Variation in Competitive Ability among Rice Varieties

(Phylogenetic Differentiation in Cultivated Rice XIX)

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It has been demonstrated by SAKAI (1953, '54, '55a, b, c, d, '56a, b) that the competitive ability of a form in relation to others of the same species is a character determined by the genotype. He conducted experiments on the occurrence of competition between plants, the influence of hybridity and polyploidy on competitive ability, the change of relative frequency of genotypes in mixed populations, the effect of environmental conditions on competition, and so on. From those experiments, it is pointed out that competition might be an important evolutionary agent.

This paper is a report of investigations on variations in competitive ability among cultivated rice varieties, which have been carried out on the basis of the principles established by SAKAI. The writer wishes to express his appreciation for Dr. SAKAI's interest in his work and valuable advices given during the course of these experimentations.

Materials and Methods

A number of rice varieties including both the Indica and Japonica or the Continental and Insular types were used. They belong to the set of materials used in the writer's previous studies (OKA 1953, etc.), and are due to random sampling from a large collection of rice varieties from various Asian countries. Among them, those used as cross-parents are described as follows:

No.	Local name	Origin	Type
563	Kinoshita-mochi	Japan	Temperate-Insular (Japonica)
115	U-kuh	Formosa	Continental (Indica)
414	P. T. B. 10	India	"
108	Pei-ku	Formosa	"
504	Taichung No. 65	"	Temperate-Insular (Japonica)

Three different methods were used for measuring the competitive ability of a strain. By the first method, the strains to be tested were mix-planted with a certain tester-strain in a plot and singly-planted in another plot, and their records were compared. By the second method, the tester strain was mix-planted with the strain to be tested in a plot and singly-planted in another plot, and the records for the tester strain from both plots were compared. This procedure is based on the premise worked out by SAKAI (1953, '55d) that when two genotypes compete with each other, the stronger one's gain may be proportionate to the loss of the weaker. For estimating the competitive ability of a strain by these methods, the panicle number per plant and plant weight, which were known to be the characters most sensitive to competition (SAKAI 1953), were recorded.

By the third method, two strains to be tested were mix-propagated in a certain initial

proportion, and after one or a few generations, their relative frequencies in the bulk population were investigated.

The experiments were conducted at the Taiwan Provincial College of Agriculture, Taichung, Formosa, or at the National Institute of Genetics, Misima, Japan, as noted against each table. The plants were grown in experimental fields by the ordinary methods of rice culture used in Formosa or Japan.

Results of Observations

1. Intervarietal variation in competitive ability.

It has been reported that rice varieties belonging to the so-called Indica or Continental type might generally be superior in competition to those of the Japonica or Temperate-Insular group (SAKAI 1955e). However, the pattern of variation in this character has not yet been sufficiently investigated. In order to find out the variation among different phylogenetic variety-groups, 53 rice varieties from various Asian countries were tested by the second of the above-mentioned three methods, using Taichung No. 65 (Strain No. 504) as the tester. 15 tester plants were grown along with about 100 plants of each variety so as to be surrounded by them, with a spacing of 25 cm between plants. Average panicle numbers of the test plants in each plot were compared with that in the adjacent singly-planted plots, which were distributed in the experimental field and being 36 in total number. The significance of differences was estimated from the results of

Table 1. Variation in competitive ability among cultivated rice varieties (Increase or decrease in panicle number of the tester strain, Taichung No. 65).

Variety-group	Weak					Strong					No. of vars.
	3	2	1	0	-1	-2	-3	-4	-5		
Continental				1	2	5	11	10	4	33	
Tropical-Insular	2		4	2	3	1				12	
Temperate-Insular			3		2	2		1		8	

(Second crop season, 1955, at TAICHUNG)

variance analysis of the data for the singly-planted plots of the tester. It was found that a difference beyond 0.88 in panicle number exceeded the 5% level of significance.

The variation in competitive ability thus found among the 53 varieties is set out in Table 1. The data in the table show that varieties of the Indica or Continental type generally have a higher competitive ability than those of the Japonica or Insular type. Tropical- and Temperate-Insular groups appeared to vary within similar ranges.

2. Variation among lines derived from hybrids.

F₁₀ lines derived from two crosses between distantly related varieties, 414 × 563 and 108 × 504 (called Crosses I and II, respectively, in the previous paper of this series; OKA 1957 a, b) were used. Those lines were the results of random selection from F₆ populations of the respective crosses which had been propagated in pedigrees or in bulk; as to its details the readers may refer to OKA (1957 a). They were thus classified into two groups, one derived from pedigree propagation and the other from bulk propagation of hybrid populations.

The competitive ability of the lines from 414 × 563 were tested by the same method as used for testing the varieties from various Asian countries. Those from 108 × 504 were tested as follows (the first method): Each line to be tested was mix-planted in two separate plots with the respective parental strains (with 108 in Plot A, and with 504 in B) so as to be surrounded by the latter, and was also singly-planted in the third plot (C). Panicle numbers were recorded for the plants of these three plots, and the competitive ability of a line was shown by the value A+B-2C. The significance of differences

was estimated from the results of variance analysis of the data for singly-planted plots of the parental varieties. It was found that a difference beyond 2.38 exceeded the 5% level of significance.

