RICE VARIETIES INTERMEDIATE BETWEEN WILD AND CULTIVATED FORMS AND THE ORIGIN OF THE JAPONICA TYPE[1]

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Variations between wild and cultivated rice forms are dealt with in this paper. Some background information will be briefly given first: The wild species genetically closely related to the cultivated rice, *Oryza sativa* L., is *O. perennis* Moench. It is distributed in various tropical countries of the world, and is thought to be the progenitor of cultivated rice (Sampath and Rao 1951, Richharia 1960, etc.) In addition to this species, another wild form, *O. sativa* f. *spontanea* Roschev., is also found in tropical Asia. The writers and their colleagues (Morishima, Oka and Chang 1961) have however considered that in view of the occurrence of a continuous array of intergrades between the two taxa, *O. sativa* f. *spontanea* can be regarded as a form of *O. perennis;* they then conventionally divided Asian wild-rice forms belonging to this group into *perennis, intermediate* and *spontanea* types. In tropical Asian countries, wild-rice populations of this group are mostly found in swamps in the proximity of rice fields. It has been known that natural hybridization occurs between the wild and cultivated rice species (Roy 1921). The present writers pointed out that hybrid swarms which contained a large amount of genetic variability could be occasionally formed between *O. perennis* and *O. sativa* (Oka and Chang 1961). They also showed that when the habitat assumes conditions of cultivated fields and introgression of cultivated rice happens, wild populations will respond to selection due to the habitat and give rise to intermediate wild-cultivated forms (Oka and Chang 1959).

The cultivated rice might have evolved from the wild species passing through a series of intermediate grades. As discussed by the writers in the above-mentioned papers, the intermediate populations due to hybridization may be considered as valuable materials for looking into the evolution of cultivated

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rice. However, for the creative evolution to proceed, there must be a large amount of genetic variability represented by various intermediate forms, which would be established under certain environmental conditions. It was found that such intermediate plants were actually occurring in a mountain region in India, the Jeypore Tract. The rice varieties collected from this closed region, either growing wild or cultivated by the native people, showed wide variations in various characters and were mostly of intermediate wild-cultivated types.

An important difference between the wild and the cultivated rice species under consideration is that varieties of the latter are differentiated into so-called Indica and Japonica types, while those of the former are not. In this connection, it will be of interest to find that some Jeypore strains resembled the Japonica type, while others resembled the Indica type. Those strains were investigated regarding variations in various characters and hybrid-sterility relationships with certain test-strains. Based on these data, the pathway along which the cultivated rice might have evolved is considered in this paper.

Materials and Methods

1) Collection from Jeypore Tract.

The Jeypore Tract comprises an about 25,000 square-kilometer area in the western part of Orissa State, India (18°-20°N; 81.5°-84°E), the altitude ranging from about 100 to 1000 meters. It is believed that this area has never been influenced by modern civilization until recent years. The greater part of this area is under forest, but rice is grown by the native people in their "shifting" farms or terraced paddies along valleys. The monsoon starts in this area usually by the middle of June and extends to the beginning of October, bringing about 150 to 200 cm of precipitation.

It was pointed out first by Ramiah (1953) that in this region are found wide variations in both wild and cultivated rice forms. Since 1955, the Indian Council of Agricultural Research has sent several collecting parties to this region, and the materials collected are being kept in the Central Rice Research Institute, Cuttack, India. When the senior writer visited that Institute in November 1957, he was allowed to use a part of the materials for his studies through the kindness of Dr. S. Govindswamy who was in charge of the project. Further, Mr. T. Narise, who was accompanying the senior writer, was permitted to join a collecting party and visited some parts of the Jeypore Tract. Thus, a number of genetic stocks collected from this area became available for the writers.

The seed samples thus obtained consisted of "wild" and "cultivated" groups, obtained from plants recognized by the collector as such. According to Govindswamy (1957), villages in the Jeypore Tract are isolated from one another and each has its own varieties which have been grown from time immemorial. The native people in this area have not learned to use fertilizers nor do they know modern cultivation practices.

2) Other materials.

Together with the Jeypore materials, a number of varieties of *O. perennis* and *O. sativa* were observed for the sake of comparison. Those of *O. perennis* (called "wild control-strains" in this paper) were raised from seed-samples each representing a natural population, which were collected by the senior writer during his trip in India in 1957. They ranged from *perennis* to *spontanea* types; for detailed explanations the readers may be referred to Morishima, Oka and Chang (1961). The *sativa* varieties used ("cultivated control-strains") were the inbred lines which had been used by the senior writer for various variation studies (Oka 1953a, 1958, etc.). They are due to random sampling from a large collection of rice varieties from various Asian countries.

3) Conditions of field experiments.

The plants to be studied were grown in the experimental field of Taiwan Provincial Agricultural College, Taichung (24°N), Taiwan, in 1958 and 1959. Seeds were water-soaked for germination on June 22 in both years, and seedlings raised in pots for three weeks were transplanted into the paddy field, spacing at 25 cm × 25 cm (single plant per hill). No fertilizer was applied, but the loamy paddy soil in the field supplied sufficient nutrients. Further, for evaluating photoperiodic responses of the strains by comparing heading dates between plants seeded at different dates (c. f. Oka and Chang 1960), another seeding was made one month in advance (water-soaking on May 23). These plants headed mostly from early October to early November; the average temperatures of the growing periods were about 26° to 27°C, while the temperatures in the heading time ranged approximately from 23° to 27°C.

Most of the strains, except for the cultivated ones used as controls, seemed to be mixtures of different genotypes. Five plants per strain were grown, and if they appeared to be similar to one another, one of them was arbitrarily taken for multiplying self-pollinated seed which represented the given strain in the next generation. The same plant was also used as the pollen-parent of crosses as will be mentioned later. However, the wild-rice strains used as controls were populations each consisting of more than forty plants, and from their selfed seeds, several lines per population were raised in the next generation.

4) Characters investigated.

Records were taken on a single plant basis for all the plants raised, while the strain means were used for variation studies. The characters investigated were: (group 1) Anther length, ligule length (of the second and third leaves from the top), panicle length, plant height, spikelet width, pollen fertility, regenerating ability of plants after maturity, (group 2) degree of grain shedding, seed dormancy, weight of 100 grains, spikelet number per panicle, rachis number per panicle, awn length, (group 3) phenol reaction of hulls, potassium chlorate resistance, low temperature resistance, apiculus hair length, (group 4) spikelet length, length-width ratio of spikelets, presence or absence of pigmentation at various plant parts, glutinous *vs.* non-glutinous starch in endosperm, and heading date. The above division of characters into four groups is based on findings of Morishima, Oka and Chang (1961); characters of group 1 are useful for classifying wild forms into *perennis* and *spontanea* types, those of group 2 for classifying the whole materials into wild (*O. perennis*) and cultivated (*O. sativa*) forms, and those of group 3 for classifying cultivated varieties into Indica and Japonica types, while those of group 4 are not related to a particular direction of variation. Measuring methods for some of these characters are briefly given as follows:

Pollen fertility: About 200 pollen grains per plant, stained with 0.2% iodine potassium iodide solution, were observed under microscope to determine the percentage of good pollen.

