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Viability Selection at an Allozyme Locus During Development in European Beech (Fagus sylvatica L.)

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(Received 18th March 1985)

Summary

The genetic structures at one leucine aminopeptidase locus (LAP-A) of nuts, seedlings raised in the greenhouse and seedlings raised in the forest, all originating from the two beech provenances Germany and Rumania, were investigated and compared. In many pairwise comparisons, significant differences in genotypic structures as well as genic structure were ascertained between different developmental stages. In both provenances, the allele A_2 seems to have an advantage in the seedlings raised under both types of conditions. Homozygous carriers of the allele A_2 survived best in the greenhouse, while heterozygous carriers possessed great viability under more variable environmental conditions, Since distinctly different genetic backgrounds were present in the two base populations, the identical effect of the allele A_2 confirms the adaptive role of this locus. With the aid of measures such as the 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 under the aspect of the adaptation of this long-lived tree species to a heterogeneous environment.

Key words: Fagus sylvatica, genic structure, genotypic structure, enzyme gene-locus, viability selection, seed, seedlings, genetic distance, environmental heterogeneity.

Zusammenfassung

Viabilitätsauslese an einem Enzym-Genlocus während der Entwicklung der europäischen Buche (*Fagus sylvatica* L.).

Die genetischen Strukturen an einem für Leucinaminopeptidase kodierenden Genlocus (LAP-A) an Bucheckern sowie im Gewächshaus bzw. im Bestand angezogenen Sämlingen einer deutschen und einer rumänischen Herkunft wurden untersucht und verglichen. In vielen paarweisen Vergleichen wurden signifikante Unterschiede sowohl der genotypischen als auch der genischen Struktur verschiedener Entwicklungsstadien festgestellt. In beiden Herkünften scheint der Besitz eines Allels A_2 für Sämlinge unter beiden Anzuchtbedingungen einen Vorteil zu haben. Homozygote Träger von A_2 überlebten im Gewächshaus am besten, während heterozygote Träger unter variableren Umweltbedingungen hohe Viabilität besaßen. Da die beiden Ausgangspopulationen unterschiedlichen genetischen Hintergrund hatten, bestätigt der in beiden identische Effekt von A_2 die adaptive Rolle dieses Genlocus. Der Charakter der aufgetretenen Viabilitätsauslese wird mit Hilfe von Maßen wie dem Viabilitätsparameter und dem genetischen Abstand im einzelnen erklärt. Die mögliche Bedeutung dieses Genlocus in diesem frühen ontogenetischen Stadium wird unter dem Aspekt der Anpassung dieser langlebigen Baumart an eine heterogene Umwelt diskutiert.

1. Introduction

Recent investigations using isozyme analysis have shown large amounts of genetic variation within and between populations of flowering plants (for reviews see NEVO 1978, BROWN 1979, HAMRICK *et al.* 1979). Long-lived woody plants seem to possess higher levels of genetic variation than do other species (HAMRICK *et al.* 1979), although further investigations of many different enzyme systems are necessary to confirm this. GREGORIUS *et al.* (1979) presented a testable hypothesis that the genic diversity of each individual is important for trees exposed to temporally and spatially heterogeneous environments during their long lives. The environmental situations of a tree could be quite different for each developmental stage. The influence of the ecological factors at a given stage on the loci active at this stage also varies over the carriers of different genes and genotypes. In order to cope with these demands, i. e. for survival of these carriers, as many of these loci as possible should be heterozygous.

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This study was supported by a grant from German Academic Exchange Service (DAAD).

In a given environment, the available genetic potential 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 strucure at this stage. During ontogeny, natural selection acts continuously on different phenotypic characters, so that only those individuals better adapted to the given environments can survive. Therefore, the individuals surviving in later ontogenetic stages have possibly been strongly selected.

