EVOLUTION OF RESPONSES TO GROWING CONDITIONS IN WILD AND CULTIVATED RICE FORMS

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This study was undertaken in an attempt to penetrate into the complex of responses to growing conditions of rice varieties from the viewpoint of evolution cultivated forms. The supposed wild progenitor of cultivated rice, the Asian perennial form of *Oryza perennis,* grows in natural swamps. For cultivated rice, the systems of cultivation differ from locality to locality. In the primitive systems, it is generally found that a land which can retain water or is innundated in the rainy season is ploughed and puddled, and seeds are broadcasted by hand. No further agricultural procedure then is taken until harvest. In other systems, seedlings raised in a nursery bed are transplanted to a puddled swampy field; transplanting may be regarded as an advanced method if compared with the above broadcasting method, which is practiced either in large paddy fields along rivers, or in small terraced paddies in mountainous areas.

In contrast, according to the improved systems, seedlings raised in a fertilized nursery bed and kept at proper density are space-transplanted in rows. Chemical fertilizers are applied to the field as basic and top dressings, and weeding is made several times after transplanting. Insecticides and fungicides are also used if necessary.

Thus, transplanting, weeding and fertilizer application may be regarded as the factors for advanced rice culture in Asia. With the view to visualizing the evolution of responses to these basic growing conditions, a series of varieties ranging from wild to improved forms were tested in different combinations of the above three factors. The field experiments were made at the College of Agriculture, Chung-Hsing University, Taichung (24°N), Taiwan, in 1960 and 1961. The writers are indebted to Mr. Hai Yuan for his cooperation in conducting the experiment. We are also grateful to Dr. H. W. Li, Institute of Botany, Academia Sinica, for his kind review of the manuscript. It was concluded

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from the results obtained that the evolution of responses to cultivation might proceed in parallel with the advancement of cultivation techniques.

Materials and Methods

Materials: The following ten rice varieties (A to J) were used.

A (W 203): A *spontanea* or annual wild form of *Oryza perennis* Moench, or *O. sativa* f. *spontanea* Roschev., collected by the senior writer from a swampy patch in the suburb of Cuttack, Orissa, India. As discussed by the writers (Oka and Chang 1962), we may assume that the wild progenitor of *O. sativa* is the Asian perennial form of the same species. But it is difficult to gather a sufficient amount of seeds of the perennial form for field experimentation. Accordingly, the annual form was used as a representative of wild forms.

B (JW 18): A wild strain belonging to *O. perennis*, collected from the Jeypore Tract, Orissa, India. As shown in Table 1, this strain was in grain shedding and other characters intermediated between wild and cultivated forms. It may be considered as a wild form approaching cultivated rice.

C (JC 191): A cultivated strain (*O. sativa;* same for C to J) Collected from the Jeypore Tract. It has some characters of wild rice, so that it may be regarded as a primitive cultivated variety.

D (JC 178): A cultivated strain of the Jeypore Tract, showing almost completely the characters of cultivated rice. The writers assume that rice varieties are differentiated into the Indica and the Japonica types as they approach to cultivated forms (Oka and Chang 1962). This strain has characters of the Indica type.

E (JC 45): A cultivated strain of the Jeypore Tract, showing characters of the Japonica type, *i.e.*, negative phenol reaction, a high resistance to potassium chlorate, long apiculus hairs, etc. It may be regarded as a primitive Japonica variety. In the Jeypore Tract, the native people grow rice either by shifting (burning forests) or by broadcasting on small non-terraced or terraced fields. Irrigation, weeding and fertilizer application are not known in this area.

F (647): A native variety obtained from Celebes, Indonesia, the local name being Padi ase banda. Japonica (Tropical-Insular) type. It is not known whether it is grown by transplanting or broadcasting.

G (423): A strain obtained from the Agricultural Research Station at Pattambi (Malabar), Madras, India, called P.T.B. 9. Indica type. Varieties like this are grown in tropical summer-monsoon areas mostly by broadcasting.

H (124): A native variety of Taiwan, Shuang-chiang, having passed through pureline selection conducted some forty years ago. Indica type.

This strain is suitable for the second crop of Taiwan, which may be compared with the summer-monsoon crop in tropical Asian countries.

I (108): A native variety of Taiwan, Pei-ku having passed through pureline selection. Indica type. This strain is suitable for the first crop of Taiwan, which is raised in spring months with artificial irrigation. In Taiwan, an intensive transplanting system is used for growing rice.

J (504): A Ponlai (Horai) variety of Taiwan, Taichung 65 selected from a hybrid between two Japanese varieties. Japonica type. It is adapted to both first and second crops, and is known to have a high yielding capacity and a wide regional adaptability.

These and other traits of the ten strains used are briefly listed in Table 1. These strains make up in the listed order a series from wild to modern improved forms. The Indica-Japonica differentiation is also involved in the series.

Table 1. *Description of the ten strains used.*

Strain no.	Species & Type	Habitat	Origin	Discriminant score X_1	X_2
A W203	*O. perennis* (annual)	Wild	Cuttack, India	-5.6	5.9
B JW18	*O. perennis* (annual)	Wild	Jeypore, India	-4.0	6.0
C JC191	*O. sativa*	Culti.	Jeypore, India	-2.8	6.1
D JC178	*O. sativa* (Indica)	Culti.	Jeypore, India	-2.3	5.9
E JC45	*O. sativa* (Japonica)	Culti.	Jeypore, India	-3.0	3.3
F 647	*O. sativa* (Japonica)	Culti.	Celebes	-2.1	1.7
G 423	*O. sativa* (Indica)	Culti.	Malabar, India	-2.2	6.2
H 124	*O. sativa* (Indica)	Culti.	Taiwan	-2.3	6.1
I 108	*O. sativa* (Indica)	Culti.	Taiwan	-2.1	6.4
J 504	*O. sativa* (Japonica)	Culti.	Taiwan	-2.1	2.0

