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GENETIC POLYMORPHISM OF ACID PHOSPHATASE IN POPULATION OF RYE, *SECALE CEREALE* L. s. l.

Introduction

In a recent paper (Яаска, 1975) we reported about the occurrence of extensive intrapopulational genetic polymorphism of acid phosphatase with similar electrophoretic variants in annual self-incompatible ryes, wild and cultivated. The genetic basis and quantitative characteristics of the observed polymorphism, however, remained obscure. In this paper we show that the polymorphism of major acid phosphatase isoenzymes present in the coleoptile and root tissues of young seedlings of *Secale cereale* L. s. l. fits the model of four alleles at a single gene locus, and compare allele frequencies at the acid phosphatase locus in some wild, weedy and cultivar populations of rye.

Materials and methods

The accessions of self-incompatible annual rye *Secale cereale* L. s. l. used were: (1) cultivars 'Priekuli 2', 'Jõgeva 120', 'Belorusskaya 23' and 'Harkov 60' of the cultivated rye *S. cereale* ssp. *cereale*, one accession of each grown at the Plant Breeding Station in Jõgeva (Estonian SSR); (2) the accession AL-8/72 of a weedy non-fragile rye *S. cereale* ssp. *segetale* collected by the author in 1972 from a drought-failed wheat field near village Hanaga in the Nakhitshevan ASSR; (3) accessions AL-2a/71, AL-2b/71 and AL-51/75 of a weedy fragile-rachis rye *S. cereale* ssp. *ancestrale* s. l. (=*S. vavilovii* Grossh. s. l., non sensu Khush) collected by the author in 1971 and 1975 from local sub-populations south-east of Yerevan in the Armenian SSR; (4) eight inbred lines of rye kindly provided by Dr. V. Smirnov of Leningrad State University (USSR).

Polyacrylamide gel electrophoresis of tissue extracts and histochemical staining of gels to locate the acid phosphatase activity were carried out as described previously (Jaaska, 1978; Яаска, 1974).

The term «isoenzyme» is used here, as in our other publications, in its broadest operational sense, involving all multiple molecular forms of the same enzyme independent of their nature, i. e., both genetic and epigenetic enzyme isoforms.

Results

1. Developmental changes in the rye acid phosphatase during germination.

Significant changes in the rye acid phosphatase electrophoretic pattern, occurring in the course of seed germination and seedling growth, are

evident from the data in Fig. 1. At least four electrophoretic groups of soluble acid phosphatase of different developmental pattern during germination and of independent individual variation, suggesting their genetic control by separate gene loci, can be distinguished. These phosphatases will be designated: A — dominant in the embryo, B — dominant in the coleoptile and root tissues, C — a fast-migrating leaf phosphatase, and D — a slow-migrating leaf blade phosphatase.

The first three phosphatases of similar developmental pattern were previously described in *Triticum* (Яаска, 1976) and *Aegilops* (Jaaska, 1978) species, while phosphatase D was observed in only some of them.

Phosphatase A is revealed on the enzymograms of embryos, quiescent or germinated for one day, as one major band of invariant and identical electrophoretic mobility for all rye forms and species, annual and perennial. This phosphatase disappears in young 3—6-day-old etiolated seedlings where new isophosphatases of different electrophoretic mobility appear. The coleoptile and root tissues of etiolated seedlings reveal a highly variable system of phosphatase B isoenzymes, accounting for 2 to 4 major and 3 to 5 minor bands in different rye individuals, as a major soluble phosphatase.

In the primary leaf, two additional electrophoretically and developmentally clearly distinguishable isophosphatase groups, C and D, appear. Phosphatase C is represented by a band of higher electrophoretic mobility in comparison with phosphatase B bands and is especially expressed in the basal part of the primary leaf. In the leaf blade of older seedlings, a group of slowly and closely migrating isophosphatases appears, on enzymograms, as a broad band of phosphatase D, the staining intensity of which, as a rule, increases with the seedling's age, reflecting a significant rise in the enzyme activity.

