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PHYLOGENETIC DIFFERENTIATION OF CULTIVATED RICE, XXIII. POTENTIALITY OF WILD PROGENITORS TO EVOLVE THE INDICA AND JAPONICA TYPES OF RICE CULTIVARS

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SUMMARY

Studies of intermediate wild-cultivated plants suggested that the Indica-Japonica differentiation of cultivars of *Oryza sativa* L. has taken place with the domestication of wild plants. The wild progenitor, which is considered to be the Asian form of *O. perennis* MOENCH, shows no trace of differentiation into two such types as the Indica and Japonica. To elucidate the potentiality of the wild progenitor to evolve the two types when domesticated, the selfed progenies from an Indica × wild and a Japonica × wild cross were examined with regard to three characters known to be useful for distinguishing between the two types. The data showed that Japonica-like plants were derived from the Indica × wild cross and Indica-like plants from the Japonica × wild cross. The Indica-Japonica differentiation was considered to have resulted from selection of incipient domesticates having such potentiality under different climatic conditions; the dynamics was discussed.

INTRODUCTION

The diverse cultivars of *Oryza sativa* L. are largely divisible into the Indica and Japonica types. The wild progenitor of *O. sativa* is considered to be the common wild rice distributed in tropical Asia, the Asian form of *O. perennis* MOENCH (OKA, 1964a, 1974b). This wild species is comprised of different varieties and shows a perennial-annual continuum (MORISHIMA et al., 1961; OKA & MORISHIMA, 1967; OKA, 1976); intermediate perennial-annual populations seem to be most probably the immediate progenitor of cultivated rice (SANO et al., 1980). However, the varieties of this wild species show no trace of differentiation into two such types as the Indica and Japonica (MORISHIMA el al., 1961; OKA & CHANG, 1962).

An examination of intermediate wild-cultivated plants collected from the Jeypore Tract, India, where the people had been isolated from modern civilization until recent years, indicated that the Indica-Japonica differentiation might have gradually proceeded with the domestication of wild plants (OKA & CHANG, 1962; OKA, 1974b). This suggests that the wild progenitor of *O. sativa* has a genetic potentiality to bring about the two types when domesticated.

To elucidate the supposed potentiality, a wild strain was crossed with an Indica and a Japonica cultivar, respectively, and the selfed progenies of the hybrids were observed with respect to Indica-Japonica differentiation. The result of this experiment is the main subject of the present paper.

BACKGROUND INFORMATION

The Indica-Japonica differentiation of rice cultivars is a well known fact since the pioneering work by KATO et al. (1928). Papers on comparisons between the two types are too numerous to summarize briefly. Oka (1958) has investigated whether or not the two types really exist as natural varietal groups, and has concluded that the presence of the two types could be recognized on the basis of character-association patterns although there was no single criterion discriminating between them. Indeed, there were various intermediate Indica-Japonica varieties distributed in the hilly areas of tropical Asia (MORISHIMA et al., 1980).

Phenol reaction of the hull, controlled by a dominant gene *Ph,* is one of good criteria; most Indicas show a positive (dominant) while most Japonicas show negative (recessive) reaction. Other characters useful for discrimination were potassium chlorate resistance of seedlings, drought resistance of young plants (by the *Mimosa* method), cold tolerance, time required for seed germination, and apiculus hair (bristle) length, all being multi-genic (OKA, 1958). When two or more discriminative characters were combined, the distinction between the two types could be shown more clearly. This has led us to the use of discriminant functions (OKA & FANG, 1957; OKA & CHANG, 1962; MORISHIMA et al., 1962). The principal component analysis of correlations among 11 characters has demonstrated the presence of two types quite clearly (MORISHIMA & OKA, 1981).

Many characters of agronomic importance show a difference between the two types although the variations overlap. Even the races of the blast fungus, *Piricularia oryzae,* were found to be differentiated into two groups, one tending to be pathogenic to Indica hosts and the other to Japonica hosts, when the data on their differential pathogenicities were subjected to multivariate analysis (MORISHIMA, 1969). This suggests that the Indica and Japonica types have many genic differences controlling vertical resistances to the fungus, and the fungus has become differentiated consequently.

The partial sterility of F_1 plants between distantly related rice cultivars is well known since the early days (KATO et al., 1928; TERAO & MIZUSHIMA, 1939; OKA, 1958). Generally, Indica-Japonica crosses exhibited the F_1 sterility more frequently than crosses within Indica and within Japonica, but the sterility relationships were complex and did not discriminate between the two types clearly (TERAO & MIZUSHIMA, 1939; OKA, 1958, 1964b; MORISHIMA & OKA, 1981). On the other hand, many strains of the Asian form of *O. perennis* were found to produce fertile F_1 plants with different cultivars which were inter-sterile (HINATA & OKA, 1962).