X_1: Classifying wild and cultivated forms,
X_1: Classifying Indica and Japonica types.
(c.f. Oka and Chang 1962)

Conditions of experiments: The three growing conditions mentioned in the introduction, *i.e.*, transplanting vs. direct seeding (T:O), weeding vs. no weeding (W:O), and fertilizer application vs. no fertilizer (F:O), were combined in eight different ways as follows:

1. TWF (Transplanted, weeded, fertilizer)
2. TWO (Transplanted, weeded, no fertilizer)
3. TOF (Transplanted, no weeding, fertilizer)
4. TOO (Transplanted, no weeding, no fertilizer)
5. OWF (Direct-seeded, weeded, fertilizer)
6. OWO (Direct-seeded, weeded, no fertilizer)

7. O O F (Direct-seeded, no weeding, fertilizer)
8. O O O (Direct-seeded, no weeding, no fertilizer)

The split-plot design with three replications was adopted, the main plots representing the above eight treatments and sub-plots representing strains. The same experiment was repeated twice, in 1960 and 1961; when the data were analysed, year was considered as a main-plot treatment. The main plots, each comprising ten sub-plots, were sectioned by dykes. The size of a sub-plot was $1\,m \times 2.5\,m$, or 40 plants in the transplanted plots.

The seeds, sterilized with organic mercury and soaked in water for two days, were sown in an ordinary nursery bed, or directly in the experimental field. In the latter case, about 150 seeds per m^2 were sown and were covered with soil at the depth of ca. 1 cm. This seeding rate (ca. 40 kg/ha) is less than half of that commonly adopted in tropical Asian countries. But in those countries, they usually puddle the land after seeding to cover the seeds, lowering the germination rate. In the present experiment, 100 to 150 plants per m^2 emerged. The directly seeded plots may then be considered to be characterized not only by direct seeding but also by a dense plant stand. In the transplanted plots, seedlings grown in the nursery bed for 18 days, having four to five leaves, were planted spaced at $25\,cm \times 25\,cm$.

In the fertilized plots, N 4 gm. P_2O_5 4 gm and K_2O 4 gm per m_2, in the form of ammonium sulfate, calcium superphosphate and potassium sulfate, respectively, were applied before puddling the field as the basic dressing, and N 4 gm/m^2, divided into two parts, was top-dressed 10 and 20 days after transplanting, or 28 and 38 days after seeding.

In the weeded plots, weeding was made by hand 10, 20 and 30 days after transplanting, or 18, 28, 38 and 48 days after seeding. The same arrangement of main plots was adopted in both 1960 and 1961; owing to the abundant dispersion of weed seeds in 1960, the non-weeded plots in 1961 had much more weeds than those in 1960. The weeds were a mixture of several annuals with broad leaves.

Seeding date was July 13 in 1960, and June 25 in 1961. The varieties tested reached the heading stage between September 25 and October 30 in 1960, and between September 15 and October 15 in 1961, when the temperatures were still high enough for maturation (above 23°C on the average of the period from heading to maturity). In both years, no serious damages due to diseases, insect pests or typhoons were recorded.

Measurements were taken on a sub-plot basis regarding heading date, plant height, panicle number (per m^2), spikelet number per panicle, single panicle weight, seed fertility, plant weight, grain weight, and the weight of weeds (at the harvesting time). The averages on 20 to 100 panicles were recorded except for the latter three characters recorded for the whole sub-plot.

Results of Experiments

1. *An outline of the results.*

The data for plant weight, grain yield and other characters (averages of three replications and two years) are given in Table 2. In general, transplanting did not increase plant weight much, but increased grain yield. In most varieties, fertilizer application and weeding increased both plant weight and grain yield, and in transplanted condition, the increase of grain yield due to fertilizer application or weeding was apparently larger than at direct seeding. However, these effects markedly differed according to varieties.

Table 2. *Mean measurements of various characters of strains A to J in respective treatments.*

a) Plant weight (fresh; 10 gm/m^2)

Treatment	A	B	C	D	E	F	G	H	I	J
TWF	134	237	211	175	156	162	242	180	233	159
TWO	90	167	154	117	99	116	164	141	171	106
TOF	96	131	119	126	108	97	136	137	145	112
TOO	106	106	103	84	95	85	111	113	106	71
OWF	108	181	187	197	150	129	218	182	132	96
OWO	78	190	146	157	121	127	173	118	114	69
OOF	105	181	162	156	141	117	186	136	132	108
OOO	80	145	135	147	125	109	150	112	120	103

b) Grain yield (dry; gm/m^2)

Treatment	A	B	C	D	E	E	G	H	I	J
TWF	112	186	374	357	360	204	391	278	384	440
TWO	93	174	338	271	239	196	362	263	343	301
TOF	59	127	224	196	203	144	256	176	231	135
TOO	82	102	161	131	148	100	188	153	174	119
OWF	95	116	245	226	226	127	261	175	155	137
OWO	92	147	242	244	193	159	238	140	163	96
OOF	60	84	143	144	115	59	161	85	86	5
OOO	55	74	130	152	96	55	164	67	73	8
Grain Wt./Plant Wt. in TWF (%)	9.4	7.9	17.7	20.4	23.0	12.6	16.1	15.4	16.5	27.6
Score/Mean*	0.45	0.74	0.88	0.68	0.95	1.00	0.83	1.17	1.46	2.31

* Score given by the second component vector (Table 8), divided by mean grain yield (See Fig. 1).

c) Panicle number (per m²)

