栽培イネにおける特異的酸性フォスファターゼ・ザイモグラムの遺伝的収斂

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GENETIC CONVERGENCE OF THE SPECIFIC ACID PHOSPHATASE ZYMOGRAMS IN *ORYZA SATIVA*[1]

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In our previous paper (Shahi *et al.* 1969a), the variations in acid phosphatase isozymes were compared among four groups of rice, *i. e.*, 1) cultivars of *Oryza sativa* L., 2) semi-wild or intermediate *perennis-sativa* forms collected from Jeypore, India, 3) Asian and other wild forms belonging to *O. perrennis* Moench, and 4) various other *Oryza* species. The wild forms, especially perennial type of *perennis*, showed various zymograms, *i. e.*, in total 147 strains contained 31 different zymograms, while in 115 *sativa* cultivars and in 26 strains of the semi-wild forms only two were located. Moreover, it was noted among cultivars that the Indica and Japonica types generally differed in their zymograms.

Since cultivated rice, *O. sativa*, is believed to have originated from the Asian group of a wild rice, *O. perennis*, it may be rather natural that the two zymograms of cultivars were observed in the wild forms. In the present paper, genes specifying the the zymograms were analyzed in order to compare two cultivars with two wild strains having the same zymograms. A discussion follows about the convergence of genic systems specifying the zymograms during the course of rice domestication.

MATERIALS AND METHODS

Two *perennis* and two *sativa* strains preserved in the National Institute of Genetics, Misima, were mainly used for crossing. The former were W107 (P_1, annual) and W1294 (P_2, perennial), both mentioned in our previous papers (Shahi *et al.* 1969b; Endo 1971). The latter were 108 (P_3, Indica type) and T65 (P_4, Japonica type). These were pure lines, except for W1294 which was homozygous for the isozymic characters examined. Parental, F_1, F_2 and B_1 plants were observed.

Zymographic examinations in *O. perennis* were carried out mainly of lemma and palea taken together and partly of leaf blade and leaf sheath, but the latter two were chiefly examined in *O. sativa*. Experimental details for the extraction of cell sap, starch

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gel electrophoresis and locating the acid phosphatase bands on the gels were already reported (Shahi *et al.* 1969a).

RESULTS

The cell saps from lemma plus palea as well as mature leaf sheath of the two *Oryza* species gave fine acid phosphatase zymograms of P_1, F_1 and P_2 plants. The P_1 plants (W107) had one major band, 3A, and, at least, four minor bands, 4A', 2A, 1A and 1C. The P_2 plants (W1294) had one major band, 5A, and, at least, five minor bands, 6A, 4A', 3A', 2A and 1A. In the F_1 plants, three major bands, 5A, 4A and 3A, and, at least, four minor bands, 6A, 2A, 1A and 1C, were detected. The 4A band of F_1 plants seems to be a dimeric hybrid band composed of 3A and 5A monomer components from P_1 and P_2 strains, respectively. This band may also overlap the 4A' band from both parents. Band 3A in P_1 showed the same mobility as 3A'in P_2 and the two bands may overlap in F_1. Since there is no evidence for hybridization between 3A' and 5A bands in the plants, both bands must be specified by non-allelic genes.

It may be interesting that the zymograms of the two wild strains, W107 (P_1) and W1294 (P_2), correspond to those of two cultivars, 108 (P_3) and T65 (P_4), respectively. This was examined in F_1 plants from $P_1 \times P_3$ and from $P_2 \times P_4$, and no difference was found in the zymograms among the F_1 and parents. The leaf sheath zymograms of P_3, F_1 ($P_3 \times P_4$) and P_4 are showh in Fig. 2. There was no appreciable difference between the acid phosphatase zymograms from lemma plus palea and from mature leaf sheath or leaf blade of the same plants, though the intensity of each isozyme band was more or less changing due to the aging of organs during the summer season. It should be noted that a set of anodal bands was located near 6A band toward the anode in leaf blade of all four strains in the autumnal season, but there was no difference among them. We have confirmed that the zymograms of P_1, F_1 ($P_1 \times P_2$) and P_2 closely resemble those of P_3, F_1 ($P_3 \times P_4$) and P_4, respectively.