Degree of grain shedding: Panicles were run over by a rubber roller (500 gm, 3 cm in diameter) six times on a board inclined at 3°, and the number of grains dropped before and after this test was recorded in per cent of the total grain number.

Seed dormancy: Germination tests were made three times, 50, 90 and 180 days after heading, with hulled and unhulled seeds. The seeds to be tested were stored in a desicator with calcium chloride at room temperatures, and were tested on moistened filter paper in petri dishes at 30°C for 10 days. From each test the percentage of germination and the mean number of days for germination were obtained. The germinating activity in general was then evaluated as: $(\% \text{ of germin.}) \times \frac{1}{10}$ (11— no. of days for germin.). The number of days required for the above index for germinating activity to reach 40% (in hulled seeds) or 20% (in unhulled seeds) was calculated as a relative measure of dormancy (starting from the tenth day after heading). They were transformed into common logarithms, and the average for unhulled and hulled seeds was used as an index.

Phenol reaction: Unhulled seeds were soaked in 1.5% phenol solution for six hours, and coloration of hulls was observed next day.

Potassium chlorate resistance: Seedlings were treated with different concentrations of $KClO_3$ solution, and the concentration necessary for producing a certain degree of damage was shown in common logarithm.

Low temperature resistance: Shown by index-numbers representing the degree of damage to seedlings treated at 0°–1°C for three days.

Further, hybrid-sterility relationships were surveyed as follows: One plant was taken from each of the Jeypore strains which had been purified once or twice by self-fertilization from a single plant, and was crossed with the test-strains given below. The F_1 plants were grown as already mentioned (in 1960 and 1961), and were investigated regarding pollen fertility and some other characters. The test-strains used (except for 504) were the ones which had been used by Oka (1953b, 1958) for cultivated varieties of various Asian countries, and also by Hinata and Oka (unpubl.) for various wild strains. The F_1 fertility data obtained for Jeypore strains could then be compared with the previous data for cultivated and wild forms.

Test-strains

Strain no.	Species and Type		Origin	Local name
108	*O. sativa*,	Indica	Taiwan	Pei-ku
414	„	„	India	P. T. B. 10
521	„	Japonica	Japan	Kisshin
563	„	„	Japan	Kinoshita-mochi
647	„	„	Celebes	Padi ase banda
504	„	„	Taiwan	Taichung no. 65

Presentation of Data

1) Variations in various characters of Jeypore strains.

In each of the 22 characters investigated, the distribution of measurements of Jeypore strains was compared with those for wild (Indian wild-rice forms) and cultivated (varieties of various Asian countries) control-strains. The results showed, in general, that the Jeypore strains, though originating from a limited area, had variation ranges as wide as, or wider than, the wild and cultivated control-strains. For saving room, only a part of the results are shown in Table 1, a-g.

Table 1a shows that in length-width ratio of spikelets, the Jeypore materials contain as large a variability as the cultivated varieties of various Asian countries, while the wild forms are relatively uniform. It is found in Tables 1b and 1c that in panicle length and ligule length, in which the *perennis* and the *spontanea* types of wild rice markedly differ, Jeypore strains vary over wider ranges than the wild and cultivated control-strains. The same tendency was also found in spikelet number per panicle and weight of 100 grains. However, in anther length, the difference between *perennis* and *spontanea* types was larger than the variation range of Jeypore strains.

Table 1. Distributions of measurements of several characters among Jeypore strains, compared with those among Indian wild-rice forms (*O. perennis*) and cultivated varieties of various Asian countries (*O. sativa*).

a) Length-width ratio of spikelets.

Group	1.8	2.0	2.2	2.4	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.2	4.4	No. of strains
O. perennis,															
type *spontanea*							1	6	2	1					10
type intermed.								2	5	5	1	1			13
type *perennis*									1	4	1	2			8
Jeypore strain,															
"wild"				1	2	15	15	16	7	5	2	2			65
"cultivated"		7	18	30	26	23	37	25	22	11	3	2	4	6	214
O. sativa,															
type Continental (Indica)	1		3	12	23	12	10	7	5	1		2	2		78
type Insular (Japonica),															
Tropical		2	6	10	7	11	7	3	1	2					49
Temperate		4	15	6											25

b) Panicle length.

Group	11 cm	14	17	20	23	26	29	32	35	38	No. of strains
O. perennis,											
type *spontanea*	3	5	1								9
type intermed.		1	3								4
type *perennis*				3	4						7
Jeypore strain,											
"wild"		2	2	10	29	15	5				63
"cultivated"		3	5	19	59	53	27	18	9	2	195
O. sativa,											
type Continental (Indica)		2	10	17	16	4	1				50
type Insular (Japonica),											
Tropical				5	5	9	4				23
Temperate		2	5	3	3	1					14

c) Ligule length.

Group	1.0 cm	1.5	2.0	2.5	3.0	3.5	4.0	No. of strains
O. perennis,								
type *spontanea*	6	3						9
type intermed.		1	2	1				4
type *perennis*		1	3	3				7
Jeypore strain,								
"wild"		16	19	18	6	2	2	63
"cultivated"	1	17	67	76	29	4	1	195
O. sativa,								
type Continental (Indica)	3	26	17	2	2	1		51
type Insular (Japonica),								
Tropical	4	13	5					22
Temperate	7	6						13

d) Percentage of grain shedding.

Group	0%	20	40	60	80	100	No. of strains
O. perennis,							
type *spontanea*					1	6	7
type intermed.					2	2	4
type *perennis*					5	1	6
Jeypore strain,							
"wild"	4	3	14	4	6	3	34
"cultivated"	41	76	9	1			127
O. sativa,							
type Continental (Indica)	33	12					45
type Insular (Japonica)	33	3					36

e) Dormancy index (No. of days for overcoming dormancy, in log.).

Group	1.0	1.25	1.5	1.75	2.0	2.25	2.5	No. of strains
O. perennis,								
type *spontanea*					6	1		7
type intermed.						4		4
type *perennis*					1	2	2	5
Jeypore strain,								
"wild"		2	14	16	2	1		35
"cultivated"	9	26	91	2				128
O. sativa,								
type Continental (Indica)	37	6	2					45
type Insular (Japonica)	24	8	1					33

f) Potassium chlorate resistance (Conc. of $KClO_3$ solution, in log).

Group	-1.33	-1.67	-2.00	-2.33	-2.67	-3.00	-3.33	-3.67	No. of strains
O. perennis,									
type *spontanea*				1	4	1			6
type intermed.					1		4		5
type *perennis*			1	1	1	1			4
Jeypore strain,									
"wild"			1	3	3	10	16	2	35
"cultivated"		1	3	12	34	28	45	5	128
O. sativa,									
type Continental (Indica)	1		6	7	4	1	8	46	73
type Insular (Japonica),	33	15							48
Tropical									
Temperate	6	19							25

g) Sensitivity to photoperiod (TDM degree; c.f. Oka and Chang 1960).