The sterile F_1 plants showed no disturbances in chromosome pairing which were responsible for the sterility. The genetic basis of the F_1 sterility was analyzed by the use of three-varietal crosses (OKA, 1957d) and of isogenic lines carrying a sterility gene (OKA, 1974a). It was gametophytic and controlled by a number of sets of duplicate genes governing gametic development. Gametes possessing a double recessive combination of the genes deteriorated during development. In addition to this, cytoplasmic pollen sterility with a gametophytic fertility-restoring gene was also detected (SHINJYO, 1969).

In the F_2 and later generation hybrids, even in those from fertile F_1 plants, partly sterile segregants were frequently found, and true-breeding partly sterile lines were obtained in the selfed progenies of such segregants (OKA & DOIDA, 1962). The F_2 sterility was mainly sporophytic and controlled by duplicate genes governing gametic development through sporophytic tissues; plants with recessive combinations of those genes showed partial sterility (OKA & DOIDA, 1962; OKA, 1978). The occurrence of sterile and weak (OKA, 1957c; a similar genetic basis) plants in the F_2 and subsequent generations were considered to indicate the tendency of the hybrids to break down. This might have played a role in varietal differentiation as will be discussed later.

MATERIALS AND METHODS

The following three strains, which were progenies of repeated self-pollination and self-fertilization from a single plant, were chosen as the parents for crosses: Wild parent (P_W) – W152, an annual or intermediate perennial-annual type of *O. perennis*, collected in a roadside swamp at Taragoone, Chinsurah, West Bengal, India. Indica parent (P_I) – Ac108, a native cultivar of Taiwan showing typical Indica characteristics, locally named Peiku. Japonica parent (P_J) – Taichung 65 or T65, a representative Japonica (Ponlai) cultivar of Taiwan, selected from a cross between two Japanese cultivars, Kameji and Shinriki.

Two crosses, $P_I \times P_W$ and $P_J \times P_W$, were made, and the F_2 populations each consisting of 200 plants were raised in the 1960 winter season at Taichung. One panicle from each of 50 randomly sampled F_2 plants were bagged to produce selfed F_3 seeds. In each cross, 50 F_3 lines each consisting of five plants were grown in the next summer season and a plant randomly selected from each line was bagged to produce F_4 lines. The F_4 to F_7 lines were propagated in the same manner, raising two successive generations a year (cf. OKA & MORISHIMA, 1971, second experiment). In each F_7 line, panicles were harvested from two plants for further observations.

To evaluate the F_7 plants for their likeness to the wild or the cultivated type, measurements were taken for the percentage of seed shedding (panicles were run over by a rubber roller six times on an inclined board and the number of grains dropped before and after the test was recorded in percent of total grain number), single grain weight (in mg, mean for 100 ripened grains), and spikelet number per panicle (cf. OKA & MORISHIMA, 1971). To evaluate them for their likeness to the Indica or the Japonica type, the F_8 seeds representing the F_7 plants were tested for the following three characters at Misima, Japan.

Potassium chlorate resistance – Four lots of seedlings (plumules ca. 1 cm long) were soaked in 0.05%, 0.2%, 1% and 4% $KClO_3$ solution, respectively, for 24 hours, washed and kept wet at 30°C for 5 days, with two replications. The degree of $KClO_3$ injury was graded into 5 classes on a single seedling basis, and the concentration giving a medium degree of injury (class 3), computed from common logarithms of concentrations (log 1% = –2.0, etc.), was used for evaluating the resistance of a sample.

Cold tolerance – Seedlings (plumules ca. 1 cm long) were kept wet at 1°C for three days and at 30°C for three days more, with two replications, and the degree of cold injury was graded into five classes with scores 1 (complete death) to 0 (no injury) on a single seedling basis. The tolerance of a sample was shown by the mean of scores.

Apiculus hair length – Ten or more hairs (bristles) on several spikelets were measured under a microscope with low magnification.

Phenol reaction was not included in the test since it was a monogenic trait; P_I and P_W showed a positive while P_J showed a negative reaction. The seeds from part of the F_7 plants were insufficient in number for completing all these tests. The number of F_7 plants with complete records were 82 in $P_I \times P_W$ and 68 in $P_J \times P_W$.