2. Phosphatase B electrophoretic phenotypes.

Of the four soluble phosphatases specified, only phosphatase B showed a distinct individual variation which was studied in greater detail to be described below. Enzyme extracts from coleoptiles of young 4—7-day-old etiolated seedlings were used as most suitable for the electrophoretic separation of phosphatase B isoenzymes.

Figure 2 presents electrophoretic phenotypes of the soluble coleoptile phosphatase encountered among the rye individuals. The number of major isophosphatase bands in a single phenotype varies from 2 to 4, giving a total of 7 distinct and widely spaced band groups numbered 1 to 7 in decreasing order of their electrophoretic mobility.

Ten phosphatase phenotypes, four two-banded, two three-banded, and four four-banded ones, could be observed in the rye populations most frequently.

The two-banded phenotypes obviously correspond to homozygotes, since such phenotypes characterize rye individuals in inbread lines. The two major bands are each accompanied by a minor band of higher electrophoretic mobility which appears on enzymograms upon prolonged incubation in the histochemical reaction mixture. The isophosphatases which comprise homozygous phenotype presumably represent epigenetic isoenzymes arisen through some unknown kind of post-translational modification. The relative staining intensity of isophosphatase bands in homozygotes varies depending on the seedling's age and tissue. On the enzymograms of younger seedlings, the faster major band dominates in the staining intensity, indicating that it may be the primary product of gene activity, modified to epigenetic isophosphatases in older tissues.

The four-banded and three-banded phosphatase phenotypes combine bands of different pairs of homozygotes and, therefore, represent codominantly expressed heterozygotes. Two three-banded phenotypes appear instead of four-banded ones due to overlapping, in the electrophoretic mobility, of isophosphatases in two heterozygous combinations, as evident from the enzymograms in Fig. 2.

In conclusion, the observed pattern of individual variation of the ten most frequent phosphatase B electrophoretic phenotypes is exactly consistent with the model of their genetic control by four alleles at a single locus which will be designated as *Ph-2*. The four alleles will be labelled as 2^a, 2^b, 2^c, and 2^d in decreasing order of electrophoretic mobility of the major isophosphatase band doublets controlled by them. Thus, the allele 2^a specifies the phenotype with bands 1 and 3 (enzymogram *3* in Fig. 2), the allele 2^b — bands 2 and 4 (*11* in Fig. 2), 2^c — bands 3 and 5 (*13* and *15* in Fig. 2), and 2^d — bands 4 and 6 (*4*, *8*, and *17* in Fig. 2).

Ph-2 heterozygotes reveal additive combinations of homozygous phenotypes with no hybrid isophosphatase band of intermediate electrophoretic mobility, indicating that phosphatase B is a monomeric enzyme.

In addition to the described four common alleles, several rare alleles were occasionally encountered in some single individuals. Enzymogram *18* in Fig. 2 illustrates a rare allele labeled 2^e, specifying isophosphatase bands 5 and 7, in a heterozygous genotype with the allele 2^a. In several cases slight shifts in the electrophoretic mobility of the four basic isophosphatase doublets were noted, presumably reflecting other rare alleles.

Table 1

Distribution of *Ph-2* genotypes in populations of cultivated, weedy, and wild rye