Group	0	10	20	30	40	50	60	70	80	90	No. of strains
O. perennis,											
type *spontanea* (Class 1)					2	2	4	5	1	2	16
type *perennis* (Class 2)								2	3	6	11
Jeypore strain,											
"wild"						1	1	3	15	8	28
"cultivated"					1	3	10	5	16	59	94
O. sativa	30	44	11	5	1	7	11	12	16	26	163

Tables 1d and 1e show that the wild and cultivated controls differ markedly in the degree of grain shedding as well as in seed dormancy, while the difference is covered by the variation range of Jeypore strains. Table 1f shows that in potassium chlorate resistance, which is a character differentiating the Indica and the Japonica types of cultivated rice, Jeypore strains vary in a fairly wide range. Similar patterns of variation were found in low temperature resistance and apiculus hair length, in which the Indica and the Japonica types also differed significantly. It is known that most Indica varieties have positive phenol reaction, while most Japonicas are negative; in the Jeypore material, two out of 35 wild strains, and 21 out of 126 cultivated ones, showed negative reaction, while the rest were positive. Regarding endosperm character, no glutinous plant could be found among the strains investigated. According to Govindswamy (1957), however, two out of 1,072 strains were glutinous.

The writers have recently pointed out that Asian wild-rice forms belonging to *O. perennis* are mostly sensitive to photoperiod, while cultivated varieties can be divided into sensitive and insensitive groups (Oka and Chang 1960). Photoperiodic sensitivities of the Jeypore strains were measured by the same method as previously adopted, comparing the heading dates of plants seeded on May 23 and June 22. As shown in Table 1g, all the Jeypore strains were found to be sensitive to photoperiod, as is the case with wild-rice forms.

2) Directions of differentiation in the Jeypore materials.

In this chapter, variations in character-complexes are dealt with instead of those in individual characters. The writers and their colleagues (Morishima, Oka and Chang 1961) have shown, by using the technique of principal component analysis (c.f. Kendall 1957), that the primary direction of variation of Asian wild-rice forms can be represented by their differentiation into *perennis* and *spontanea* types, though a continuous array of intergrades occurs between them. In addition to this, the wild-rice populations showed a tendency to vary in the direction of cultivated forms, which was given out as the second component of variation. They did not seem, however, to be differentiated into the Indica and the Japonica types, for they did not vary so widely in characters differentiating the two types. In contrast, in cultivated rice, it is apparent that the primary direction of variation is represented by their differentiation into the Indica and the Japonica types. Thus, we can recognize in this group of rice species three major directions of differentiation, which are represented by *perennis vs. spontanea,* wild *vs.* cultivated, and Indica *vs.* Japonica types, respectively. It has been suggested in the former chapter that variations in all these directions may be found among the Jeypore strains.

The above-given directions of differentiation can be each represented by an axis on which the plants under observation are distributed according to their character-combination. For obtaining such axes, discriminant functions which maximize the difference between two given types by combining measurements of several characters were computed by the method devised by Fisher (1936). The characters to be combined were chosen, examining the data of our previous work, from among those showing relatively high t values between two given types, and the measurements of thus selected characters for a number of strains typically showing the characteristics of the given types were used for constructing variance-covariance matrices from which the computation started. The discriminant formulas thus obtained (standardized) were as follows:

For classifying *perennis* and *spontanea* types,

$$X_1 = -Sw + 14.61\ L + 6.59\ P + 14.42\ An,$$

where Sw: spikelet width, L: ligule length, P: panicle length, and An: anther length.

For classifying wild and cultivated forms,

$$X_2 = -Sh + 0.04\ Gw + 0.67\ Sn - 0.38\ Rn - 1.33\ D,$$

where Sh: percentage of grain shedding, Gw: weight of 100 grains, Sn: spikelet number per panicle, Rn: rachis number per panicle, and D: index of seed dormancy.

For classifying Indica and Japonica types,

$X_3 = -K + 0.75\ Lt - 0.22\ Hr + 0.86\ Ph$,

where K: concentration of $KClO_3$ solution which causes a certain degree of damage, Lt: index-number for damage to seedlings treated at 0°–1°C, Hr: apiculus hair length, and Ph: phenol reaction (1:0).

These discriminant formulas were found to be highly effective for the respective classifying purposes, giving F values as high as 1000 for between-group variances. The scores given by these discriminant formulas were computed for

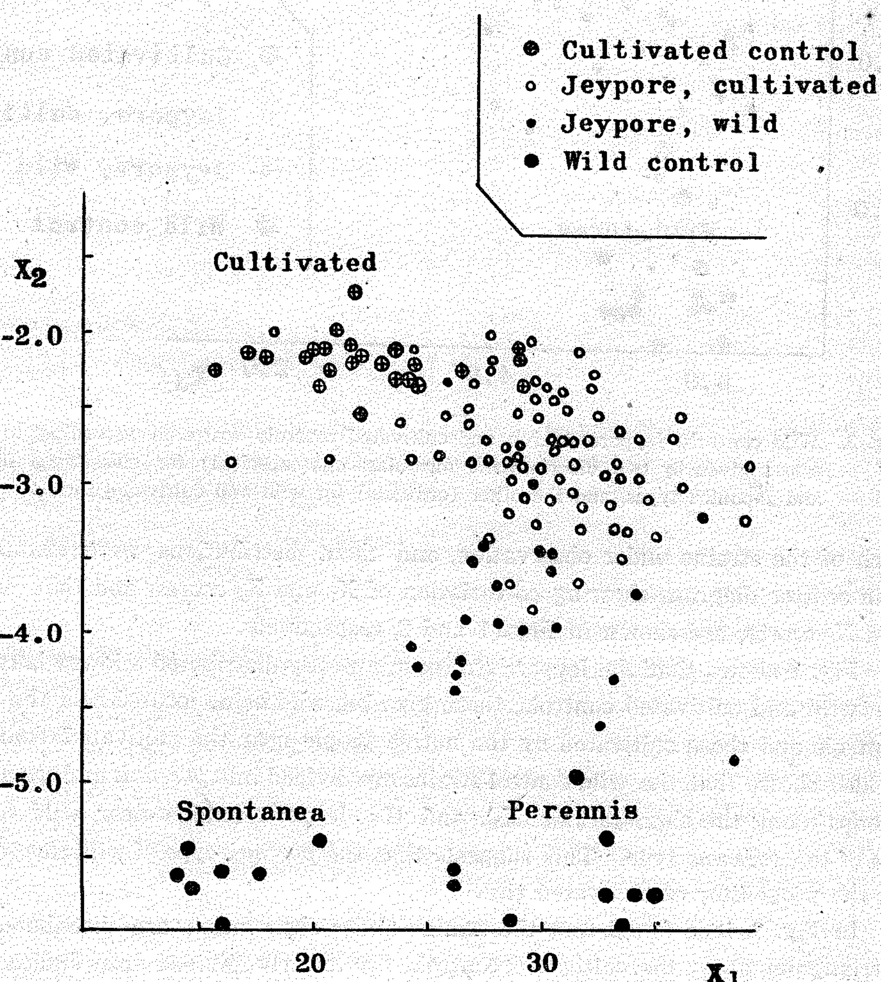

Fig. 1. Wild controls, Jeypore strains, and cultivated controls scattered according to the scores given by two discriminant formulas, one (abscissa) for classifying *perennis* and *spontanea* types, and the other (ordinate) for wild and cultivated forms.