RESULTS

The F_1 plants from both $P_I \times P_W$ and $P_J \times P_W$ were fully fertile in both the percentages of normal pollen and seed setting; in contrast, those between P_I and P_J, observed elsewhere, gave a pollen fertility of 48% and an about 40% seed fertility. Although the F_2 and later-generation plants were not recorded for fertility, they were generally fully fertile and grew normally.

The distributions of measurements of potassium chlorate resistance, cold tolerance, and apiculus hair length among the F_7 and parental plants are given in Table 1. The table shows that the Indica (P_I) and Japonica (P_J) parents distinctly differed in the three characters. With regard to potassium chlorate resistance, P_I was susceptible while P_J and the wild parent (P_W) were resistant. The F_7 plants from the two crosses varied similarly in a wide range, those from $P_I \times P_W$ showing a higher frequency of susceptible plants than those from $P_J \times P_W$. The $P_J \times P_W$ cross produced a few susceptible progenies although both parents were resistant.

In cold tolerance, P_I and P_W were non-tolerant while P_J was tolerant. The F_7 plants from both crosses varied in a wide range, those from $P_J \times P_W$ showing a higher frequency of tolerant plants than those from $P_I \times P_W$. In the same manner as was observed in potassium chlorate resistance, the $P_I \times P_W$ cross produced a few tolerant plants although both parents were non-tolerant. In apiculus hair length, P_J and P_W had longer hairs than P_I. The variations observed among the F_7 plants were transgressive, the plants from $P_I \times P_W$ generally having shorter hairs than those from $P_J \times P_W$.

To evaluate the plants with intermediate character values on their likeness to the Indica or the Japonica parent, a discriminant function maximizing the difference between the two types by combining the measurements of potassium chlorate resistance (K), cold tolerance (C), and apiculus hair length (H) was constructed by Fisher's (1936) method, using the data for 52 Indica and 55 Japonica strains from different Asian countries (cf. Oka & Chang, 1962). It was, when standardized: $X_1 = -K + 0.67C - 0.23H$. The X_1 scores ranged from 0.46 (typically Indica) to 0.15 (typically Japonica) among the F_7 plants examined.

The F_7 plants also varied between the wild and cultivated types. This variation was evaluated by another discriminant function combining the measurements of percent seed shedding (S), single grain weight (W), and spikelet number per panicle (N), which was computed to maximize the difference between 20 typically wild and 30 cultivated strains (Oka & Morishima, 1971). It was, when standardized: $X_2 = S$

Table 1. Variations in three Indica- Japonica discriminative characters among F_7 plants of two crosses and the parental plants, tested with the seeds produced by them.

a) Potassium chlorate resistance of seedlings.

Material	$KClO_3$ concentration in log						Number of plants	Mean
	-1.67	-2.00	-2.33	-2.67	-3.00	-3.33		
P_I					2	2	4	3.17
P_J	1	1	2				4	2.08
P_W	1	1					2	1.83
$P_I \times P_W$	26	31	11	11	7	4	90	2.16
$P_J \times P_W$	34	22	6	4	1	1	68	1.94

b) Cold tolerance of seedlings.

Material	Score for degree of injury						Number of plants	Mean
	0	0.2	0.4	0.6	0.8	1.0		
P_I			1	2	1	4	0.8	
P_J	3	1					4	0.05
P_W				1	1		2	0.7
$P_I \times P_W$	2	2	2	15	36	33	90	0.80
$P_J \times P_W$	5	10	6	9	26	12	68	0.62

c) Apiculus hair length (mm).

Material	Hair length (mm)								Number of plants	Mean
	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9		
P_I		2							2	0.3
P_J				1	1				2	0.55
P_W				2					2	0.5
$P_I \times P_W$	1	7	48	26	4				86	0.43
$P_J \times P_W$			9	42	22	14	6	2	95	0.57

P_I = Indica parent; P_J = Japonica parent; P_W = wild parent.

– 0.42W – 0.28N. The X_2 scores ranged from 65 (typically wild) to –24 (typically cultivated) among the F_7 plants. These three characters were weakly intercorrelated as was reported by OKA & MORISHIMA (1971). It is known that awn development also characterizes the wild type; the X_2 score showed weak correlations with awn diameter ($r = 0.16$ in $P_I \times P_W$; $r = 0.25$, significant at 5% level, in $P_J \times P_W$), and with the length of bristles on awn surface ($r = 0.21$, 5%, in $P_I \times P_W$; $r = 0.34$, 1%, in $P_J \times P_W$).

To obtain an integrated picture of the variations, the F_7 plants were scattered according to their X_1 and X_2 scores. The scatter diagram obtained is shown in Fig. 1.