Rye accessions	*Ph-2* genotypes: numerator — observed, denominator — expected										Heterozygotes	Deviation statistics	
	a/a	*b/b*	*c/c*	*d/d*	*a/b*	*a/c*	*a/d*	*b/c*	*b/d*	*c/d*		χ^2	P (d.f.=6)
'Harkov 60'	8 / 6.2	1 / 1.4	1 / 1.4	25 / 26	8 / 6.0	4 / 6.0	22 / 25.5	1 / 2.9	13 / 12.2	17 / 12.2	65 / 65	5.8	>0.45
'Belorusskaya 23'	6 / 4.8	4 / 2.6	2 / 1.7	26 / 25	4 / 6.6	4 / 5.7	24 / 22	6 / 3.9	12 / 16	12 / 13	62 / 67	5.6	>0.47
'Priekuli 2'	9 / 8.4	0 / 0	0 / 0	45 / 44	2 / 3	0 / 0	0 / 0	37 / 38.2	7 / 6.6	0 / 0	46 / 48	0.4	>0.99
'Jõgeva 120'	3 / 1.7	1 / 0.4	1 / 1.2	50 / 49	1 / 1.6	2 / 2.9	17 / 18	2 / 1.3	7 / 8.4	16 / 15.4	44 / 48	3.2	>0.78
AL-8/72	2 / 2.6	3 / 2.3	5 / 4.0	27 / 24	5 / 4.8	8 / 6.4	15 / 15.7	6 / 6.0	13 / 14.7	16 / 19.6	63 / 67	2.2	>0.90
AL-51/75	4 / 2.7	3 / 1.7	9 / 11	14 / 14	2 / 4.3	11 / 11	12 / 12.4	10 / 8.6	8 / 9.8	27 / 25	70 / 71	3.7	>0.71
AL-2a/71	0 / 0	2 / 2.0	7 / 9.6	25 / 28	2 / 0.6	1 / 1.2	1 / 2.1	7 / 8.7	15 / 14.8	40 / 33	66 / 60	6.7	>0.34
AL-2b/71	1 / 1.6	3 / 1.7	20 / 18.4	10 / 9.3	6 / 3.3	9 / 10.7	7 / 7.6	8 / 11.2	6 / 8.0	29 / 26	67 / 67	5.2	>0.51

3. *Ph-2* genotype and allele frequencies.

Distribution of *Ph-2* genotypes in all the eight rye populations studied, as seen from the data given in Table 1, closely corresponds to that expected from the Hardy-Weinberg equilibrium for four alleles at a single locus. This provides an additional support for the proposed model of genetic control of phosphatase B electrophoretic variants by alleles at a single locus.

The total number of heterozygotes in all population samples closely or exactly corresponds to the Hardy-Weinberg expectations. The proportion of *Ph-2* heterozygotes in rye populations is high, amounting 0.62 to 0.70. In two populations (cv. 'Harkov 60' and AL-2a/71) a small excess of $2^c/2^d$ heterozygotes was observed, contrasted by a slight deficiency in an another population (AL-8/72). However, no permanent excess of any particular *Ph-2* heterozygote or homozygote could be observed in the rye seedling samples analyzed. The small deviations recorded may reflect sampling fluctuations.

Table 2

Allele frequencies at the *Ph-2* locus in populations of cultivated, weedy, and wild rye

Accessions	*Ph-2* allele frequencies			
	2^a	2^b	2^c	2^d
'Harkov 60'	0.25	0.12	0.12	0.51
'Belorusskaya 23'	0.22	0.15	0.13	0.50
'Priekuli 2'	0.29	0.04	0.00	0.67
'Jõgeva 120'	0.13	0.06	0.11	0.70
AL-8/72	0.16	0.15	0.20	0.49
Al-51/75	0.165	0.13	0.33	0.375
AL-2a/71	0.02	0.14	0.31	0.53
AL-2b/71	0.125	0.13	0.43	0.305

The four common *Ph-2* alleles exhibited considerable variation in their frequency between rye populations (Table 2). The two cultivars, 'Harkov 60' and 'Belorusskaya 23', however, had similar frequencies of the alleles 2^c and 2^d and revealed only a small difference in the proportion of the remaining two alleles, 2^a and 2^b. The *Ph-2* allele frequencies in a population on non-fragile weedy rye from Transcaucasia (AL-8/72) proved quite similar to those in the two cultivar populations, differing only in the proportion of the alleles 2^a and 2^c. At the same time, considerable differences in the frequency of three *Ph-2* alleles were revealed in samples collected from two adjacent sub-populations from the same geographic locality in the Armenian SSR.