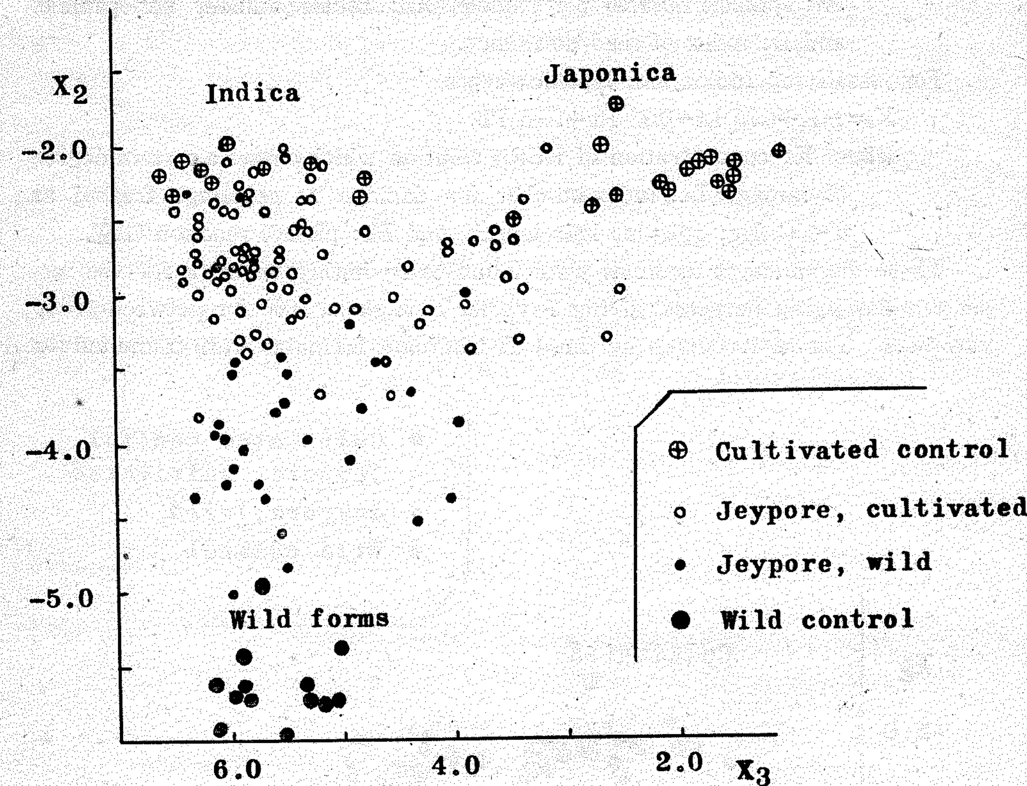

Fig. 2. Wild controls, Jeypore strains, and cultivated controls scattered according to the scores given by two discriminant formulas, one (abscissa) for classifying Indica and Japonica types, and the other (ordinate) for wild and cultivated forms.

each of the strains under observation, and their distributions were examined. The scatter diagram showing co-variation of X_1 and X_2 scores, and that of X_2 and X_3 scores, are shown in Figs. 1 and 2, respectively.

Fig. 1 shows that the Jeypore strains are mostly distributed midway between the wild and cultivated controls, those growing wild being located near the wild controls and those cultivated by the native people near the cultivated controls. It also shows that the wild control-strains are divided into *perennis* and *spontanea* groups along the abscissa axis (X_1), and the Jeypore strains near wild forms are of the *perennis* type. This suggests that the *perennis* type of wild rice might be the progenitor of cultivated rice.

In Fig. 2, it is found that the strains under observation are distributed in a triangular area; the cultivated controls are clearly divided into Indica and Japonica groups, while the wild controls are not, and among the Jeypore strains, it appears that the nearer the plants approach cultivated forms, the larger becomes the distance between the two types. This indicates that the

Indica and the Japonica types are monophyletic, and the differentiation might have been advanced with the approach to cultivated forms. As shown in Table 2, some of the Jeypore strains distributed in the upper-right part of the scatter diagram in Fig. 2 had a good association of characters of the Japonica type, *i.e.*, negative phenol reaction, high resistances to potassium chlorate and low temperature, long apiculus hairs, etc.

Table 2. Measurements of characters of some Japonica-like strains obtained from the Jeypore Tract.

Strain	Phenol reaction	$KClO_3$ resist.	Damage by low temp.	Apiculus hair Lth	Lth/width spikelets	Awn	Discrim. score X_3
Jeypore strain,							
JC 7	—	-2.10	0.65	0.425mm	2.1	+	3.17
JC 13	—	-1.70	0.60	0.570	2.0	+	2.61
JC 14	—	-2.31	0.65	0.463	2.3	—	3.36
JC 45	—	-2.79	0.43	0.599	2.1	+	3.35
JC 75	—	-2.27	0.42	0.604	2.3	—	2.81
JC157	—	-1.97	0.43	0.565	2.1	—	2.55
Cultivated control-strain, Japonica (Tropical-Insular type)							
325	—	-1.68	0.30	0.421	2.2	+	2.07
647	—	-1.33	0.30	0.475	2.1	+	1.70
Japonica (Temperate-Insular type)							
504	—	-2.02	0.10	0.426	2.1	—	2.02
521	—	-1.79	0.00	0.697	2.2	—	1.48
Indica (Continental type)							
108	+	-3.61	0.70	0.262	2.7	—	6.39
414	+	-2.76	0.50	0.196	2.9	—	5.18

It may be assumed that the three variation axes, X_1, X_2 and X_3, are orthogonal in relation to one another. If we combine them in a cubic space, the 3-dimensional distribution of Jeypore strains found there may be regarded as a model showing the evolution of cultivated rice.

3) Hybrid-sterility relationships of Jeypore strains.