Beech in Europe is mainly naturally regenerated and is therefore considered as a species well-adapted to the 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 relatively large differences in genetic constitution between different beech populations. Poor development of seedlings in natural regeneration can be attributed to many factors, namely, low germination percentage of nuts (see ROHMEDER 1972) as well as biotic and abiotic environmental factors during wintering of nuts and development of seedlings, for instance, kind of soil preparation, weather conditions, etc. (BURSCHEL *et al.* 1964). According to these authors, in two stands receiving different ground preparations the maximum seedling numbers in the spring amounted to 8%—60% and 2%—23% of nuts fallen in the preceding autumn. In the summer these numbers were decreased further to 4%—12% and 1%—15%. Under natural conditions, the seedling number on the unprepared control plots amounted only to 4%—15% and 1%—2% in the two stands.

Since beech is mainly naturally regenerated and also characterized by a drastic reduction of population size during the first few years, this tree species is very interesting with respect to population genetics. As a result of such a reduction, the genetic structure of a base population could change. Besides chance effects, such a change can be caused only by differing viabilities of the genotypes (viability selection). The present paper describes viability selection at one allozyme locus (leucine aminopeptidase; E.C.3.4.1.1; LAP-A) during several early developmental stages in two beech populations. The ontogenetic studies and the genetic control of these allozymes have already been described in detail (see KIM 1979, 1980).

2. Materials and Methods

(i) *Plant materials and field collection.* For the present investigations the nuts of two different provenances were supplied. Since there was no mast in 1978 in West Germany, one lot came from Rumania (whose detailed information was not available) and the other from the southern part of West Germany (provenance area 81013 "Schwäbische Alb und Bayerischer Jura"); this latter lot was stored since its collection in 1977.

A random sample of 6000 nuts per provenance served as base populations. Cotyledons were used for electrophoresis.

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

An experimental plot, about 80 m^2 in size, sloping slightly (11°) to the east-southeast and with relatively good light conditions, was selected in ca. 120-year-old pure beech stand. Because of heavy snowfall in the winter of 1978/79, the nuts could not be spread on this plot until the end of Feb. 1979, and then only by removing about 20 cm depth of snow. A proper soil preparation was not possible. Vegetation was removed and the ground was flattened after plowing. After uniformly spreading the nuts, the surface was covered again with snow. For each provenance a 20 m^2 large seedbed (300 nuts per m^2) was made available. In order to avoid any injury to nuts and seedlings by wild animals, a 1 m high wire fence was set up and a net was stretched over the entire plot.

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

ii) *Electrophoresis.* Starch gel zone-electrophoresis was performed using a modified discontinuous buffer system as described by POULIK (1957). The extraction and staining procedures as well as other experimental methods have already been described in detail (KIM 1980).

The genetic structures at the LAP-A locus in three different developmental samples (the nuts, the seedlings raised in the greenhouse, and in the forest) were investigated and compared.

Results

(i) *Comparison of genetic structures of the different developmental stages. Table 1* shows the genic and genotypic structures at the LAP-A locus in three developmen-

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 the genotypic structure at ach 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	nuts	.255	.188	.181	.010	.086	.140	.008	.115	.012	.005	592	256.6***	.372	.294	.311	.023
	Seedlings greenhouse	.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	nuts	.047	.194	.498	.005	.047	.130	.008	.048	.005	.018	599	368.6***	.139	.244	.596	.021
	Seedlings greenhouse	.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 level α: 0.05*, 0.01** and 0.001***.

tal stages. As is evident from the *Table*, there was a distinct difference in genotypic structure between the base populations (nuts). The most frequent genotype A_1A_1 in the German provenance amounts to 26%, but only to 5% in the Rumanian provenance. Another homozygote A_3A_3 amounts to only 18% in the German provenance, whereas it is the most frequent genotype in the Rumanian provenance (50%). As regards genic structure, the allele A_1 comprises 37% in the German but only 14% in the Rumanian provenance, while A_3 comprises 31% and 60%, respectively.

The genotypic structures of the two base populations showed large deviations from the Hardy-Weinberg expectations. Thus they contained a great excess of homozygotes, as was determined by comparison of the observed heterozygotes with the number expected under Hardy-Weinberg equilibrium. This value amounts to .54 in the German and .45 in the Rumanian provenance. It means that the observed proportion of heterozygotes in both provenances corresponds to about half of that expected.