Discussion

From the data presented here it follows that individual variation in electrophoretic variants of the soluble coleoptile acid phosphatase in rye populations is controlled by the segregation of four common and several rare alleles at a single locus, *Ph-2*. This result revises our previous hypothesis (Яаска, 1975), explaining the observed increase in the number of isophosphatases in the annual rye *S. cereale* L. s. l. in comparison with the perennial rye *S. montanum* Guss. s. l. as caused by the duplication and following divergence of the phosphatase locus. *S. montanum* s. l. has been found (Яаска, 1975) to possess isophosphatases electrophoretically corresponding to those in *S. cereale* s. l. controlled by the allele 2^d. Individual variation in *S. montanum* was contributed by the presence or absence of an additional slow-moving isophosphatase not found in

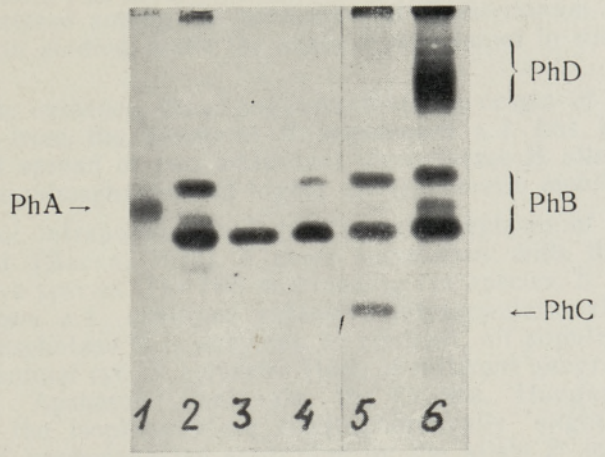

Fig. 1. Polyacrylamide gel electrophoretic enzymograms of rye phosphatases: *1* — embryo, 20 h, *2* — coleoptile, 4 days, *3* — primary roots, 4 days, *4* — primary leaf, 4 days, *5* — basal portion of a 8-day-old primary leaf, *6* — leaf blade of a 8-day-old primary leaf. The origin is at the top, the anode at the bottom.

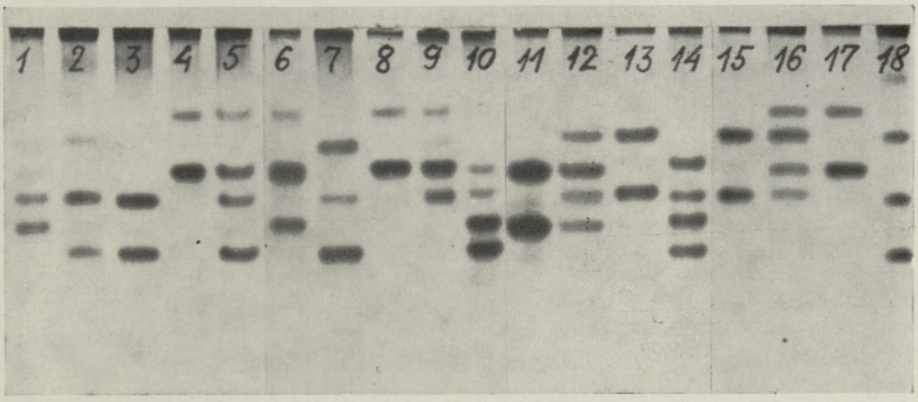

Fig. 2. Polyacrylamide gel electrophoretic enzymograms of the soluble phosphatase B in rye individuals (coleoptiles). *Ph-2* genotypes: *1* — *b/c*, *2* — *a/c*, *3* — *a/a*, *4* — *d/d*, *5* — *a/d*, *6* — *b/d*, *7* — *a/c*, *8* — *d/d*, *9* — *c/d*, *10* — *a/b*, *11* — *b/b*, *12* — *b/c*, *13* — *c/c*, *14* — *a/b*, *15* — *c/c*, *16* — *c/d*, *17* — *d/d*, *18* — *a/e*. The origin is at the top, the anode at the bottom.

S. cereale and by a slight shift in the electrophoretic mobility of isophosphatases encoded by the allele 2^d. The two isophosphatases of highest electrophoretic mobility, B^1 and B^2, controlled by the alleles 2^a and 2^b were not encountered among the accessions of *S. montanum* of different geographic origin studied, while the allele 2^c was found in some samples only.