It is generally thought that the F_1 hybrids between Indica and Japonica types of *O. sativa* are partially sterile, while those between varieties of the same type are fertile. Actually, fertile F_1s between the two types, as well as partially sterile ones between varieties of the same type, are frequently found, and it is known that the hybrid-sterility relationship is not completely correlated with the two types which are recognized as character-association groups (Terao and Mizushima 1939, Oka 1953b, 1958). Regarding [the hybrid-sterility relationships of wild-rice strains, Hinata and Oka (unpubl.) found that strains of both *perennis* and *spontanea* types tended to show high F_1 fertilities in their mutual hybrids as well as in hybrids with cultivated varieties of different types. It was also found, however, that wild-rice populations, especially those of the *perennis* type, contained differences in various sterility factors; partially sterile plants occur in the populations at different frequencies. Further, when crossed with a certain test-strain, plants of the same population show a variation in the fertility of F_1 plants, and even the F_1 plants from a single cross may differ in fertility.

As mentioned already, the Jeypore strains, purified at least once by self-fertilization, were each crossed with the same set of test-strains as formerly used for the cultivated and wild control-strains. In each cross-combination a single cross was made, and two to five F_1 plants per cross (in a few crosses only one) were raised. It was found that in about one fourth of the crosses (*viz.* 32 out of 121 crosses with test-strain 108, and 25 out of 98 crosses with 504), F_1 plants from the same cross differed significantly in pollen fertility; from a study of sampling variations with other materials, a difference exceeding 15% in 1960, and 12% in 1961, was considered to be significant. This suggests that the plants in their original habitats might have been highly heterozygous for genes causing the sterility of F_1 hybrids, possibly in the same degree as in wild-rice populations.

Hybrid-sterility relationships of those strains were then surveyed as follows: When a significant difference in pollen fertility was found between F_1 plants of the same cross, the fertility of the cross-combination was represented by

Table 3. Distributions of F_1 pollen fertilites of Jeypore strains as tested with four *sativa* strains.

a) Test-strain: 108 (Indica)

Group	% of good pollen									No. of strains
	100	90	80	70	60	50	40	30	20	
Wild control	5	7	1							13
Jeypore strain,										
"wild"	11	13	4	1	1					30
"cultivated"	18	64	17	3	6	2				110
Cultivated control,										
Continental (Indica)	24	19	7	3	1		1			55
Insular (Japonica),										
Tropical	1	10	15	5	3	5	1			40
Temperate			3	6	2	5	1	2		19

b) Test-strain: 414 (Indica)

Group	% of good pollen									No. of strains
	100	90	80	70	60	50	40	30	20	
Wild control	5	5	1	1			1			13
Jeypore strain,										
"wild"	5	6	4	2	2					19
"cultivated"	5	33	20	2	3	2				65
Cultivated control,										
Continental (Indica)	8	3	6	6	16	14	2			55
Insular (Japonica),										
Troppical			4	13	10	9	3	1		40
Temperate		1	5	2	4	2	3	2		19

c) Test-strain: 521 (Japonica)

Group	% of good pollen									No. of strains
	100	90	80	70	60	50	40	30	20	
Wild control	2	5	4					1		12
Jeypore strain,										
"wild"	1	4	3	2	2					12
"cultivated"	4	21	8	2	6	3				34
Cultivated control,										
Continental (Indica)		3	12	7	8	10	11	3	4	58
Insular (Japonica),										
Tropical	8	10	4	6	6	3	3			40
Temperate	7	5	1	2	3	1				19

d) Test-strain: 563 (Japonica)

Group	% of good pollen										No. of strains
	100	90	80	70	60	50	40	30	20	10	
Wild control	2	2	4		2	1					11
Jeypore strain,											
"wild"	1	2	2	1	1	2					9
"cultivated"	4	12	9	4	2	1	1	1			34
Cultivated control,											
Continental (Indica)		11	2	6	8	11	7	8	2	3	58
Insular (Japonica),											
Tropical	7	10	11	5	3		3				39
Temperale	7	6	1	2	2						18

the average of higher values, discarding lower ones. Distributions of F_1 pollen fertilities with four test-strains, thus found, are given in Table 3. The data in the table show that, as pointed out by Hinata and Oka (unpubl.), wild control-strains mostly produced fertile F_1 hybrids with any of the test-strains, while cultivated strains had a more restricted affinity and displayed a wide range of

F_1 fertility; the same table also shows that a majority of the Jeypore strains had high F_1 fertilities as the wild controls.

With the view to illustrating the above-mentioned facts more clearly, the mean value of F_1 pollen fertilities with five test-strains, 108, 414, 521, 563 and 647, was examined. Its distributions are shown in Table 4. The table shows that wild control-strains have apparently higher values than cultivated ones, and the Jeypore strains are in both mode and variation range intermediate between the wild and cultivated controls. Among the Jeypore strains, those growing wild and cultivated appear to resemble the wild and the cultivated controls, respectively. This suggests that with the approach of wild genotgpes to cultivcted ones, mutually partially sterile groups would have developed among the Jeypore strains.

Table 4. Distributions of average F_1 pollen fertility with five test-strains.

Group	% of good pollen												No. of strains
	100	95	90	85	80	75	70	65	60	55	50	45	
Wild control	1	2	3	2		2							10
Jeypore strain,													
"wild"		1	4	2	3	1	1						12
"cultivated"		2	7	9	12	7	1	1					39
Cultivated control,													
Continental (Indica)				3	4	11	10	8	8	1	1	2	48
Insular (Japonica),													
Tropical			1	7	8	10	4	1	3	1			35
Temperate				4	3	4	3	3	1				18

Next, how the variation in hybrid-sterility relationship of the Jeypore strains could be related to their Indica-Japonica differentiation was observed. Distribution of F_1 pollen fertilities with two test-strains, 108 (Indica) and 504 (Japonica), with which a relatively large number of crosses have been made, is shown in the scatter diagram in Fig. 3. The figure shows that a part of the Jeypore strains showed partial sterility with one or the other of the two test-strains in the same manner as control-strains of the Indica or the Japonica type, though most of them showed high F_1 fertility. However, as already mentioned, hybrid-sterility relationships among rice varieties are too complicated to classify them into two groups. A discriminant function which maximized the difference between the Indica and the Japonica types by combining F_1 pollen fertilities with five test-strains, 108, 414, 521, 563 and 647, was then constructed using data for 80 cultivated strains (from Oka 1953b). It was found to be:

$$Y=1.0\ (108)+0.177\ (414)-0.120\ (521)-0.584\ (563)-0.615\ (647).$$

Distributions of the score given by this discriminant formula are given in Table 5. The table shows that among the cultivated controls the distributions of Indica and Japonica types overlap each other in part, though they differ in the mean, and the distribution of Jeypore strains extends from the values of Indica type to those of Japonica type. It may be inferred from this fact that differences of sterility factors as found between varieties of the Indica and Japonica types are involved in the Jeypore strains.