Comparison of these basic structure with those of seedlings in the greenhouse makes evident the increase of homozygotes A_2A_2 and the corresponding decrease of heterozygotes A_1A_2 and A_1A_3 of both provenances in the greenhouse. With regards to allele frequencies, allele A_1 is decreased for the benefit of allele A_2. The genotypic structures of seedlings of both provenances in the greenhouse still show great deviations from the expected Hardy-Weinberg proportions.

The change in genetic structure of seedlings in the forest shows a different tendency. The heterozygotes, especially carriers of allele A_2, increased in the forest. The corresponding decrease of homozygotes amounts to 10% for A_1A_1 and A_2A_2 in the German provenance and for A_3A_3 in the Rumanian provenance. Among the heterozygotes, A_1A_3 and A_2A_3 in the German provenance increased two-fold and A_1A_2 increased four-fold in both provenances. The substantial deviation of the genotype frequency from Hardy-Weinberg proportions at the beginning diminished considerably in the Rumanian provenance and is no longer significant in the German provenance. Despite this great difference in genotype frequency, the allele frequencies of both seedling stages in the German provenance do not show any distinct differences.

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

(ii) *Comparison of genotypic and genic viability parameters.* The interpretation of this observed change in genetic structure by viability selection should be ascertained with a measure which directly reflects the differences in viability of certain genotypes or alleles. To this end, the following viability parameter was used. The survival probability (I^S_{ij}) of the genotype composed of alleles A_i and A_j from the beginning till the stage S is:

$$I^S_{ij} = \frac{N^S_{ij}}{N^B_{ij}}$$

where N^S_{ij} is the number of individuals of this genotype at stage S and N^B_{ij} is the number in the base population.

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

$$V^S_{ij} = I^S_{ij} \frac{N^B}{N^S} = \frac{P^S_{ij}}{P^B_{ij}}$$

where N^B and N^S are the total number of individual in the base population and at stage S, respectively. $\frac{N^B}{N^S}$ is the reduction of the poulation size from the beginning to stage S. P^B_{ij} and P^S_{ij} are the relative frequencies of genotype A_iA_j in the base population and at stage S, respectively.

This parameter is equal to 1 for a given genotype and stage, whenever the population at that stage possesses the same proportion of the genotype as he base population. This means that the survival rate of this genotype is identical to the reduction of the total population (selection neutrality). If this parameter exceeds 1, the corresponding genotype has a selective advantage; if it is smaller than 1, the genotype has a selective disadvantage. This principal meaning of the viability parameter is analogously applicable to alleles, where the number of individuals of each genotype is replaced by that of each allele.

In *Table 3*, the genic and genotypic viability parameters in two different samples are given. The allele A_4 and the genotypes with this allele, which in most cases amounted to under 3%, were left out. In the forest as well as in the greenhouse, the allele A_2 shows the largest value of this parameter in both provenances *(Table 3a)*. The parameters of the alleles A_3 and A_1 are less than 1 or show neutrality. This advantage of allele A_2 can be directly connected with the genotypic viability parameters *(Table 3b)*. Among the three homozygotes, the parameters of A_2A_2 and A_3A_3 exceed 1, the selective advantage of A_2A_2 being more distinct. On the other hand the parameters of all heterozy-

Table 2. — Statistical test for difference in genic and genotypic structures at locus LAP-A between different developmental stages. Significance levels were determined for pairwise comparisons by a G-test. The first row in each is for genic and the second for genotypic structure.

Provenance	Pairwise comparisons			Pooled
	Nuts vs. seedlings in the greenhouse	Nuts vs. seedlings in the forest	Seedlings in the forest vs. greenhouse	
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***.