The available evidence, thus, suggests that the origin of the annual *S. cereale* s. l. from the perennial *S. montanum* s. l. has lead to the appearance and spread of two additional phosphatase B alleles, 2^b and 2^a, controlling isophosphatases of higher electrophoretic mobilities.

The extent of intrapopulational genetic polymorphism of acid phosphatase showed (Яаска, 1975) a close correlation with the breeding system of the rye species. The two outbreeding rye species, *S. cereale* s. l. and *S. montanum* s. l., exhibited extensive intrapopulational individual variation in phosphatase B isoenzymes. In contrast, all populations of the cleistogamous annual rye, *S. sylvestre* Host, of different geographic origin (Turkmenistan, Apsheron Peninsula, the Crimea, Hungary) shared (Яаска, 1975) the isophosphatase electrophoretically slightly differing from the major isophosphatase controlled by the allele 2^c in *S. cereale*. A sample of a self-compatible annual wild rye originally collected by Dr. H. Kuckuck in Iran (Kuckuck, Kranz, 1957) was monomorphic with respect to the isophosphatase phenotype controlled by the allele 2^c in *S. cereale*. This self-compatible cleistogamous rye has been previously treated as *S. vavilovii* Grossh. s. str. (Kuckuck, Kranz, 1957; Khush, 1963; Jaaska, 1975), but was recently named *Secale iranicum* Kobyl. (Кобылянский, 1975) to distinguish it from self-incompatible wild annual ryes which were proposed to be included under the name *S. vavilovii* Grossh. s. l. (Гандилян, 1976).

There seems to be a general correlation between the breeding system and the extent of intrapopulational genetic variation. Drastic differences in the extent of intraspecific polymorphism of phosphatase B between auto- and allogamous species were observed (Jaaska, 1978) in the grass genus *Aegilops* L. Self-fertilizing diploid *Ae. tauschii* Coss. was found monomorphic at the locus *Ph-2* throughout its large distribution area from Transcaucasia to Afghanistan and Kirghiz SSR. In contrast, *Ae. speltoides* Tausch., an outbreeding diploid of much more restricted geographic distribution, displays extensive genetic polymorphism of phosphatase B with five or six alleles at the locus *Ph-2*.

To explain the observed differences, it has been speculated (Jaaska, 1974, 1978) that the process of genetic recombination itself characteristic of allogamous species may generate new allelic variation at the loci encoding for proteins and enzymes through inducing a set of specific intragenic recombinations. Intragenic recombination, occurring at frequencies higher than spontaneous mutation, is considered as a potential source of new allelic variation by several investigators (Ohno, 1967; Stebbins, 1969; Watt, 1972).

The result of the present study, showing that the same four *Ph-2* alleles are common and occur in high frequencies in populations of the annual self-incompatible rye *S. cereale* s. l. of different geographic origin and growth habit (cultivated, weed or wild), requires a special consideration. Thus, *Ph-2* allele frequencies in cultivar populations grown in the Estonian SSR and in a weedy population from a drought-failed wheat field in the Nakhitshevan ASSR, i. e., under contrasting climatic conditions, showed only small differences. At the same time, two sub-popula-

tions of wild fragile-rachis rye from the same locality in the Armenian SSR and some rye cultivars grown in the Estonian SSR revealed clear-cut differences in the frequency of *Ph-2* alleles.

These data give no indication that natural selection for a particular set of external ecological environment should be considered as a main directive force of the observed intrapopulational genetic polymorphism. Instead, it seems reasonable that a random genetic drift in isolated local sub-populations of rye may account for the observed differences in the *Ph-2* allele frequencies.

There was also no permanent excess in the total number or particular kind of *Ph-2* heterozygotes in the rye seedling samples analyzed to indicate gametophytic or juvenile zygotic selection to maintain the polymorphism.