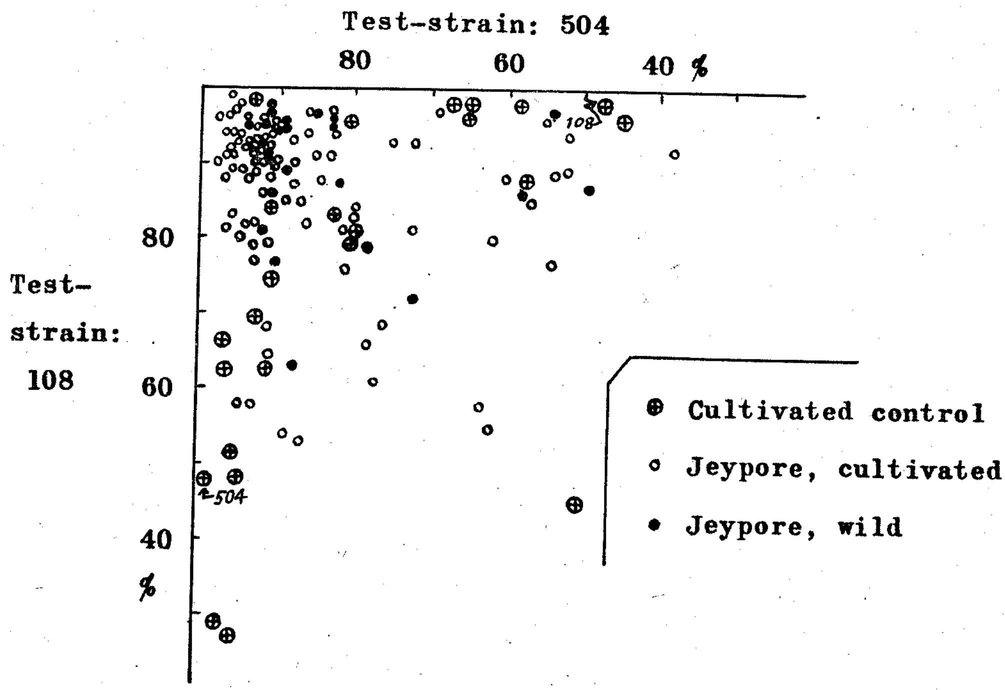

Fig. 3. Scatter diagram showing the relation between F_1 pollen fertilities with two test-strains, 108 (Indica) and 504 (Japonica).

Table 5. Distributions of discriminant score combining F_1 pollen fertilities with five test-strains so as to maximize the difference between Indica and Japonica types.

Group	Indica				Japonica				No. of strains
	70	50	30	10	-10	-30	-50	-70	
Wild control			1	3	6				10
Jeypore strain,									
"wild"			1	2	8	1			12
"cultivated"			4	8	18	7	2		39
Cultivated control,									
Continental (Indica)	3	3	15	16	8	3			48
Insular (Japonica),									
Tropical				4	13	11	3	5	36
Temperate					4	4	5	4	17

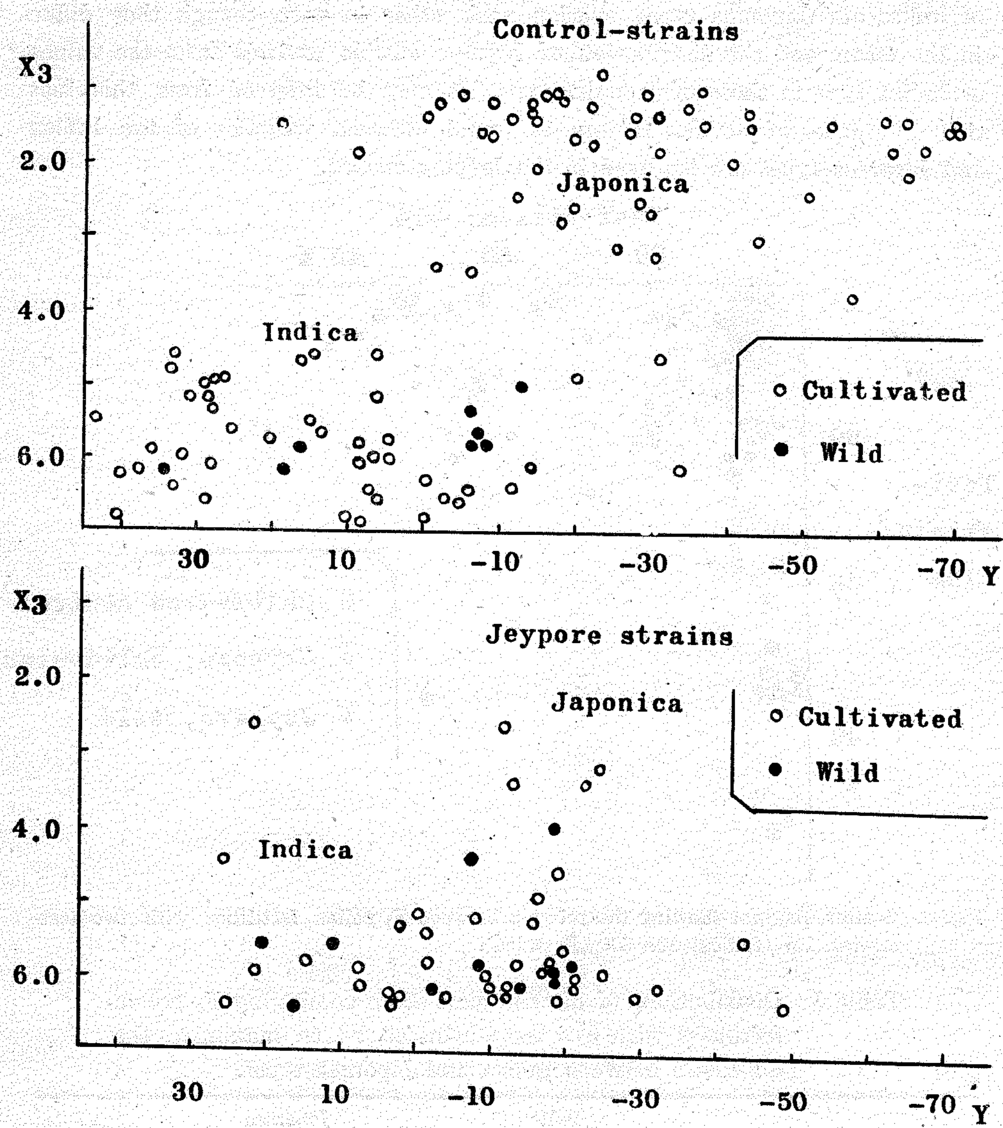

Fig. 4. Scatter diagrams showing the relation between two discriminant scores for classifying the Indica and the Japonica types, one (abscissa) combining F_1 pollen fertilities with five test-strains, and the other (ordinate) measurements of four characters.
Upper: Cultivated and wild control-strains.
Lower: Jeypore strains.