Treatment	A	B	C	D	E	F	G	H	I	J
TWF	619	297	221	232	177	192	198	244	214	200
TWO	547	216	190	202	115	132	137	206	181	124
TOF	353	174	154	137	100	112	116	153	148	102
TOO	352	142	105	113	76	74	104	126	113	74
OWF	453	492	298	379	227	240	293	358	346	195
OWO	598	426	386	379	306	269	266	366	362	203
OOF	252	377	254	316	175	114	300	294	253	28
OOO	279	265	262	266	206	139	231	218	245	27

d) Spikelet number per panicle

Treatment	A	B	C	D	E	F	G	H	I	J
TWF	28	64	106	80	141	78	134	79	109	80
TWO	27	59	88	73	129	88	142	74	87	83
TOF	27	67	91	70	128	93	154	68	85	67
TOO	24	54	76	63	108	73	114	62	64	50
OWF	27	59	101	69	112	74	131	60	64	75
OWO	26	55	85	60	95	77	111	56	60	57
OOF	27	61	89	59	96	68	120	57	62	22
OOO	24	47	74	48	79	50	110	48	45	13

e) Seed fertility (%)

Treatment	A	B	C	D	E	F	G	H	I	J
TWF	—	81	92	91	94	84	95	88	88	80
TWO	—	82	95	91	93	90	88	91	92	88
TOF	—	86	94	93	92	88	93	89	95	85
TOO	—	85	95	95	94	87	94	91	95	91
OWF	—	75	83	87	93	84	93	82	64	64
OWO	—	75	85	91	90	89	89	80	70	72
OOF	—	79	87	92	92	77	94	87	75	34
OOO	—	79	89	93	91	83	94	87	73	42

The results of variance analysis of the data are given in Table 3. The table shows that the variance due to treatment, variety, and treatment×variety were mostly significant. The difference between two years and its interaction with treatments and variety were also highly significant; the large values of of variance due to T×W×Y is accounted for by that the non-weeded plots in

Table 3. *Variance analysis of plant weight, grain yield and other characters.*

Source of variation	D. F.	Plant weight (100 gm/m²) M. S.	σ^2/M^2	Grain yield (10gm/m²) M. S.	σ^2/M^2	Panicle no. (per 1/10m²) M. S.	σ^2/M^2	Spikelet no. $(\times/\sqrt{10})$ M. S.	σ^2/M^2
Replication	2	255**	0.80	325*	0.55	694	0.58	15	—
T	1	12	—	9,001**	11.70	11,215**	—	3,029**	2.27
W	1	1,164**	1.61	12,571**	16.52	12,960**	8.50	1,556**	1.15
F	1	1,227**	1.73	886**	—	430	—	1,276**	0.86
TW	1	484**	1.29	500**	—	209	—	15	—
TF	1	71	0.21	560**	1.33	565	—	1	—
WF	1	138*	0.19	1	—	41	—	163*	0.18
TWF	1	45	—	4	—	457	0.88	50	—
Year	1	51	0.06	15,519**	20.66	2,255**	1.57	3,325**	2.51
TY	1	1,249**	5.48	243*	0.51	11,850**	17.63	44	0.02
WY	1	447**	1.89	228*	0.47	1,699**	2.30	20	—
FY	1	452**	1.91	916**	2.31	2,069**	2.86	159	0.18
TWY	1	197**	1.55	1,983**	10.32	363	0.57	107	0.20
TFY	1	14	—	64	0.06	2,425**	6.79	86	0.15
WFY	1	97	0.65	9	—	6	—	43	0.02
TWFY	1	56	0.58	51	—	166	—	55	0.09
Error (a)	30	23.4	0.91	51.9	1.12	176.4	2.29	39.2	0.41
Variety	9	300**	2.62	1,608**	8.96	3,578**	13.07	4.009**	14.82
VT	9	61**	0.01	287**	3.01	784**	3.31	143**	0.81
VW	9	35**	0.25	133**	1.39	369**	1.12	103**	0.53
VF	9	8	—	41*	—	91*	—	32*	0.11
VTW	9	19**	0.43	31	—	43	—	23	—
VTF	9	9	0.12	26	0.16	84	0.50	39*	0.35
VWF	9	3	—	23	0.15	14	—	6	—
VTWF	9	9	0.26	12	—	16	—	35*	0.37
VY	9	66**	1.32	267**	3.34	115*	0.49	124**	0.82
VTY	9	60**	2.40	62**	1.19	346**	4.47	39*	0.33
VWY	9	24**	0.78	28	0.30	221**	2.58	34*	0.27
VFY	9	9	0.12	55**	1.02	91*	0.62	16	—
VTWY	9	9	0.22	58**	2.17	127**	2.32	24	0.22
VTFY	9	5	—	19	0.11	51	0.03	17	—
VWFY	9	9	0.23	16	—	49	—	9	—
VTWFY	9	4	—	29	1.33	62	0.73	22	0.35
Error (b)	288	6.5	3.47	17.1	5.47	49.9	9.05	16.7	3.06

M. S. Mean square, abridged numerals are shown.
σ^2/M^2 Variance component/square of mean measurement, in %.
** Significant at 1% level; * Significant at 5% level.

1961 had, as already mentioned, more weeds than those in 1960, especially in directly seeded plots.

It was also a noticeable fact that plant weight did not differ much between the two years, but grain yield in 1960 was much larger than that in 1961. Plant weight represents the total amount of assimilation, while grain yield is its fraction primarily determined by the transportation of nutrients to grains. It seems that the rate of transportation is easily affected by the presence of weeds and other conditions.

The relative magnitude of variations due to various causes may be read from the values of variance components given in Table 3; they were estimated on the assumption that the treatments, T, W and F, are fixed, while year is random, and are shown in percent of the square of mean measurement (σ^2/M^2 in %). Further analysis of variance was made of the data for individual varieties separately, as will be mentioned below.