To explain the above results it seems reasonable to consider all the four common *Ph-2* alleles inherent in *S. cereale* as essentially neutral with respect to each other, since they have already undergone selection and passed through the «bottleneck» of natural selection in ancient times, in the course of origin of the annual self-sterile *S. cereale* s. l. from the perennial rye, *S. montanum* s. l. In contemporary populations of *S. cereale* the four alleles are spreading mainly by random genetic drift, possibly even without significant mutation pressure. A low pressure of spontaneous mutation in modern populations of *S. cereale* is thought to account for the appearance of only rare alleles encountered sporadically in single individuals. The common *Ph-2* alleles are considered as having arisen during and the speciation process which has led to the divergence of *S. cereale* from ancestral forms of *S. montanum*.

It has been suggested (Stutz, 1972; Яаска, 1975) that *S. cereale* has arisen through the hybridization of *S. montanum* with a self-fertile annual rye which has already had originated from *S. montanum* and carries one of the two chromosomal translocations differentiating *S. cereale* from *S. montanum*. Stutz (1972) has referred to *S. sylvestre* as a link between *S. cereale* and *S. montanum*. This view has been argued (Яаска, 1975) on the grounds of isoenzyme data, showing that *S. sylvestre* is characterized by the presence of isoperoxidases and isophosphatases not encountered in other rye species. Therefore, *S. sylvestre* has been considered as a lateral branch of evolutionary divergence from *S. montanum*, not related to the origin of *S. cereale*.

The isoenzyme data, however, support *S. iranicum*, another cleistogamous annual rye, as a proper candidate to form an immediate link between *S. montanum* and *S. cereale*. *S. iranicum* carries one major chromosome translocation and the allele $Ph\text{-}2^c$, which are also characteristic of *S. cereale*. It may be assumed that genetic recombination in the hybrid progeny from *S. montanum* and *S. iranicum* has given rise to a second chromosomal translocation and to an increased level of a specific set of intragenic recombinations which have generated two new alleles, $Ph\text{-}2^b$ and $Ph\text{-}2^a$.

At present, the occurrence of extensive intrapopulational enzyme polymorphism is a well-known phenomenon (see reviews: Selander, Johnson, 1973; Powell, 1975; Nevo, 1978). The forces maintaining enzyme polymorphisms have, however, remained obscure in most cases, and have been a subject of discussion and controversy (reviews: Johnson, 1973; Lewontin, 1974; Harris, 1976; King, 1976). Most investigators have agreed (Johnson, 1973; Lewontin, 1974; Ayala, Gilpin, 1974; Bryant, 1974; Nevo, 1978, a. o.) that isoenzyme polymorphisms can be best explained by the

classic neo-Darwinian concept of microevolution, according to which natural selection operating on stochastic gene mutations is the sole vectorial process governing the direction of evolution. M. Kimura (1968), J. King and T. Jukes (1969) and others (reviews: Harris, 1976; King, 1976), however, have argued that molecular evolution, in contrast to evolution of organisms, does not follow and cannot be explained by neo-Darwinian doctrines. They have favoured the so-called «neutralist» theory, according to which two stochastic processes — neutral mutation in combination with random genetic drift — account for the molecular evolution and polymorphism.

It seems to us that the selectionist—neutralist doctrines are two extreme approaches which may be combined and should be developed further to explain various cases of genetic polymorphism in different species. Both doctrines, selectionist as well as neutralist, are based on the concept of spontaneous mutation as a stochastic and undirected process. It is evident and can be accepted that the mutation process is indeed stochastic with respect to selection pressures, external or internal, acting on populations. However, at present there is sufficient, although fragmentary, evidence suggesting that molecular structure of the genome itself and internal factors inherent in the DNA replication process govern the rate and direction of the mutation process and favour some specific types of mutations. Enhanced mutability of particular DNA sequences is a well-documented phenomenon (see review: Clarke, Johnston, 1976).