Correlation between hybrid-sterility relationship and character-combination is a point of interest in dealing with the problem of Indica-Japonica differentiation. In regard to this problem, the discriminant score combining measurements of four characters (X_3, in the previous chapter) and that combining F_1 pollen fertilities with five test-strains (Y), both for classifying the Indica and the

Japonica types, were compared. The scatter diagram showing their relation is presented in Fig. 4. The figure shows that the two discriminant scores are correlated among cultivated control-strains, but not among Jeypore strains. It may be noticed, however, that a few Jeypore strains had an association of hybrid-sterility relationship and other characters which was characteristic of the Japonica type. It may be said that the Jeypore strains have a potentiality to be differentiated into types such as the Indica and Japonica.

Discussion

Whether the *perennis* or the *spontanea* type of wild rice is more probably the progenitor of cultivated rice has been a problem of dispute. From systematic view-points, Roschevicz (1931) as well as Chatterjee (1948, 1951) considered that *spontanea* might be the ancestral form of cultivated rice. On the other hand, Sampath and Rao (1951) and other Indian workers (c.f. Richharia 1960) are inclined to consider that *perennis* might be the ancestral form and *spontanea* could be a hybrid derivative between *perennis* and cultivated forms. Regarding this problem, the present writers and their colleagues (Morishima, Oka and Chang 1961) have shown that populations of the *perennis* type occur in relatively stable habitats such as deep swamps and can be propagated both sexually and asexually, while those of the *spontanea* type in relatively unstable habitats are propagated only by seeds, and that *perennis* populations contain a larger amount of genetic variability than *spontanea* populations. They then concluded, supported by Stebbins's hypothesis (1958) that plant species with such features as mentioned above for *perennis* can be regarded in many cases as the ancestral form, that the *perennis* type may presumably be the progenitor of both *spontanea* and cultivated types. This view was evidenced in the present work; the intermediate wild-cultivated forms collected from the Jeypore Tract, especially those approaching wild rice, were of the *perennis* type, and those strains formed an array of intergrades connecting *perennis* with cultivated varieties.

We may then consider the evolutionary pathway from wild to cultivated rice forms. It may be pointed out that: 1) Because of its partially allogamous breeding, pronounced seed dormancy and partially asexual propagation, the *perennis* type of wild rice is liable to accumulate in its populations genetic variations, which is supplied by mutations and hybridization. This was theoretically corroborated by Dr. M. Kimura of the Japanese National Institute of Genetics after a mathematical study of such a population model (unpubl.). 2) *Perennis* populations were actually found to contain a large amount of genetic variability, as already mentioned. Hybrid swarms between *perennis* and cultivated forms, which appeared to be formed occasionally in nature, were found to have stored up a great deal of variability which, if released, could cover the range from wild to cultivated forms (Oka and Chang 1961). 3) However, when the plants approach cultivated forms, the probability of selfing increases and seed dormancy is weakened (as proved by the writers in a semi-wild form established as weed in rice fields; Oka and Chang 1959). These changes will result in a restriction of the capacity to preserve genetic variability of populations; variations released thereby will give rise to different forms. 4) It may be taken for granted that wild and cultivated forms take an advantage in wild and cultivated habitats, respectively, and so do the intermediate ones in intermediate wild-cultivated habitats. The above-mentioned semi-wild form established as weed in rice fields can serve as an example showing this relation; it might have been established as a result of its response to the pressure of cultivation in the habitat.

These considerations will lead us to the following speculation: In the Jeypore Tract rice culture by the native people is so primitive that the environmental conditions in rice fields are in some respects close to those in natural habitats, and as the rice fields are shifted year by year, wild forms growing in swamps can find their niches in fields left in fallow. The wild-rice populations containing a large amount of genetic variability will then respond to the pressure of cultivation and will give rise to diverse varieties. Some of them may be picked up by the native people for cultivation. Those plants might be intermediate wild-cultivated types and show wide variations in various characters, as illustrated in this study. The occurrence of such intermediate wild-cultivated forms may therefore be regarded as suggesting how cultivated rice can be created from wild plants. It remains unexplained however why plants approaching cultivated forms tend toward self-pollination.

Another important problem involved in the origin of cultivated rice is why cultivated varieties are differentiated into the Indica and the Japonica types. It has been shown in the present study that the two types are monophyletic and the distance between them increases as the plants approach cultivated forms. The relatively small number of Japonica-like strains in the Jaypore material may be explained by assuming that the environmental conditions prevailing there might be relatively favorable for Indica-like plants. It may then be strongly suggested that the wild progenitor of cultivated rice has a potentiality to bring about such a differentiation.

The senior writer (Oka 1953c, 1957a) formerly demonstrated that the partial sterility of hybrids between distantly related rice varieties could be accounted for by assuming sets of duplicate genes which in double-recessive combinations interrupt the development of both micro- and mega-spores carrying them (*gametic-development genes*). Based on this hypothesis, wild-rice plants which show high F_1 fertilities with test-strains of different types would have double-dominant combinations of those genes. Then, recessive mutations or deficiencies at one or the other of the duplicated loci will give rise to plants which are partially sterile in their mutual F_1 hybrids.

In addition to the gametic-development genes, we have evidence showing that rice has many duplicate genes: 1) Genes for awnedness, empty-glume length, etc. (Chao 1928). 2) Genes for auricle and empty-glume colorations (Mitra and Ganguli 1932). 3) Genes for coloration of the junctura, auricle and ligule (Rice in India, 1956). 4) "Runners" *vs.* "Non-runners" (Ramirez *et al* 1960). 5) It was suggested by Mizushima and Kondo (1960) that the loci of genes for apiculus pigmentation would differ if distantly related varieties were compared. 6) The senior writer (Oka 1957b) showed that the occurrence of weak plants in F_2 and later generations of hybrids between distantly related rice varieties could be accounted for by duplicate genes which in certain recessive combinations would interrupt the growth of the plants (complementary semi-lethals). 7) He also found similar duplicate genes for true-breeding partial sterility which appeared in the F_2 and later generations of intervarietal crosses (*duplicate-fertility genes*), and considered that those genes could be responsible for the tendency of such hybrids to break down (Oka, in press).

Why rice has many duplicated gene loci is an important problem; it is however outside the scope of this paper. When genes are duplicated, as discussed by the senior writer before (Oka 1957a), a recessive mutation at one locus may be concealed by the non-mutated duplicate gene at the other locus, so that genic changes which are otherwise fatal may be retained in the population. The species will then enjoy a large amount of potential variation. Further, differences in duplicate genes will result in a restriction to free recombination of other independent genes, since certain recombinations are eliminated by gametic or zygotic selections. In view of these respects, it may be assumed that the potentiality of wild rice to produce different cultivated types such as the Indica and Japonica is essentially due to the duplication of genetic materials.