2. *Varietal differences in the responses to treatments.*

a) *Effect of transplanting:* Directly seeded non-weeded plots generally had a larger amount of weeds than transplanted non-weeded plots. In order not to involve the interaction between transplanting and weeding, comparisons between transplanted and directly seeded plots were made of the data obtained from weeded plots. The T/O ratios in different characters, and the components of variances due to transplanting (in per cent of the square of mean measurement) estimated for various varieties are given in Table 4.

Table 4. *Responses to transplanting of strains A to J.*

Character	A	B	C	D	E	F	G	H	I	J
Plant weight, T/O (weeded plots)	1.02	1.09	1.10	0.83	0.96	1.10	1.08	1.06	1.65	1.54
σ^2_T/M^2 (%)	0.7	0.2	0.1	3.4	1.0	—	0.3	—	3.5	1.4
Grain yield, T/O (weeded plots)	1.17	1.52	1.54	1.47	1.43	1.40	1.56	2.05	2.53	4.21
σ^2_T/M^2 (%)	1.7	5.4	6.3	1.7	5.1	9.9	6.2	16.6	32.1	77.1
Fraction of σ^2_T due to regression on plant weight (%)	(−) 32.1	(−) 3.4	(−) 19.9	(−) 0.4	(−) 29.5	(−) 9.6	(−) 14.9	(+) 14.3	(+) 71.3	(+) 47.2
r btw. grain yield and straw weight (based on T+Error)	—	-0.27	-0.06	-0.37	-0.15	-0.08	-0.10	0.18	0.79	0.70
$\frac{\text{Grain Wt.}}{\text{Plant Wt.}}$, T/O	1.09	1.40	1.39	1.79	1.48	1.27	1.45	1.94	1.61	2.58
Panicle number, T/O (weeded plots)	0.67	0.56	0.60	0.58	0.57	0.67	0.63	0.62	0.58	0.87
Spikelet number, T/O (weeded plots)	1.05	1.08	1.05	1.19	1.31	1.11	1.13	1.31	1.65	1.30
Plant height, T/O (weeded plots)	1.09	1.09	1.09	1.10	1.08	1.19	1.12	1.29	1.30	1.30

Transplanting increased most character except for plant weight, while varieties H, I and J showed higher rates of increase than others. As already mentioned, H and I have been grown in Taiwan for many years by the transplanting system, and the Ponlai variety J was selected under the condition of transplanting. Their high responses to transplanting and proper spacing may be regarded as reflecting their history of origin. It is also found from Table 4 that the increase of grain-yield/plant-weight ratio due to transplanting tended to be high in the order of varieties A to J. This suggests that the response to transplanting might have advanced with the evolution of cultivated rice.

In wild as well as primitive cultivated varieties, the variance of grain yield due to transplanting was found to be negatively correlated with that of plant weight. The fraction of variance of grain yield due to its regression on plant weight was estimated for each variety by the method of covariance analysis. The variances due to regression (in per cent of the variance due to transplanting) are given in Table 4. The data in the table show that varieties A to G had negative regressions of grain yield on plant weight in the variation caused by transplanting. This implies that in those plants the transportation of nutrients to grains is rather reduced when assimilation is promoted in a properly spaced condition. Those plants seem to have a tendency to compensation between vegetative growth and sexual reproduction.

With the view to estimating the tendency to compensation between vegetative and sexual activities, the correlation coefficients between straw and grain weights were computed for each variety, using the sums of squares and products due to treatment+error. The results are also given in Table 4. The correlation coefficients seem to become high with the evolution toward modern varieties. All wild and primitive cultivated forms seem to be the more adapted ones to direct seeding at a high density.

b) *Effect of fertilizer application:* The F/O ratios in various characters and the components of variances due to fertilizer application are given in Table 5. In both transplanted and directly seeded plots, fertilizer application increased plant weight, panicle number, spikelet number per panicle, and other characters. The improved variety J had apparently higher ratios of increase than other varieties. The two primitive Japonica varieties, E and F, showed relatively high F/O ratios in panicle number, which according to Oka (1954, 1956), may be used as an index of fertilizer response. This is consistent with the previous findings of the senior writer that varieties of the Japonica (Insular) type, either Temperate or Tropical, tend to have higher fertilizer response than Indicas (Oka 1954, 1956). It was also found that in transplanted plots fertilizers increased grain yield, but in directly seeded plots grain yield decreased in all

Table 5. *Responses to fertilizer application of strains A to J.*

Character	A	B	C	D	E	F	G	H	I	J
Plant weight, F/O (transpl. plots)	1.18	1.35	1.27	1.52	1.34	1.25	1.36	1.23	1.36	1.52
F/O (direct. seed.)	1.28	1.11	1.26	1.15	1.26	1.05	1.32	1.42	1.15	1.22
σ^2_F/M^2 (%)	2.50	1.16	1.62	1.54	0.36	0.23	2.25	1.92	1.47	4.45
Grain yield, F/O (transpl. plots)	1.06	1.12	1.22	1.33	1.42	1.17	1.14	1.07	1.20	1.56
F/O (direct. seed.)	1.04	0.85	0.85	0.75	1.10	0.86	0.96	1.22	0.94	1.36
σ^2_F/M^2 (%)	0.13	—	—	—	0.11	—	—	0.40	0.53	7.98
Fraction of σ^2_F due to regression on plant weight (%)	58.7	—	—	—	82.1	—	—	57.2	78.5	99.1
$\frac{\text{Grain Wt.}}{\text{Plant Wt.}}$, F/O	0.86	0.83	0.86	0.84	0.98	0.90	0.79	0.86	0.93	1.13
Panicle number, F/O (transpl. plots.)	1.08	1.32	1.28	1.16	1.45	1.50	1.29	1.21	1.24	1.69
F/O (direct. seed.)	0.84	1.29	0.92	1.22	0.89	1.04	1.51	1.13	1.07	1.17
Spikelet number, F/O (transpl. plots)	1.08	1.15	1.21	1.11	1.13	1.08	1.13	1.10	1.30	1.10
F/O (direct. seed.)	1.08	1.18	1.21	1.19	1.19	1.18	1.13	1.11	1.18	1.45

but three varieties, J, H and E. Fertilizers reduced grain-yield/plant-weight ratio in most varieties.