The data obtained from these experiments were arranged first for making a comparison between the classes derived from bulk and pedigree propagations. The results are given in Table 2.

As the data in Table 2 show, lines derived from bulk propagation tended to have higher competitive ability than those derived from pedigree propagation, though in both classes the range was much wider than the parental difference. Table 2(b) shows that the competitive abilities of those lines were generally higher than the parental means. These facts indicate that plants with high competitive abilities increase in hybrid populations, especially in those propagated in bulk.

Secondly, correlations between competitive ability and other characters were examined. It was found (Table 3) that competitive ability was not significantly correlated with most of the agronomic characters. It might be of some interest to note that no significant correlation was found between competitive ability and panicle number per plant (in singly-planted plots), though the former was measured by the increase or decrease in the latter.

However, characters differentiating the Indica and Japonica, or the Continental and Insular types were found to some extent to be correlated with competitive ability. For example, the two types are largely represented by positive and negative phenol reactions, respectively (OKA 1953). As shown in Tables 4 and 5, the hybrid lines with positive phenol reaction tended to have higher competitive ability than those with negative reaction. In this manner, lines resembling of the Continental type with respect to the manner of character association or reaction-type of hybrid sterility had a tendency toward higher competitive ability than those resembling the Insular type (Table 4). It was pointed out in the author's previous papers (OKA 1957 a, b) that in hybrids between distantly related rice varieties, there occurs a tendency toward restriction of character recombinations. The correlation found between competitive ability and the characters differentiating these phylogenetic variety-groups may be explained by the restriction of recombinations [in hybrids. It may be note-worthy that among lines derived from 108×504, those showing resistance to blast disease (caused by *Piricularia oryzae*) tended to have a high competitive ability (Table 5).

Table 2. Variation in competitive ability among F_{10} lines derived from 414 × 563 and 108 × 504
a) Lines from 414×563 (Tester : Taichung No. 65).

Propagation method	Weak				Strong		No. of lines	Mean
	1	0	-1	-2	-3	-4		
Pedigree	1	5	11	4	1	1	23	-1.09
Bulk	2	3	9	16	9	1	40	-1.75

(Second crop season, 1955, at TAICHUNG)

b) Lines from 108×504 (Decrease due to mix-planting in parental varieties).

Propagation method	Weak						Strong		No. of lines	Mean
	4	2	0	-2	-4	-6	-8	-10		
Pedigree	2	8	9	14	9	4	3		49	-1.80
Bulk		1	5	7	11	4	3	2	33	-3.77

(Second crop season, 1954, at TAICHUNG)

Table 3. Correlation coefficients between competitive ability and agronomic characters.

Characters	414×563	108×504
Plant height	0.30*	-0.08
Panicle length	0.14	
Panicle number	0.16	-0.14
Seed number per plant	0.12	0.25*
No. of days of growing period		0.17
Resistance to shedding of grains	-0.18	0.02
Germination speed	0.14	0.07
Length/width ratio of grain	0.31*	0.13
Index-number of alkali-test	-0.30*	-0.16

* Exceeds 5% level of significance.

3. Inheritance of competitive ability.

F₂ and F₃ lines of the cross 563 × 115 were used for this experiment. In this cross, though the parental varieties were distantly related, the F₁ was almost completely fertile with respect to pollen and seed setting. The lines of the parental varieties, F₂ and F₃ were tested for competitive ability using a Japanese variety, Yaeho, as the tester. A plot consisted of a row of 15 plants of the above-given materials, and in each row, between each two of those plants spaced at 25 cm, two plants of the tester strain were inserted, reducing the distance between plants to about 8 cm. A set of plots was consisted of six plots belonging to the parental varieties, three belonging to F₂ and 40 belonging to the respective F₃ lines. Those plots were randomized with four replications. It was assumed that the two tester-plants standing on the both sides of a plant to be tested would show the effect of competition with the given plant. Then, the sums of measurements for such two tester-plants were recorded, and were used for variance analysis. Panicle number and plant weight were recorded, and partitioning of variance components was made by Mather's method. The results are given in Table 6.

The data in Table 6 show that the inheritance of competitive ability can be analysed by the same method as used for ordinary quantitative characters, if a proper design of experiment is adopted. This suggests that the competitive ability is controlled by Mendelian genes. In the present experiment, however, the number of effective factors could not be estimated owing to too large values of variance of variance of F₃ lines.

Table 4. Variation in competitive ability among lines with different characters (414 × 563).

Class	Weak				Strong		No. of lines
	1	0	-1	-2	-3	-4	
Phenol reaction :							
+	2	6	9	15	7	2	41
-	1	2	11	5	3		22
Character combination group :*							
I (Similar to Continental type)			2	7	3		12
II	2	1	5	4	3	1	16
III	1	5	3	4	2	1	16
IV			3	3	2		8
V, VI (Similar to Temp.-Insular type)	2	7	2				11
Reaction-type group of hybrid sterility : **							
I (Continental type)	1	1	2	9	4		17
II		1	7	5	3	1	17
III			2	1			3
V				1			1
VI (Temp.-Insular type)	1	1	5	2	1	1	11

* For details see OKA 1957 a. ** For details see OKA 1957 b.