Internally. directed mutations specified by peculiarities of the DNA molecular structure and replication process and occurring at elevated rates at certain critical stages of speciation should significantly contribute to the direction of molecular evolution by forming a high pressure of specific mutations and generating certain alleles at higher frequencies. Such mutations may be named directional mutations, to distinguish them from ordinary spontaneous mutations arising at low rates and presumably supported by accidental mistakes in the process of DNA replication. Stochastic mutations supported by spontaneous replication mistakes may account for the appearance of rare neutral or dominant advantageous alleles. Directional mutations inherent in a particular state of molecular structure of a species genome and occurring at some critical periods of its evolutionary history may account for common alleles which are essentially neutral with respect to each other and are spreading in modern populations by random drift.

The concept favoured above differs from the ordinary neutral mutation—random drift hypothesis in its deterministic nature, by emphasizing the role of directional mutations in the origin of common neutral alleles maintained in populations by random drift. It is hoped that the application of the deterministic version of neutral mutation—random drift concept presented here will aid to overcome controversies and difficulties in explaining many cases of enzyme polymorphisms in the state of Hardy-Weinberg equilibrium described in literature. At the same time, this concept does not diminish the significance of natural selection as a final and directing force in adaptive evolution and in supporting several other cases of enzyme polymorphism.

Electrophoretic analysis of phosphatase B genotype and allele frequencies may be of potential value in the rye breeding programs as a quantitative measure of genetic distinctiveness, stability or dynamics of breeding stocks and cultivar populations.

Conclusions

Individual variation of electrophoretic multiple forms of the soluble coleoptile phosphatase observed in the populations of the annual self-incompatible rye *Secale cereale* L. s. l. follows the model of four common and several rare alleles at a single gene locus labelled *Ph-2*. Genotype and allelic frequencies at the *Ph-2* locus in 8 rye populations of different geographic origin (Transcaucasia and Estonia) and growth habit (cultivated, weedy, wild) are compared.

A deterministic model of neutral mutation—random drift concept is presented to explain isoenzyme polymorphisms maintained in natural populations in the state of Hardy-Weinberg equilibrium. Specific directional mutations inherent in the molecular structure of a species genome and arising at certain critical stages of speciation are postulated to have given rise to common alleles which are essentially neutral with respect to each other and are spreading by random drift. Stochastic mutations are thought to account for the appearance of rare neutral and dominant advantageous alleles.

REFERENCES

Ayala, F. J., Gilpin, M. E. Gene frequencies comparisons between taxa: support for the natural selection of protein polymorphisms. — Proc. Natl. Acad. Sci. USA, 1975, v. 71, p. 4847—4849.

Bryant, E. H. On the adaptive significance of enzyme polymorphism in relation to environmental variability. — Amer. Nat., 1974, v. 108, p. 1—19.

Clarke, C. H., Johnson, A. W. B. Intragenic mutational spectra and hot spots. — Mutat. Res., 1976, v. 36, p. 147—163.

Harris, H. Molecular evolution: the neutralist—selectionist controversy. — Fed. Proc., 1976, v. 35, p. 2079—2082.

Jaaska, V. Electrophoretic studies of seedling phosphatases, esterases and peroxidases in the genus *Triticum* L. — Eesti NSV TA Toim., Biol., 1969, v. 18, p. 170—183.

Jaaska, V. Electrophoretic analysis of acid phosphatase isoenzymes in the genus *Aegilops* L. — Biochem. Physiol. Pflanzen, 1978, v. 173, p. 133—153.

Johnson, G. B. Enzyme polymorphism and biosystematics: the hypothesis of selective neutrality. — Ann. Rev. Ecol. System., 1973, v. 4, p. 93—116.

Khush, G. S. Cytogenetic and evolutionary studies in *Secale*. IV. *Secale vavilovii* and its biosystematic status. — Z. Pflanzenzüchtg., 1963, v. 50, p. 34—43.

Kimura, M. Evolutionary rate at the molecular level. — Nature, 1968, v. 217, p. 624—626.

King, J. L. Progress in the neutral mutation—random drift controversy. — Fed. Proc., 1976, v. 35, p. 2087—2091.

King, J. L., Jukes, T. H. Non-Darwinian evolution. — Science, 1969, v. 164, p. 788—798.