Among 60 F_2 segregants from a cross between the two *perennis* strains, there were found no new zymograms other than those of P_1, F_1 and P_2 types, as they segregated into $8P_1$, $36F_1$ and $16P_2$ types. Some of them are represented in Fig. 3. Very similar results were obtained from the cross between the two *sativa* strains, 108 (P_3) and T65 (P_4): Namely, $163F_2$ plants segregated into $57P_3$, $70F_1$ and $36P_4$ types. Their six zymograms are shown in Fig. 4, where the band 5A of immature leaf sheath (plant No. 3-2) was relatively weak. F_3 progenies also showed the three types, $20P_3$, $38F_1$ and $12P_4$, obtained from four F_2 heterozygotes, while B_1 ($F_1 \times P_4$) progenies showed the two types, $9F_1$ and $17P_4$ (Table 1). The ratios for the three types indicate single locus segregation, though they may be modified by gametic selection. We then designated the allelic genes which specify bands 3A and 5A by Acp_1^{3A} and Acp_1^{5A} at the Acp_1 locus, respectively. Also, the genes specifying band 1C of P_1 (or $P)_3$ and its null form of P_2 (or P_4) were designated by Acp_2^{1C} and Acp_2^{0} at the Acp_2 locus, respectively. Obviously, the two loci, Acp_1 and Acp_2, are closely linked.

The genes specifying 4A', 2A and 1A bands appear to be common to both parental

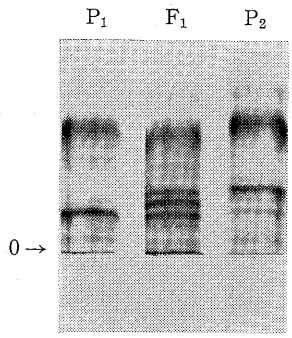

Fig. 1. Acid phosphatase zymograms from lemma plus palea of three plants in *O. perennis:* P_1, W107; F_1, $P_1 \times P_2$; P_2, W1294.

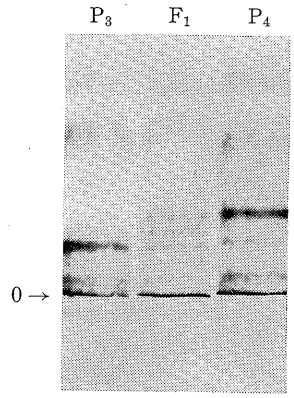

Fig. 2. Acid phosphatas zymograms from leaf sheath of three plants in *O. sativa:* P_3, 108 (Indica type); F_1, $P_3 \times P_4$; P_4, T65 (Japonica type).

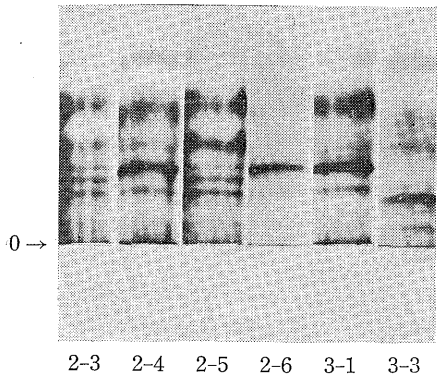

Fig. 3. Acid phosphatase zymograms from lemma plus palea of six F_2 segregants from a cross between W107 and W1294. Numbers at the bottom of the gels show plant No.

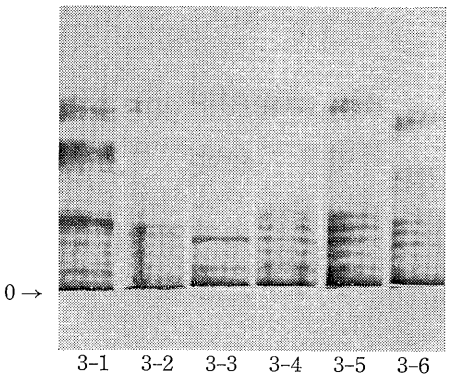

Fig. 4. Acid phosphatase zymograms from leaf sheath of six F_2 segregants from a cross between 108 and T65. Numbers at the bottom of the gels show plant No.

strains. The minor band 6A was always accompanied by 5A major band. The gene specifying the minor band may be linked with Acp_1, unless it was due to *in vivo* modification of the major band.

Thus, the present experiments revealed that the isozymic differences between the two zymograms of both species were due to alleles at Acp_1 and Acp_2 loci. Namely, the Indica type zymogram (P_1 and P_3) was specified by Acp_1^{3A} and Acp_2^{1C}, while the Japonica type zymogram (P_2 and P_4) was specified by Acp_1^{5A} and Acp_2^{0}. The inheritance of these isozyme bands is diagrammatically represented in Fig. 5.

Table 1. Segregation for acid phosphatase isozyme patterns from *perennis* and *sativa* crosses

Generation	P_1 (or P_3) type	F_1 type	P_2 (or P_4) type	Total	χ^2-test	P
O. perennis						
P_1 (W107)	3			3		
P_3 (W1294)			3	3		
F_1 ($P_1 \times P_2$)		3		3		
F_2	8	36	16	60	4.53	0.10
O. sativa						
P_3 (108)[1]	3			3		
P_4 (T65)[2]			3	3		
F_1 ($P_3 \times P_4$)		3		3		
F_2	57	70	36	163	8.66	0.01
B_1 ($F_1 \times P_4$)		9	17	26	2.34	0.25
F_3-16	4	15	3	22		
F_3-17	4	8	1	13		
F_3-25	2	7	2	11		
F_3-38	10	8	6	24		
F_3 total	20	38	12	70	2.46	0.10

1) Indica type. 2) Japonica type.