Unlike the case of transplanting *versus* direct seeding, the variation due to fertilizer application of plant weight was in all varieties positively correlated with that of grain yield. The fraction of variance of grain yield representing the regression on plant weight, estimated in each variety, is also shown in Table 5. It was as high as 99% in variety J, while lower percentages were found in primitive varieties. It seems that fertilizers may promote both vegetative and sexual activities, though the efficiency differs according to varieties.

c) *Effect of weeding and weed resistance:* The W/O ratios in various characters and the components of variances due to weeding are shown in Table 6. In the transplanted plots, most varieties showed a marked increase of plant weight and grain production in response to weeding. The varieties adapted to intensive cultivation, I and J, showed larger W/O ratios than other relatively primitive varieties. The variances of various characters due to weeding appeared to increase in the order of varieties A to J.

On the other hand, in directly seeded plots where the density of plants was high, the increase of plant weight due to weeding was generally small, and was negative in varieties I and J. When varieties I and J were directly seeded and not weeded, their grain production was almost nill, though they

Table 6. *Responses to weeding and weed resistance of strains A to J.*

Character	A	B	C	D	E	F	G	H	I	J
Plant weight, W/O (transpl. plots)	1.19	1.78	1.80	1.43	1.32	1.70	1.74	1.37	1.80	1.50
W/O (direct. seed.)	1.04	1.12	1.12	1.17	1.01	1.11	1.15	1.21	0.97	0.80
σ^2_W/M^2 (%)	—	1.50	2.65	2.45	0.42	1.71	3.01	2.23	0.96	0.23
Increase due to weeding (gm/m²), in direct. seed. plots	4	230	178	255	23	148	275	255	-33	-229
Grain yield, W/O (transpl. plots)	1.55	1.82	2.24	2.34	2.01	1.77	1.92	2.19	2.46	3.14
W/O (direct. seed.)	1.71	1.65	1.98	1.69	1.96	2.78	1.49	1.77	1.93	27.10
σ^2_W/M^2 (%)	11.4	10.9	16.3	14.8	16.4	14.5	11.1	15.4	16.8	43.7
Fraction of σ^2_W due to regression on plant weight (%)	18.1	63.3	74.4	55.2	29.8	71.0	63.0	77.6	75.9	27.0
$\frac{\text{Grain Wt.}}{\text{Plant Wt.}}$, W/O	1.48	1.29	1.57	1.63	1.73	1.57	1.28	1.61	1.71	3.58
Panicle number, W/O (transpl. plots)	1.89	1.72	1.65	1.94	1.78	1.85	1.57	1.73	1.60	2.12
W/O (direct. seed.)	1.93	1.48	1.42	1.31	1.57	1.95	1.09	1.43	1.40	8.15
Spikelet number. W/O (transpl.) plots)	0.95	1.01	1.18	1.15	1.14	1.00	1.02	1.18	1.33	1.38
W/O (direct. seed.)	1.08	1.18	1.21	1.19	1.19	1.18	1.13	1.11	1.18	1.45
Weed resistance, Weight of weeds in direct: seed. plots (gm/m²)	474	412	328	312	454	678	274	344	362	995

had larger plant weight than in weeded plots. In this case, the percentage of seed settiing was also lowered. It may be said that in directly seeded condition weeding is generally less effective than in transplanted condition, and when varieties adapted to intensive cultivation are directly seeded, non-weeding brings about a physiological disturbance.

The amount of weeds in non-weeded plots may serve as an index of weed resistance of rice varieties. The data for the amount of weeds are given in Table 6; the results of variance analysis of the data, and those of the difference in plant weight between weeded and non-weeded plots, are given in Table 7. In both weed weight and the difference in plant weight, the variances due to variety and variety×transplanting were highly significant. Judging from the weed weights in directly seeded plots, the primitive cultivated varieties, such as C, D and G, had higher weed resistance than the wild strains, while the varieties adapted to intensive cultivation, especially those of the Japonica type, seemed to have a low resistance. However, the increase of plant weight due to weeding was not parallel to the amount of weeds. In general, Indica varieties showed a larger increase, especially in transplanted plots, than Japonica varieties (Table 6). Thus, the interrelationship between the growth of rice plants and that of weeds is very complicated; the correlations of the two measurements were in most items negative, as shown in Table 7. It seems that the presence of weed may promote the vegetative plant growth to some extent, though it reduces grain production.

Table 7. *Variance analysis of weed weight and the increase in plant weight due to weeding, and correlation between them.*

Source of variation	D. F.	Weed weight (10gm/m^2) M. S.	Increase in plant weight (100gm/m^2) M. S.	r[1)]
Replication	2	73	55	
T	1	7,513(*)	969**	-0.58
F	1	765	276**	
TF	1	3,154	91*	
Year	1	50,634**	893**	0.65
TY	1	13,783*	394**	0.32
FY	1	1,879	193**	
TFY	1	3,635	112*	
Error (a)	14	1,668	15.4	-0.37
Variety	9	3,046**	70**	-0.69
VT	9	3,062**	37**	-0.29
VF	9	163	6	
VY	9	783**	48**	-0.47
Other interactions	36	324	15	
Error (b)	144	194	12.7	-0.38

1) Computed from Treatment+Error sums of squares and products.
** Significant at 1% level; * Significant at 5% level.