Table 3. — Genic and genotypic viability parameter at Locus LAP-A for two seedling stages. One 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	Germany		Rumania	
	Seedlings (greenhouse)	Seedlings (forest)	Seedlings (greenhouse)	Seedlings (forest)
A_1	.78	.78	.61	1.02
A_2	1.37	1.29	1.18	1.36
A_3	.90	1.00	1.00	.86

b) Genotypic viability parameter

Genotyp	Germany		Rumania	
	Seedlings (greenhouse)	Seedlings (forest)	Seedlings (greenhouse)	Seedlings (forest)
A_1A_1	.94	.55	.73	.83
A_2A_2	1.74	1.07	1.24	1.30
A_3A_3	1.09	.89	1.02	.82
A_1A_2	.43	1.86	.51	1.79
A_1A_3	.40	.86	.55	.84
A_2A_3	.86	1.57	1.40	1.60

gotes in both provenances lie under 1, except for A_2A_3 in the Rumanian provenance. This clearly means that selection acted against heterzygotes during the seedling stage in the greenhouse. During the seedling stage in the forest, the genotypic viability parameters show a different 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 exceeds 1. The other homozygotes were selected against.

These results can be summarized as follows: The allele A_2 has an advantage at the seedling stages in the greenhouse as well as in the forest. With the exception of the heterozygote A_2A_3, of Rumanian provenance, the homozygotes, especially A_2A_3, have a selective advantage in the greenhouse. On the contrary, in the forest all genotypes with the allele A_2 show the parameter greater than 1. But among these genotypes the two heterozygoes have a considerably larger value than the homozygote A_2A_2.

(iii) *Comparison of genic and genotypic distance.* The extent of the change in genetic structure due to viability selection can be elucidated with the aid of the 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 *Figure 1.* In the German provenance, the genic distance is .112 between nuts and seedlings in the greenhouse and .086 between nuts and seedlings in the forest *(Table 4).* The value between the seedling stages amounts to .029 and indicates again their similar genic structure. The Rumanian provenance shows another tendency: The genic distance between nuts and seedlings in the greenhouse is the smallest (.057).

In general the genotypic distance shows a tendency similar to that of the genic distance in the Rumanian provenance *(Table 4).* The value between the seedling stages is the largest, .29 in the German and .13 in the Rumanian provenance. Between nuts and seedlings in the forest, this genotypic distance is .171 in the German and .13 in the Rumanian provenance. The values between nuts and seedlings in the greenhouse are the smallest in both provenances. This means that viability selection acted in different directions in the two seedling stages, which were raised under different conditions *(Table 4, Figure 1).*

The genic and genotypic distance between the two provenances shows the largest value at the seedling stage in the greenhouse and the smallest in the forest. These estimates also indicate that the viability selection at the seedling stage acted more strongly in the German provenance than in the Rumanian provenance.

4. Discussion

The two lots of beech nuts investigated contain a large excess of homozygotes equivalent to an estimated inbreeding coefficient (see Kim 1980). In regular pedigree breeding they are about half-way between coefficient after two generations of full-sib mating and after five generations of half-sib mating (Hattemer 1982). 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 the inbreeding coefficient $\bar{F}$ by Wright (1921, 1969) can be regarded as due only to inbreeding, whenever this coefficient $\bar{F} = 1 - \frac{\sum_{i<j} P_{ij}}{1 - \sum_i p_i^2}$ meets the following condition:

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

$$P_{ij} = 2p_ip_j - 2p_ip_j \bar{F} \quad (\forall i \neq j).$$

This relationship was fulfilled in nuts of the German provenance but not in the Rumanian provenance (see Kim 1980). Therefore, in at least one of the provenances, part of the homozygote excess should be due to other causes.

