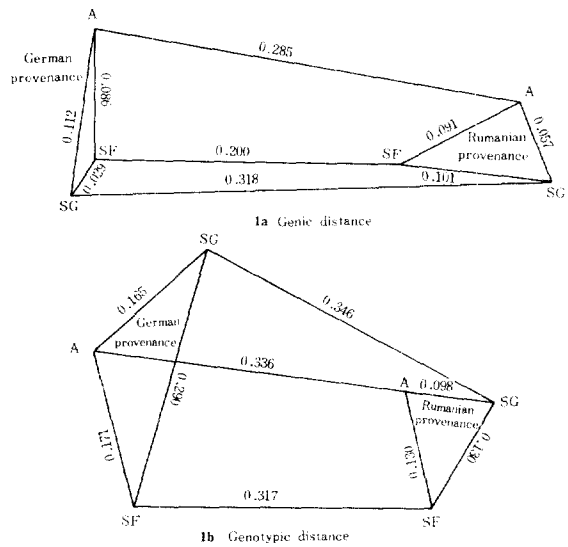

Fig. 1. Schematic illustration of genetic distance between developmental stages and between provenances (A: acorns, SG: seedlings in green house, SF: seedlings in forest).

genic distance is 0.112 between acorns and seedlings in greenhouse, and 0.086 between acorns and seedling in forest (Table 4). The value between seedling stages amounts to 0.029 and indicates again their similar genic structure. The Rumanian provenance shows another tendency: The genic distance between two seedling stages is the largest (0.101) and that between acorns and seedlings in greenhouse is the smallest (0.057).

The genotypic distance shows in general a similar tendency to genic distance in Rumanian provenance (Table 4). The value between seedling stages is the largest, 0.29 in German and 0.13 in Rumanian provenance. Between acorns and seedlings in forest, this genotypic distance is 0.171 in German, and 0.13 in Rumanian provenance. The values between acorns and seedlings in greenhouse are the smallest in both provenances. This means, that the viability selection acted in a different direction in two seedling stages which are raised under different condition (Table 4; Fig. 1).

The genic and genotypic distance between two provenances shows the largest value at the seedling stage in greenhouse and the smallest in forest (Table 4; Fig. 1). These estimates show also that the viability selection at seedling stage acted stronger in German provenance than in Rumanian provenance.

DISCUSSION

The acorn lots investigated contain large excess of homozygotes equivalent an estimated inbreeding coefficient of 0.4-0.5 (see Kim, 1980). In regular pedigree breeding they are about half-way between coefficients after two generations of full-sib mating or five generations of half-sib mating (Hattemer, in print). However there exists uncertainty as to whether this large inbreeding coefficient should be ascribed to repeated mating of relatives or to a high proportion of seeds from self-fertilization. In the case of multiple alleles the homozygote excess measured with inbreeding coefficient $\bar{F}$ by Wright (1921, 1969) can be regarded only due to inbreeding,

if this coefficient $\bar{F} = 1 - \dfrac{\sum_{i<j} P_{ij}}{1 - \sum_i P_i^2}$

meets the next condition:

$$P_{ii} = P_i^2 + P_i (1-P_i) \bar{F} \quad \text{and}$$

$$P_{ij} = 2P_iP_j - 2P_iP_j \bar{F} \; (\forall_i \neq_j)$$

This connection was fulfilled in acorns of German provenance but not in Rumanian provenance (see Kim, 1980). At least, in one of the provenances, part of the homozygote excess should be due to some other causes.

The Wahlund effect (Wahlund, 1928) probably contributed more to $\bar{F}$ than does inbreeding. Levin (1977) gave also this consideration in a population study of phlox species.

A so-called silent allele at this locus could be also responsible partly for this large heterozygote deficiency (see Kim, 1980). Besides, sexual as well as gamete selection could also play a role. However, a special controlled cross experiment is necessary to convince it.

Although the observation focusses mainly on genetic structure changes in some different developmental stages, these unexpected and different genetic structures of both provenances are very interesting and indicate once more the spread of non-panmictic reproduction system in forest trees.

Many different forms of balancing selection can maintain the genetic variation over generation in a population (Karlin & Mcgregor, 1972; Hedrick et al. 1976). One of these general explanations is heterozygote superiority observed in many animal and plant populations (Berger, 1976; Hedrick et al. 1976). The relation of genetic structure to demographic factors, for example increase of heterozygotes with age, were also observed in different organisms (Fujino & Kang, 1968; Allard et al. 1972 ; Koehn et al. 1973; Tinkle & Selander, 1973; Schaal & Levin, 1976).

In spite of careful preventive measures against possible injury factors, germination percent was very low in forest (1-3%), and not so high in green house (20-30%) also. This could be explained by the unusual climate conditions in the winter of 1978/79. The difference between provenances might be due to different quality of acorns (see Kim, 1980).

In parallel with this drastic reduction of population size, the genetic structure of base population also

changed (Table 1). There are large differences in genetic structure between acorns and seedling stages, or between the different ontogenetic stages in the same generation. The allele A_2 seems to have advantage in both seedlings raised under different conditions. Homozygous carriers of A_2 allele survived best in greenhouse, while heterozygous carriers possessed the greatest viability under variable conditions, in forest (Table 3). This result is well in line with the heterozygous advantage theory (see Fincham, 1972; Berger, 1976; Ayala, 1976). Since a conceivable different genetic background was present in the two base populations, the identical effect of the allele A_2 confirms that LAP-A locus is among the adaptive loci at this stage of life cycle. The adaptiveness of this locus can be further confirmed by a different behaviour of another allozyme locus (see Kim, 1980): An acid phosphatase locus was identified in young leaves. The change of genetic structure of this locus in two seedling stages showed another parallel tendency in both provenances. These results can not be described in detail, because the genetic structure of base population is not available.

The values of genic and genotypic distance between different developmental stages reflect well the extent and direction of occurred viability selection (Table 4; Fig. 1). It shows that the viaility selection acted in different direction under different environmental conditions. This indicates the importance of genic diversity in a population for adaptation to heterogeneous environment at each ontogenetic stage during life cycle of long lived organisms, as tree species (see Gregorius et al. 1979). For population the occurrence of four alleles at this adaptive locus is important to realize the heterozygote advantage at seedling stage in adaptation.

The large allele frequency changes by viability selection raise the question as to why such alleles were not excluded during former generation. One answer might be a unique selecting environment which was not realized before. Another explanation could be the change of selection pressure in different life stages which can maintain a stable genetic polymorphism: Selection acts against certain alleles or genotypes at one stage and acts against other alleles or genotypes at other stage. In this connection some empirical studies showed, that fitness value of one genotype could vary in relation to different life stages (Clegg & Allard, 1973; Schaal & Levin, 1976).

All these questions require further studies on the genetic structure in later stages of this long lived species.

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