3. *Multivariate analysis of the data for grain yield.*

Basing on the data of grain yield, correlation coefficients between the eight treatment combinations were computed. The correlation matrix was then analysed by the technique of principal component analysis, in order to find an integrated figure for the evolution of responses to growing conditions. The correlation matrix and the first to fourth component vectors extracted from it are given in Table 8. As shown in the table, the first component, which made a 77.5% contribution to the total variation, gave the eight treatment combinations similar positive values of direction cosines; this component may be considered as indicating that the varieties used were similarly ranked in different treatments. After subtracting this component, the second component, making a 10% contribution, showed a succession of direction cosines diminshing in the order OOO to TFW. This component vector may then be considered as showing that the

Table 8. *Matrix of correlation coefficients between treatments and component vectors extracted from it.*

Treatment	TWF	TWO	TOF	TOO	OWF	OWO	OOF	OOO	Component vector			
									1st	2nd	3rd	4th
TWF		.881	.757	.674	.746	.634	.611	.528	.331	-.509	.287	.350
TWO			.726	.666	.680	.670	.575	.590	.328	-.467	.442	-.131
TOF				.963	.914	.720	.761	.569	.367	-.215	-.428	-.150
TOO					.914	.718	.814	.599	.364	-.078	-.509	-.087
OWF						.831	.913	.766	.387	.087	-.224	.145
OWO							.820	.829	.355	.269	.232	-.760
OOF								.867	.364	.375	-.076	.428
OOO									.327	.499	.412	.219
Contribution									.775**	.100**	.070**	.024*

** Significant at 1% level, tested by Barlett's (1950) method.
* Significant at 5% level.
Computations made by the I. B. M. Co., Tokyo.

eight treatment combinations form a series of growing conditions ranging from primitive to advanced one. The implications of the third and fourth component vectors, having smaller contributions, were not clear from the data.

Taking the second component vector, the scores given by the direction cosines were calculated in each variety. The results (in per cent of mean grain yield; sign reversed) are given in the bottom row of Table 2, b. It is found that the varieties A to J form an increasing array of the scores. This score may be regarded as an index of adaptability to intensive cultivation. Inter-varietal variations in this score and the mean grain yields in TFW plots are shown in Fig. 1. Also the components of variances of grain yield due to transplanting and weeding (in per cent of the square of mean value), and the F/O ratios in panicle number are shown in Fig. 2 for comparion. The figures show that the responses have gradually advanced as wild plants approached the cultivated forms, and proceeded rapidly due to intensive cultivation and modern breeding. It is also found that the Japonica type reacts with higher responses, even the primitive varieties, than the Indica type.

In contrast, productivity seems to have rapidly increased with the domestication of wild plants. The irregular up and down of grain yield between primitive and modern varieties seem to suggest that after the initial domestication the improvement of yielding capacity has been achieved in different countries separately, through adaptation to the advancement of agricultural techniques.

4. *Comparison of modes of fluctuation among varieties.*

The measurements of many characters considerably differed between 1960

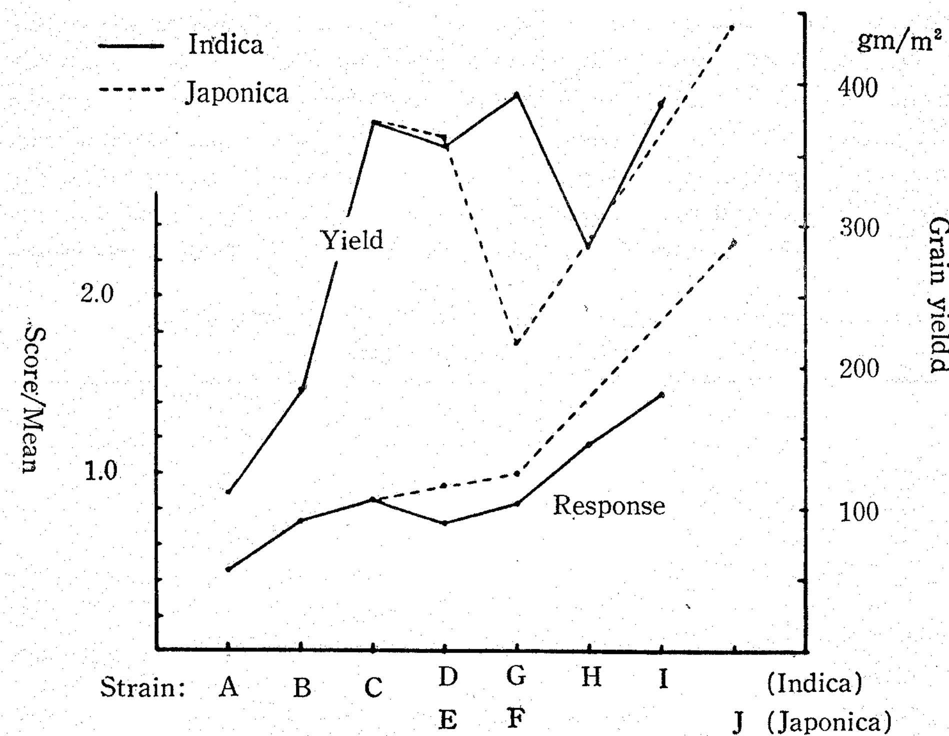

Fig. 1. Progress of response to intensive culture (score given by the second component vector) and grain yield (in TWF plots).