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

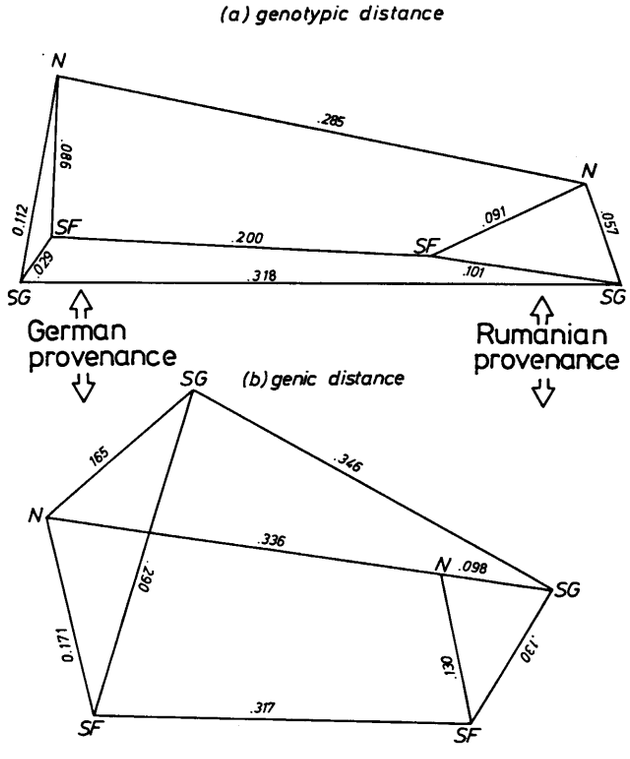
A so-called silent allele at this locus could also be partly responsible for this large heterozygote deficiency (see Kim 1980) but was never encountered in homozygous condition in this material.

Although the observation focusses mainly on genetic structure changes in several developmental stages, these unexpected genetic structures of the two provenances indicate once more the spread of a non-panmictic reproduction system in forest trees.

Many different forms of balancing selection can cause the genetic variation to be maintained over generations in a population (Karlin and McGregor 1972, Hedrick *et al.* 1976). One of the general explanations of this phenomenon is heterozygote superiority, as observed in many animal and plant populations (Berger 1976, Hedrick *et al.* 1976). A relationship between genetic structure and demographic factors, for example increase of heterozygotes with age, were also observed in different organisms (Fujino and Kang 1968, Allard *et al.* 1972, Hebert *et al.* 1972, Koehn *et al.* 1973, Tinkle and Selander 1973; Schaal and Levin 1976).

In spite of careful preventive measures against possible injury factors, the germination percentage was very low in the forest (1—3%) and not very high in the greenhouse (20—30%). This could be explained by the unusual climatic conditions during the winter of 1978/79. The difference between provenances may be partly due to different pretreatment of the nuts. Parallel to this drastic reduction in population size, the genetic structure of the base population also changed *(Table 1)*. There are large differences in genetic structure between nuts and seedling stages, as well as between the different ontogenetic stages in the same generation. The allele A_2 seems to have an advantage in seedlings raised under both conditions. Homozygous carriers of the A_2 allele survived best in the greenhouse, while heterozygous carriers possessed the greatest viability under variable conditions, namely in the forest *(Table 3)*. These results are well in line with the heterozygous advantage theory (see FINCHAM 1972, BERGER 1976, AYALA 1976). Since conceivably different genetic backgrounds were present in the two base populations, the identical effects of the allele A_2 confirm that the LAP-A locus is among the adaptive loci at this stage of the life cycle. The adaptivity of this locus can be further confirmed by the different behavior of another allozyme locus (see KIM 1980): a acid phosphatase locus was identified in young leaves. The change in genetic structure of this locus in two seedling stages showed another parallele tendency in both provenances. These results cannot be described in detail, because the genetic structure of the base population is not available.

The values of genic and genotypic distance between different developmental stages well reflect the extent and direction of occurred viability selection *(Table 4, Figure 1)*.



Figgure 1. — Schematic illustration of genetic distances between developmental stages and between provenances.
a) Genic distance
b) Genotypic distance
(A: nuts, SG: seedlings in greenhouse, SF: seedlings in forest)

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

a) Between developmental stages

Prov.	Nuts vs. seedlings in greenhouse	Nuts vs. seedlings in forest	Seedlings in the forest vs. greenhouse
Germany	.112	.086	.029
	.165	.171	.290
Rumania	.057	.091	.101
	.098	.130	.130

b) Between provenances

Nuts	Seedlings in the greenhouse	Seedlings in the forest
.285	.318	.200
.336	.346	.317

It shows that viability selection acted in different directions under different environmental conditions. This indicates the importance of genic diversity in a population for adaptation to a heterogeneous environment at each ontogenetic stage during the life cycle of long-lived organisms such as tree species (see GREGORIUS *et al.* 1979). For a population, the occurrence of four alleles at this adaptive locus is important for the realization of the heterozygote advantage at the seedling stage in adaptation.