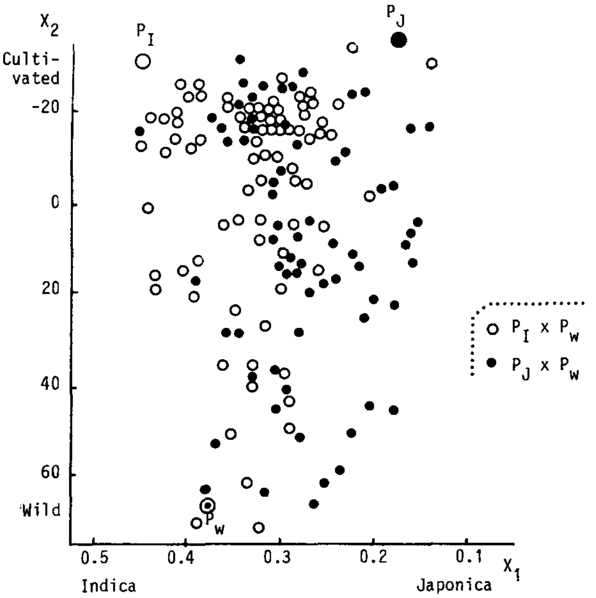

Fig. 1. F_7 plants derived from an Indica × wild and a Japonica × wild cross, scattered according to discriminant scores for classifying the Indica and Japonica types (X_1) and those for classifying the wild and cultivated types (X_2). Parents: Indica, P_I – Ac108, Japonica, P_J – T 65, and wild (*O. perennis*), P_w – W 152.

Many of the F_7 plants were close to the cultivated parents, as was discussed by OKA & MORISHIMA (1971). Although many of them were intermediate between Indica and Japonica types, among those approaching the cultivated type, there were a few Japonica-like plants derived from the Indica × wild ($P_I \times P_w$) cross and a few Indica-like plants derived from the Japonica × wild ($P_J \times P_w$) cross.

The degree of Indica-Japonica differentiation may also be evaluated by the correlations of characters distinguishing between the two types. In fact, the three characters observed were strongly intercorrelated among 120 rice cultivars from different Asian countries although they were uncorrelated among wild strains of *O. perennis* (Table 2) and also within the Indica or the Japonica group (MORISHIMA & OKA, 1981). The correlations found among the F_7 plants were generally lower than those found among the cultivars, only those between cold tolerance and apiculus hair length attaining the 5% level of significance (Table 2).

The tendency to general agreement of these characters may be evaluated by the

Tabel 2. Correlations between potassium chlorate resistance (K), cold tolerance (C), and apiculus hair length (H) in different strain groups.

Group	Number of strains	Correlation coefficient			Average (concordance)
		K-C	C-H	H-K	
Asian rice cultivars	120	0.59**	0.64**	0.68**	0.64
F_7, Indica × wild	82	0.09	0.22*	0.13	0.15
F_7, Japonica × wild	68	0.11	0.24*	0.16	0.17
Asian *O. perennis*	40	–0.03	–0.03	–0.04	0.03

*, ** Significant at 5% and 1% levels, respectively.

mean of absolute values of correlation coefficients which is proportional to KENDALL'S (1948, p. 410–415) coefficient of concordance. The concordance of characters among the F_7 plants was much lower than that observed among the 120 cultivars. This suggests that the three characters are controlled by different genes which are recombined in the hybrids, even though gene combinations resembling those of the parents could have some selective advantage as discussed by OKA (1956, 1957a, b).

DISCUSSION

The occurrence of Japonica-like plants from an Indica × wild cross and of Indica-like plants from a Japonica × wild cross may serve as an evidence for the potentiality of the wild plants to produce the Indica and Japonica types when domesticated, since the same wild strain has been used for the two crosses studied. Within the scope of the present experiment, however, the genetic basis of this potentiality remains as a matter of conjecture. To our knowledge no similar case has been reported in other organisms. A simplest explanation for the genetic basis would be to assume two loci each with three alleles which differ in the intensity of character expression or mutually suppressing in certain combinations, as follows:

Let us assume that the wild parent had $A^0A^0B^0B^0$, the Indica parent had $A^2A^2B^1B^1$, and the Japonica parent had $A^1A^1B^2B^2$ and that $A^2 > B^1$, $A^1 > B^0$, $B^2 > A^1$, and $B^1 > A^0$ in their effects on a character $(2 > 1 > 0)$, while conditions $A > B$ and $B > A$ bring about an Indica and a Japonica characteristic, respectively. It may also be assumed that either $A^0 > B^0$ or $B^0 > A^0$, etc. Then, $A^2A^2B^1B^1$ (Indica) × $A^0A^0B^0B^0$ (wild) will produce $A^0A^0B^1B^1$ expressing a Japonica character $(B > A)$, and $A^1A^1B^2B^2$ (Japonica) × $A^0A^0B^0B^0$ (wild) will produce $A^1A^1B^0B^0$ expressing an Indica character $(A > B)$. Indica cultivars would have $A^1A^1B^0B^0$, $A^2A^2B^0B^0$, or $A^2A^2B^1B^1$, and Japonica cultivars would have $A^0A^0B^1B^1$, $A^0A^0B^2B^2$, or $A^1A^1B^2B^2$. Alleles A^1 and A^2 may be mutants from A^0, and B^1 and B^2 from B^0. This model seems to account for the pattern of variations in three characters observed among the F_7 plants. Although other models may also be set up, they need assumptions of more loci and more intricate genic interactions.

With regard to the high F_1 fertility observed in the initial crosses, as discussed by HINATA & OKA (1962), it may be assumed that the wild parent had double dominant combinations of gametophytic sterility genes, like $+_1+_1+_2+_2$, and the two cultivated parents had $+_1+_1s_2s_2$ and $s_1s_1+_2+_2$, respectively. Then, the F_1 plants from both Indica × wild and Japonica × wild crosses are expected to be fertile while that between Indica and Japonica parents are partly sterile (cf. OKA, 1974a).

Observing hybrid derivatives from Indica-Japonica crosses, the senior author pointed out earlier that when the hybrid populations were propagated without deliberate selection, 1) plants having parental combinations of independent genes (*Ph*:*ph* for phenol reaction, *Rc*:*rc* for pericarp red coloration, and + : *wx* for glutinous endosperm) tended to increase against those with recombinations (OKA, 1956), 2) certain characters discriminating between the Indica and Japonica types also tended to behave in the same manner (OKA, 1957a), and 3) this tendency was associated with F_1 sterility relationships to some extent (OKA, 1957b). The tendency of parental gene combinations to increase in hybrid populations was considered to result from selective elimination of gametes and plants with double-recessive combinations of duplicate genes controlling gametophytic and sporophytic sterilities. The same tendency would also be expected if, in a genic system as postulated above, gene combinations similar to the parental ones had a selective advantage over others under certain environmental conditions. It may be asserted that in the Indica-Japonica hybrids, although genes are recombined without restriction, the selfed progenies tend to become differentiated in the direction of parental types to some extent as the result of selection (see below).

As mentioned, observations of intermediate wild-cultivated plants from the Jeypore Tract have strongly suggested that the Indica and Japonica types are monophyletic, both originating from the same ancestral plants. The potentiality of the wild rice to produce the both types as demonstrated in the present study may serve as a support of the hypothesis of monophyletic origin.

Alternatively, it may also be assumed that the two types were derived from different founders separately, possibly in different localities. On this assumption, however, the wild progenitor must have been differentiated at least latently before being domesticated, and the intermediate Indica-Japonica cultivars commonly found in the hilly areas of tropical Asia must be hybrid derivatives between the two types once established. There is no tangible evidence supporting this view although in the light of the hypothesis of diffused origins of agriculture (HARLAN, 1975), the site of rice domestication as well as the founder population may be considered reasonably to be plural. It may be inferred that there were a number of founder populations distributed over an area and they were selected in different directions in response to different environmental conditions.

Introgressive hybridization between the wild and cultivated rice species releases various types of plants (OKA & CHANG, 1961; CHU & OKA, 1970). Most probably, the evolutionary process of cultivated rice has followed 'differentiation-hybridization cycles' as discussed by HARLAN (1966); it would have been 'short cycles' as supposed for barley, since no major chromosomal rearrangement is involved (CHU et al., 1969). In the light of this hypothesis, discussion on whether monophyletic or diphyletic does not seem to make a good sense.

In Asia, rice cultivars distributed over high latitudes and high altitudes are exclusively Japonicas, and Indicas are dominant in tropical lowlands. In south-western China (YÜ, 1944) as well as in northern Thailand (OKA & CHANG, 1963), Japonicas tend to be grown on the hill and Indicas in the valley; as mentioned, Japonicas have higher cold tolerance than Indicas. On the other hand, populations of the wild rice, *O. perennis,* are distributed in marshes with stagnant water in the areas where Indicas are dominant, but not on the hillside. Intermediate Indica-Japonica cultivars are frequently found on the hillside (MORISHIMA et al., 1980). Their populations are various and contain much genetic variations in each. It may be suggested that the Japonica type was selected along with the dissemination of incipient domesticates from lowland to higher elevation.

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