However, if many recessive mutations or deficiencies of duplicate genes are combined at random, they will give rise to various genotypes which are mutually partially isolated by different kinds of barriers rather than resulting in a few major groups such as the Indica and Japonica. It seems that to some extent this situation can be actually found among the Jeypore strains—they appeared to be heterozygous for the said genes, and showed a complicated pattern of hybrid-sterility relationships which were not so much correlated with variations in other characters. A similar situation was also found among the derivatives of a hybrid between an Indica and a Japonica variety (Oka 1957c). In regard to these, it must be noticed that in any case the Indica-Japonica differentiation could be more clearly recognized by character association than by hybrid-sterility relationship. This suggests that the partial sterility of F_1 hybrids is rather an outcome of differentiation which has been advanced by other forces than an effective isolating mechanism which promotes differentiation.

In view of the differences in low temperature resistance and other physiological responses between the Indica and the Japonica types, it is readily understandable that differential adaptability of the two types to their environments may act as a forceful agent in promoting the Indica-Japonica differentiation. It was found in northern Thailand that rice varieties grown in the mountain part were mostly of the Japonica type, while those in low valleys were of the Indica type (Oka, unpubl.). The same pattern of distribution is also reported in the south-western provinces of China (Yü 1944). It is also known in China that varieties grown in the southern provinces are mostly Indicas (Sen), while those in the northern provinces are mostly Japonicas (Keng). In these cases, the two types seem to be differentiated by altitude, latitude, or by temperature response. However, varieties of the Japonica type are widely distributed in the islands of the Western Pacific, ranging all the way from Indonesia to Japan. In contrast, varieties of the Indica type are mainly grown in the plain regions of the Asian continent. In view of this fact, the senior writer has in his studies of cultivated rice varieties renamed the two types as "Continental" (Indica) and "Insular" (Japonica), respestively (Oka 1953a, 1958, etc.). Therefore, differential adaptability of the two types does not seem to be simply explained by their difference in temperature response.

According to Ting (1949), the first record of rice culture in China appeared in the inscribed oracle bones which belonged to the Shia-U dynasty (about 2,100BC), and the varieties grown in ancient times might have been Japonicas (though it might be difficult to determine); it was not until the Sung dynasty (about 980AD) that Indica varieties were introduced from Vietnam and spread out into the southern provinces. On this and other bases, some Chinese workers are inclined to consider that the Indica and the Japonica types might have originated in India and in China, respectively (Chou 1948). However, the data of the present study have indicated that Indica-Japonica differentiation may proceed with the evolution of cultivated forms. This process might be possible in any country if certain necessary conditions were provided. If we assume that the first cultivated rice was created in some place in India, we may consider that those initial plants might have had a latent tendency to be differentiated into Indica and Japonica types, and the differentiation might have been promoted by selection during the course of spreading into other countries. It is possible, however, that the same process has been repeated many times, and is still in progress even at present time.

Summary

The Jeypore Tract comprises the western part of Orissa State, India, and is thought to have never been influenced by modern civilization. A number of rice varieties collected from this region, some growing wild and others cultivated by the native people, were investigated regarding various characters, together with Indian wild-rice forms belonging to *O. perennis* (including *perennis* and *spontanea* types) and varieties of *O. sativa* (including the Indica and Japonica types) which were taken as controls. The Jeypore strains showed wide ranges of variation in almost all the characters investigated. With the view to evaluating the variations as a whole, discriminant formulas for classifying *perennis* and *spontanea* types, wild and cultivated forms, and the Indica and Japonica types were constructed, respectively, using data of the wild and cultivated control-strains. Examining the scores given by these discriminant formulas, the writers found that the Jeypore strains were mostly of intermediate wild-cultivated types, and that those approaching wild forms were of *perennis* type. This suggests that the *perennis* type of wild rice might be the progenitor of cultivated rice. It was also found that the strains tended to be gradually differentiated into Indica and Japonica types as they approach cultivated forms, suggesting that the two type are monophyletic. A greater part of the strains showed, in the same manner as wild control-strains, high F_1 fertilities with test-strains of different types which were partially sterile in their mutual F_1 hybrids. Some of them however showed partial sterilities with certain test-strains, bringing about a complicated pattern of hybrid sterility relationships. About one fourth of them appeared to be heterozygous for genetic factors responsible for F_1 sterility. On the whole, the hybrid-sterility relationship was not correlated with the character-complex which differentiates the Indica and the Japonica types. Based on these findings, the evolutionary pathway from wild to cultivated forms of rice was discussed: It was inferred that the *perennis* type of wild rice can store up a large amount of genetic variability in its populations and can release different types of plants. Those plants might have a potentiality to develop different types such as the Indica and Japonica, possibly due to the presence of many duplicated gene loci, and therefore the intermediate wild-cultivated forms of Jeypore may be regarded as still staying in the midst of differentiation.

介於野生與栽培兩型間的中間型稻之研究兼論日本型稻之起源

(中　文　摘　要)

岡　彥　一　　張　文　財

印度歐利沙省 (Orissa State) 西部的瑞坡區 (The Jeypore Tract) 是一個尚未受現代文明影響的落後地區。本研究係以該區所產的野生稻及該區土著所種的栽培稻爲材料，並採用印度本土所產的 *Oryza perennis* (包括 *perennis* 型及 *spontanea* 型) 及若干標準栽培稻 *O. sativa* (包括印度型及日本型)，以資對照。採自瑞坡區的品系，幾乎每一性狀都顯示很大的變異幅度。筆者爲分析此等品系的全盤性變異起見，乃根據對照品系 (包括野生的和栽培的) 的性狀調查資料，作成三種判別函數，分別用以區分 *perennis* 型和 *spontanea* 型，野生型和栽培型，以及印度型和日本型。就判別值之大小觀之，瑞坡區的品系大多介於野生與栽培兩型之間，其中判別值靠近野生型的品系大抵與 *perennis* 型相似，由此可以推斷，栽培稻的祖先似爲 *perennis* 型野生稻。又判別值靠近栽培型的品系有分成印度型與日本型的趨勢，可見栽培稻中的印度型與日本型似乎是單元演化的 (Monophyletic)。瑞坡區的品系與五個鑑定品系 (其相互間的 F_1 爲部分不孕) 雜交，其 F_1 大多數均爲高度可孕，一如野生對照品系與鑑定品系之 F_1 然。不過也有一部分 F_1 (瑞坡×鑑定) 爲部分不孕，結果形成複雜的雜種不孕關係 (Hybrid sterility relationships)。這些品系中約有四分之一，其不孕遺傳因子似爲雜接合狀態。大體言之，此等雜種不孕關係與區分印度型與日本型所用的複合性狀 (Character-complex) 之間並無相關。基於上述諸事實，對於稻種由野生型到栽培型的演化途徑，我們似可作如下之議論：野生稻的 *perennis* 型，其集團內可蓄積大量的遺傳變異性，由此可以釋出不同型的植物。此等植物或許含有向印度型及日本型分化的潛力，推其原因，可能由於它們含有許多重複因子的關係，而那些來自瑞坡區的介於野生與栽培兩型之間的中間型稻，則可視爲尙滯留於分化途中的產物。

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