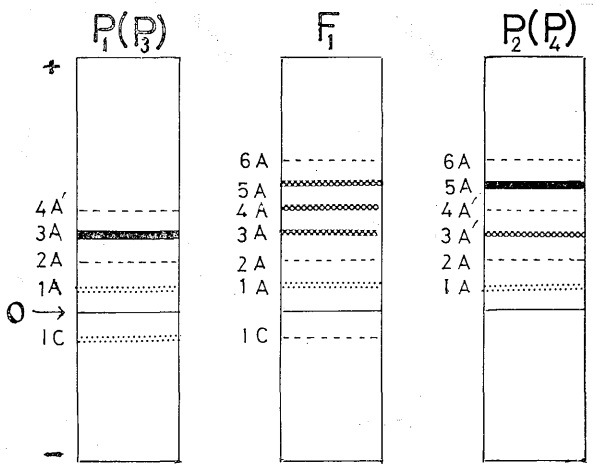

Fig. 5. A diagram for the inheritance of acid phosphatase isozymes between two strains of *O. sativa* (or *O. perennis*).

DISCUSSION

Although *perennis* wild strains and *sativa* cultivars are cytologically closely related, both species are considerably different. Morphologically and zymographically the former is polymorphic, and shows more grain shedding as well as many other wild characters. The species has a series of intergrades varying from annual to perennial forms. The latter species, including Indica, Japonica and intermediate types, shows less grain shedding and is potentially perennial, though cultivated as an annual. For cultivated

rice, the conditions of cultivation differ from locality to locality. Since any genetic system as a whole is presumbly moulded by cultivation, this may cause a convergence of the genetic systems responsible for morphological and physiological characters, resulting in the formation of local varieties. Thus, local varieties must be, more or less, different from each other. A series of intervariental morphological variation (*e.g.* Oka 1958) and of hybrid sterility has been observed (*e.g.* Hinata and Oka 1962). However, the species showed to have only two kinds in acid phosphatase zymograms, when we neglect mutant zymograms expected in any cultivar.

The present experiments revealed that the genic systems specifying the two acid phosphatase zymograms of two *sativa* cultivars almost completely corresponded to those of two *perennis* strains. Then, it appears that among cultivars the two kinds of genic systems are to the exclusion of others distributed, in contrast to the intervarietal differential genic systems controlling morphological and physiological characters.

A similar fact was already observed in leaf peroxidase zymograms of both species. In wild perennial populations the zymograms were much more polymorphic than in the annual populations. Furthermore like the case of acid phophatase, *sativa* cultivars (Chu 1967) and semi-wild *perennis-sativa* strains (Chu and Oka 1967) were found to have two kinds of perioxidase zymograms representing the Indica and Japonica types, respectively, which differed in the presence or absence (or very weak intensity) of 4C band, *i. e.*, most strains of the Indica type have this band but those of the Japonica type generally lack it.

From these results may be drawn a tentative hypothesis that even at a primitive cultivation as observed in Jeypore, India, some particular zymograms were rapidly selected and others were lost. In other words, when the genetic systems of primitive rice forms are moulded by cultivation, convergence of the genetic systems may occur at a certain isozyme level. Actually the cultivation experiments with *O. perennis* and its hybrid with *O. sativa* demonstrated that the frequency of alleles expressing cultivated characters quickly increased and that selection for the cultivated characters resulted in homozygosity, probably due to increased selfing rate (Oka and Morishima 1971). However, the correlation between the cultivated characters and specific zymograms remains to be further examined.

SUMMARY

In a number of rice cultivars, *Oryza sativa*, acid phosphatase zymograms were found to be of two kinds. Genetic experiments revealed that the isozymic difference between the two was due to alleles at Acp_1 and Acp_2 loci which are closely linked. Those two zymograms were detected in wild rice strains of *O. perennis* which is believed to be the wild progenitor of *O. sativa*. The genetic behavior of the isozymes was very similar to that of the isozymes of *O. sativa*. Although *O. perennis* showed many different acid phosphatase zymograms, semi-wild *perennis-sativa* strains were found like *O. sativa* to have the same two kinds. Probably, domestication, even in a primitive stage, may lead to genetic convergence for the genes specifying the acid phosphatase zymograms of rice.

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