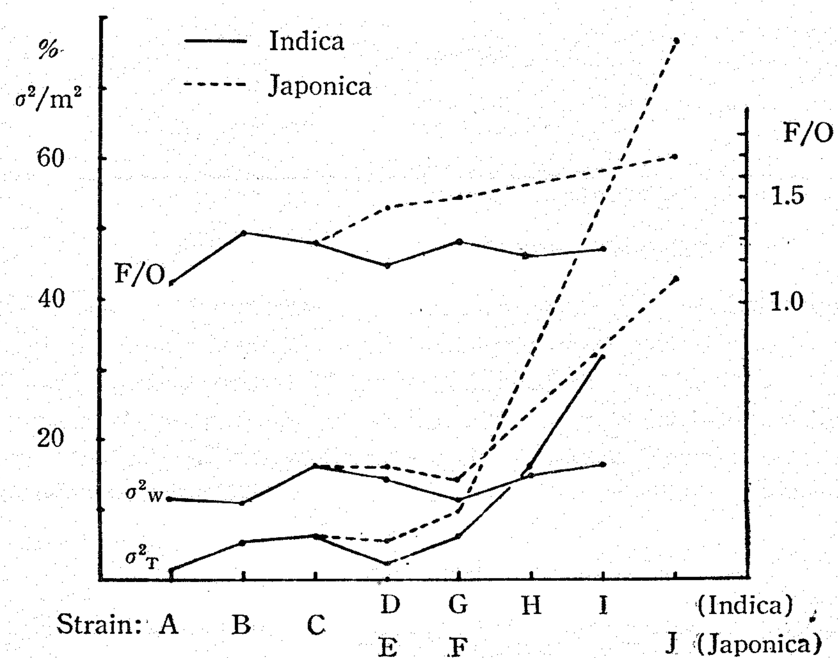

Fig. 2. Progress of responses to transplanting (σ^2_T/M^2 in %), weeding (σ^2_W/M^2 in %) and fertilizer application (F/O in panicle number).

and 1961. This could be mainly due to more vigorous growth of weeds and better germination (resulting in a higher density of plants) in 1961 in directly seeded plots than in 1960. It will be difficult, therefore, to estimate from the data whether the varieties differ in the degree of annual fluctuation or not. However, an attempt was made to compare among varieties the variances due to year, the ratios of the difference between two years to the sum of measurements, and error variances due to replication. As shown in Table 9, the results

Table 9. *Comparisons of variability due to year and replication among strains.*

Character	A	B	C	D	E	F	G	H	I	J
Plant weight, $\frac{'60-'61}{'60+'61}$ (%) (weed. plots)	17.8	15.7	6.4	5.2	8.6	8.9	9.6	6.9	4.3	2.3
σ^2_Y/M^2 (%)	6.9	0.4	0.2	1.4	0.4	0.5	0.7	1.2	1.5	0.2
σ^2_e/M^2 (%)	4.6	3.0	4.1	3.1	5.2	3.2	6.8	2.7	4.0	3.9
Grain yield, $\frac{'60-'61}{'60+'61}$ (%)[1]	16.7	16.1	14.5	13.1	18.2	1.7	14.1	22.6	9.9	6.3
σ^2_e/M^2 (%)	6.9	3.1	5.6	4.8	5.1	5.4	7.0	6.6	7.0	9.8
Fraction of σ^2_e due to regression on plant weight (%)	—	1.2	27.8	6.8	39.0	21.7	13.2	38.6	44.2	57.8
Panicle number, $\frac{'60-'61}{'60+'61}$ (%)[1]	12.1	1.7	9.1	4.3	1.3	1.2	9.6	2.1	7.4	1.7
Spikelet number, $\frac{'60-'61}{'60+'61}$ (%)[1]	2.1	5.3	3.9	4.7	5.6	11.0	18.2	16.0	2.5	10.4

σ^2_Y Component of variance due to year,
σ^2_e Error variance
1) In transplanted and weeded plots.

suggested that the wild strain, A, would have larger variances due to year of plant weight and panicle number than other cultivated strains. In the error variation, wild as well as primitive cultivated strains seem to have lower regression coefficients of grain yield on plant weight than improved cultivated strains. As will be discussed later, it is possible that in response to certain environmental conditions, wild plants are more unstable than cultivated ones.

Discussion

It is not known how cultivation was initiated in the stone age. As suggested by H. G. Wells (The outline of history, 1920–51), we may assume that first the seeds of wild plants were harvested by man, as it is found in India, West

Africa and South America even in the present days. The seeds dropped on the ground nearby their dwellings might have germinated giving rise to new populations which grow in a disturbed habitat. According to the writers and their colleagues' hypothesis (c. f. Oka and Chang 1959, Hinata and Oka 1962b), the evolutionary change of wild plants to cultivated forms might have been initiated by natural selection in a habitat disturbed by man; in such a habitat, the heterotic advantage of wild plants could be reduced due to promotion of self-pollination, and various forms could have been released from the populations. The primitive people must have harvested the plants near their dwellings, and through the repetition of this work, they might have learned how to grow plants. Then, the second step of evolution would have been selection by man, though artificial selection in the early stage could be effective only when helped by natural selection in the same direction.

The most primitive types of rice culture found at present are the "shifting" custom (direct seeding after burning forests) and direct seeding in roughly puddled natural swamps. Such would have been the situation of agriculture in the stone age in tropical Asia. The invention of other cultivation techniques, such as transplanting, might be of more recent origin, probably started in the early historical era. With the progress of cultivation techniques, rice would have spread over a large area, and many varieties with different modes of adaptability might have been established in different localities. Finally, in the present era, the advancement of systems of cultivation, based on the rise of man's scientific knowledge and industrial power, has brought about modern cultivated varieties which are adapted only to improved agricultural environments.

As mentioned in the introduction, the growing conditions taken up in this study, namely, transplanting, weeding and fertilizer application, may be considered to be the elements of intensive rice culture in Asia. As the results of multivariate analysis of the data have shown, the responses to these conditions seem to have gradually advanced during the course of evolution, and did so rapidly in response to modern cultivation and breeding. The mode of responses of various varieties to these conditions seemed to be well accounted for by the agricultural environment in which each variety is grown. It may be said that the evolution of genotype might proceed in parallel with that of the environment, when the wild progenitor has the potentiality to realize such an evolution.