The large allele frequency changes by viability selection raise the question as to why such alleles were not excluded during an earlier generation. One answer might be a unique selecting environment which was not realized before. Another explanation could be the variation in selection pressure in different life stages which can maintain a stable genetic polymorphism: Selection acts against certain alleles or genotypes at one stage and against other alleles or genotypes at an other stage. In this connection, some empirical studies have shown that the fitness value of a given genotype could vary with the different life stages (CLEGG and ALLARD 1973, SCHAAL and LEVIN 1976).

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

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Quantifying Uniformity of Gamete Production in Seed Orchards

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(Received 2nd April 1985)

Summary

Genetic uniformity of seed orchards is often discussed in subjective terms such as asymmetry of gamete production, pollen contamination levels, etc. A quantitative index of orchard uniformity, U, that integrates gamete production and foreign pollen contamination is proposed. This index provides forest geneticists with a quantitative method of comparing orchards or evaluating changes in annual production of a single orchard. Index calculation requires estimates of microspore and megaspore production levels for individual clones and an estimate of the degree of pollen contamination.

Key words: variance, strobili, gamete production.

Zusammenfassung

Die genetische Einheitlichkeit von Samenplantagen wird oft unter einseitigen Gesichtspunkten wie z. B. der Asymmetrie der Gametenproduktion, dem Pollenkontaminations-Niveau usw. diskutiert. Ein quantitativer Index für die Plantagenuniformität, U, der die Gametenproduktion und die Fremdpollenkontamination miteinbezieht, wird vorgeschlagen. Der Index versorgt die Forstgenetiker mit einer quantitativen Methode, Samenplantagen zu vergleichen oder Unterschiede in der jährlichen Produktion einer einzelnen Plantage zu errechnen. Eine Index-Berechnung erfordert Schätzungen des Mikro- und Megasporen-Produktionsniveaus der Einzelklone und eine Schätzung des Grades der Pollenkontamination.

Introduction

Success or failure of a tree improvement program is largely dependent on the breeders' ability to identify genetically superior trees and to use them to produce progeny that out-perform trees derived from unimproved sources. A program's success can be measured by the realized level of improvement in the progeny and more specifically by the realized genetic gain. Improvement programs for many coniferous tree species rely on wind-pollinated seed orchards for large-scale seed production efforts. The value of these seed orchards is a function of their total seed yield and the realized genetic gain of their seeds.

Realized genetic gain is often calculated as a deviation of progeny test scores from a checklot (TALBERT, *et al.* 1985) rather than by comparing the checklot to trees grown from bulk samples of seed orchard seed. Estimation of realized genetic gain in seed orchard seed using progeny test data is often based on the assumption of uniformity of gamete contributions among clones. Complete genetic uniformity requires several conditions: a) equal production of microspores and megaspores by each clone in the orchard; b) equal viability of microspores and megaspores; c) synchronized production of microspores and megaspores; d) random union of gametes among all non-related pairs of clones and e) negligible levels of alien pollen. Several studies have documented variation in microspore and megaspore production and effectiveness (BERGMANN 1968, MÜLLER-STARCK 1982, SCHMIDTLING 1983) by use of field counts of flowers and electrophoretic studies of seed. Field counts of male and female flowers can serve as rudimentary estimates of potential gamete contributions and electrophoretic analysis of bulk seed lots may enable breeders to quantify the actual gamete contributions of each clone to the final seed crop. Variation in gamete production needs to be incorporated into the calculation of genetic gain or erroneous estimates will be obtained.

Orchards that vary from the assumptions stated above are said to be less uniform but uniformity is usually described in subjective terms that specify the degree of departure from optimum productivity. Such subjectivity makes it difficult to compare the annual productivity of a single orchard or to compare productivities among several orchards. The purpose of this paper is two-fold. First, to

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