Kuckuck, H., Kranz, A. R. A genetic analysis of rye populations from Iran. — Wheat Inf. Serv., 1957, v. 6, p. 20—21.

Lewontin, R. C. The Genetic Basis of Evolutionary Change, Columbia Univ. Press, New York, 1974.

Nevo, E. Genetic variation in natural populations: patterns and theory. Theor. Pop Biol., 1978, v. 13, p. 121—177.

Ohno, S. The spontaneous mutation rate revisited and the possible principle of polymorphism generating more polymorphism. — Can. J. Genet. Cytol., 1967, v. 11, p. 457—467.

Powell, J. R. Protein variation in natural populations of animals. — Evolut. Biol., 1975, v. 8, p. 79—119.

Selander, R. K., Johnson, W. E. Genetic variation among vertebrate species. — Ann. Rev. Ecol. System., 1973, v. 4, p. 75—91.

Stutz, H. C. On the origin of cultivated rye. — Amer. J. Bot., 1972, v. 59, p. 59—70.

Watt, W. B. Intragenic recombination as a source of population genetic variability. — Amer. Natur., 1972, v. 106, p. 737—753.

Гандилян П. А. К систематике рода *Secale* L. и его разнообразие в Армянской ССР. I. Видовая дифференциация. — Биол. ж. Армении, 1976, т. 29, с. 27—35.

Кобылянский В. Д. К систематике и филогении рода *Secale* L. — Бюл. ВНИИ растениеводства, 1975, вып. 48, с. 64—71.
Яаска В. Происхождение тетраплоидных пшениц по данным электрофоретического изучения ферментов. — Изв. АН ЭстССР. Биол., 1974, т. 23, № 3, с. 201—220.
Яаска В. Эволюционная изменчивость ферментов и филогенетические взаимосвязи в роде *Secale* L. — Изв. АН ЭстССР. Биол., 1975, т. 24, № 3, с. 179—198.
Яаска В. Геном- и тканеспецифическая регуляция изоферментов эстеразы и кислой фосфатазы у тетраплоидных пшениц при прорастании. — Изв. АН ЭстССР. Биол., 1976, т. 25, № 2, с. 132—145.

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HAPPELISE FOSFATAASI GENEETILINE POLÜMORFISM RUKKI *SECALE CEREALE* L. POPULATSIOONIDES

Ühcaastase isesobimatu rukki *Secale cereale* L. s. l. populatsioonides täheldatav lahustuva happelise fosfataasi isoensüümide individuaalne varieeruvus on tingitud neljast sagedasest ja mitmest haruldasest alleelist ühe ja sama geeni lookuses. Artiklis on esitatud võrdlevad andmed fosfataasi genotüüpide ja alleelide sageduse kohta 8 erineva geograafilise päritolu (Taga-Kaukaasia ja Eesti) ja ökoloogiaga (kultuur-, umbrohu- ja metsiku rukki) populatsioonis ning teoreetiline mudel polümorfismi mõistmiseks.

Велло ЯАСКА

ГЕНЕТИЧЕСКИЙ ПОЛИМОРФИЗМ КИСЛОЙ ФОСФАТАЗЫ В ПОПУЛЯЦИЯХ РЖИ *SECALE CEREALE* L.

Генетический полиморфизм кислой фосфатазы колеоптиля в популяциях однолетней самонесовместимой ржи обусловлен четырьмя частыми и несколькими редкими аллелями одного локуса. Представлены данные о частоте генотипов и аллелей этого локуса в популяциях ржи различного географического происхождения (Закавказье и Эстония) и типа произрастания (культурные, сорные и дикие). Для объяснения случаев полиморфизма изоферментов в состоянии равновесия Харди—Вайнберга выдвинута детерминистическая модель концепции нейтральных мутаций. Согласно этой модели специфические мутации, свойственные геному данного вида и возникающие в определенные периоды видообразования, обусловливают появление селективно нейтральных по отношению друг к другу и распространяющихся путем случайного генетического дрейфа частых аллелей. Случайные мутации обусловливают появление селективно нейтральных редких аллелей и полезных доминирующих аллелей.