Of the three elements of intensive rice culture, transplanting might be of particular importance. In the present experiment, transplanting showed large values of interaction variances with other treatments, and it was found that weeding as well as fertilizer application were generally more effective in transplanted condition than at direct seeding. This suggests that weeding and the use of home-made manures have become efficient after the adoption of transplanting method.

Transplanting brought about an increase in plant weight and grain production in most varieties. However, in wild as well as in primitive cultivated forms, the covariance due to transplanting of grain yield with plant weight was negative: in other words, vegetative growth and grain production were negatively correlated in response to transplanting. From this viewpoint, only the three varieties of Taiwan, H, I and J, were really adaptive to transplanting, though the response to transplanting might have advanced with the evolution toward the present varieties.

On the other hand, the resistance to weeds is a character which must always be subjected to the pressure of natural selection. Taking the amount of weeds per unit area as its index, weed resistance was found to have become high as the wild plants were domesticated, but the evolution thereafter toward the present varieties has reduced the competitive ability against weeds, especially in the Japonica type. This indicates that all those varieties have been selected in weeded condition. It was found, however, that the increase in plant weight due to weeding was not parallel with the amount of weeds in the non-weeded plots, and also that the increase in grain production due to weeding was not correlated with that in plant weight. In all the weeding response in grain yield may be said to have advanced with the evolution toward the present varieties. Thus, the physiology of weed resistance is complicated. When the three varieties of Taiwan which are not adapted to direct seeding were directly seeded, the co-existence of weeds increased plant weight and reduced grain production, bringing about a negative correlation between plant and grain weight. On the contrary, according to Dr. K. I. Sakai of National Institute of Genetics, Japan (unpublished), cases were found in Ceylon in which weeds reduced plant weight and increased grain yield due to improved fertility.

In general, seed production of plants will be in different degree negatively correlated with vegetative growth. For instance, wild plants compete with one another by both vegetative and reproductive means, and the populations can be maintained through a delicate balance between the two phases. It was suggested from the data of the present study that in respect to environmental fluctuation (error variation), wild and primitive cultivated forms might have a stronger tendency to negative correlation between vegetative and reproductive activities than modern cultivated varieties. It was also suggested that wild forms might have due to year larger variances of plant weight and other characters than cultivated forms.

We have no established knowledge as to how the responses to minor enviromental fluctuation can be compared with those to growing conditions, such as weeding vs. non-weeding. Hypothetically, we may assume that wild plants are more sensitive to minor environmental conditions than cultivated ones, while the latter are more sensitive to conditions provided by man than the former. If this were true, wild plants would have relatively low selection coefficients in their populations, and annual fluctuation of environmental conditions inducing selections in different directions would help the populations to store up genetic variations. In contrast, cultivated plants are relatively stable in development, and their populations are relatively homogeneous. This might be partly due to that the more genetically homogeneous a population, the less would be the pressure of intrapopulational competition. Thus, it may be assumed that with the domestication of wild plants, populations become homogeneous and the sensitivity to minor environmental factors is reduced. This would result in deterioration of the compensating tendency between plant and seed weight, in sofar as the plants are grown within the range of a certain adaptive environment.

In was also found from the present experiment that yielding capacity rapidly increased with the domestication of wild forms, but its progress thereafter was rather slow; it might have advanced in different countries through adaptation to given environments. The reason for the initial rapid progress remains unexplained within the scope of the present experiment. It is difficult to compare experimentally wild and cultivated environments, unless an experimental field can be set up near a natural population of wild plants and detailed observations can be made. Genetic studies of yielding capacity from this viewpoint will be needed in the future.

Another problem remaining unsolved is how the Indica and Japonica types have differentiated in the course of evolution toward cultivated forms, as the two types are monophyletic. As discussed by Oka and Chang (1962) and Hinata and Oka (1962a), the wild progenitors might have had a potentiality to to differentiate into various types, but the actual differentiation might have resulted from differential responses to certain environmental factors involved in the conditions of cultivation. It is interesting to find in this connection that primitive Japonica varieties have relatively high responses to transplanting, weeding and fertilizer application though they have not yet been selected in an intensive cultivation system. The Japonica type seems to have a capacity to become adapted to intensive cultivation more rapidly than the Indica type.

In view of the rapid adaptation of rice varieties to intensive cultivation in recent years, we may expect that plants with higher responses than the present ones will come about in the future if the growing conditions are more and more intensified. The writers assume that it will be an important breeding objective to select a type that would be more respondent to the conditions provided by man but not sensitive to natural conditions which cannot be controlled by man.

Summary

A set of ten rice varieties ranging from wild (*spontanea* type, *Oryza perennis*) to improved cultivated forms (*O. sativa*), in which intermediate wild-cultivated forms from the Jeypore Tract, India, and native varieties of tropical Asian countries (Indica and Japonica) were included, were tested in different combinations of three basic growing conditions, namely, transplanting, weeding and fertilizer application, which were regarded as the elements of intensive rice culture in Asia. It was found in general that responses to these growing conditions might have gradually advanced during the course of evolution toward the present varieties, while their rapid progress was due to the pressure of modern cultivation and breeding. It was pointed out that the evolution of genotype and that of environment might proceed in parallel.

生長環境對野生稻和栽培稻進化的影響

岡 彥 一 張 文 財

十種野生稻和栽培稻系統，其中包括印度 Jeypore 地區的中間型稻和亞洲熱帶的在來種(印度型和日本型)，應用移植，除草和施肥等三種不同的基本栽培條件，探討種植法和稻種進化的關係。本試驗顯示，對這些栽培條件的反應性係爲伴隨稻種的進化而漸進的，然而其急速的進步是由近代耕作及育種的加壓而成。亦可以說因子型和環境的進化是雙方同時進行的。

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