Table 5. Competitive ability of lines differing in phenol reaction and resistance to blast disease (108 × 504).

Class	Weak				Strong			No. of lines
	3	2	0	-2	-4	-6	-8	
Phenol reaction :								
+	1	7	9	15	9	10	5	58
-	1	3	6	6	12	4	1	33
To blast disease :*								
Resistant			5	2	5	5	1	18
Intermediate		3	1	4	6	3	3	21
Susceptible	2	7	9	14	9	6	2	50

* Tested by natural infection at Tonhsu, Formosa.

Table 6. Variance components for the increments or decrements in test strain due to competition with hybrid or parental plants of the cross 563 × 115.

Population	Panicle number		Plant weight	
	Observed	Expected	Observed	Expected
V _{F₂}	12.47	12.57	347.3	348.8
V _{F₃}	3.20	3.20	30.8	30.8
V _{F₃}	12.02	11.79	344.7	341.6
E ₁	10.90	11.01	332.9	334.4
E ₂	1.72	1.70	21.2	20.6
D		2.96 ± 1.07		17.74 ± 14.57
H		0.33 ± 2.92		22.12 ± 40.01

(1957, at MISIMA)

4. Effects of growth conditions on competition.

In order to find out the effects of fertilizer, plant number per hill, and the duration of nursery-bed period on the competition between rice varieties, a mixed population of Taichung No. 65 (Strain 504) and Pei-ku (Strain 106) with the initial 50 : 50 proportion was grown successively for three generations together with pure populations of these varieties (the third method). The treatments were (1) no fertilizer, single plant per hill, (2) no fertilizer, 5 plants per hill, (3) no fertilizer, single plant per hill, the period in the nursery bed being twice as long as usual, and (4) a large quantity of fertilizer (16.4 g/m² N), single plant per hill. These plots were randomized with two replications, and the competitive ability of Taichung No. 65 under these conditions was shown by its proportion in plant number and in seed number (mix-harvested).

It was found that the proportion of Taichung No. 65 decreased in all of the four treatments, the rate of decrease being different for each. The relative propagation rates under those conditions were estimated from the data for pure plots of the two varieties. Using those values, the competitive ability of Taichung No. 65 in each generation was computed by the following formula, which was derived from that devised by SAKAI (1955 d),

$$p = \frac{a_1 - a_0 + (1 - a_1) a_0 q}{a_0 (1 - a_0)},$$

where p and $(1 - q)$ stand for the relative propagation rate and competitive ability of Taichung No. 65, and a_0 and a_1 stand for its proportion in plant number and in seed number, respectively.

The results of this computation are given in Table 7. As the data in the table show, the competitive ability of Taichung No. 65 was relatively low in highly fertilized plots, and became higher when the nursery bed period was prolonged. It is known, however, that in order to get better crops, Taichung No. 65, rather than Pei-

Table 7. Competitive ability (p) and relative propagation rate ($1 - q$) of Taichung No. 65 to Pei-ku under different conditions.

Growing condition	First crop		Second crop	
	$1 - q$	p	$1 - q$	p
1) No fertilizer, single plant	0.872	-0.398	0.925	-0.122
2) " , five plants	0.815	-0.536	0.912	-0.129
3) " , single plant, long nursery bed period	0.807	-0.203	0.938	0.038
4) High dosage of fertilizer, single plant	0.949	-0.603	1.368	-0.597

(1954~1955, at TAICHUNG)

ku, is suited for large quantities of fertilizer, but it often yields a poor crop when the nursery bed period is too long. It is interesting to find a variety which apparently shows a higher competitive ability under conditions relatively unfavorable to it.

Secondly, the effect of lowland vs. upland growing was investigated using one lowland (Sizuoka-aikoku No. 1) and two upland (Rikuto-norin No. 18 and "Red-rice") varieties of Japan. The "Red-rice" belongs to the Indica type, and is known to be a weed in some upland rice farms in Japan. According to S. IYAMA (unpublished), it seems to be maintained in the Japanese upland-variety populations owing to its strong competitive ability. Singly-planted plots of these three varieties were compared with mix-planted ones in which two of them were alternately planted, under lowland and upland conditions. A plot consisted of a row of 30 plants (spaced 8 cm apart), the spacing between rows being 50 cm. The plots were randomized with three replications.

The recorded panicle number and plant weight in singly-planted plots and the increment or decrement due to competition in mix-planted plots are given in Table 8. No

Table 8. Competition between lowland and upland varieties in lowland and upland conditions.

Variety	Condition	Panicle number, Surrounded by			Plant weight, Surrounded by		
		S. 1	R. 18	Red	S. 1	R. 18	Red
Sizuoka-aikoku No. 1 (Lowland)	Low.	7.6	- 1.0	-1.9	55.7 ^{gm}	- 6.6	-13.1
	Up.	7.8	- 0.6	-1.5	26.4	+ 1.9	- 6.6
Rikuto-norin No. 18 (Upland)	Low.	-0.4	5.5	-0.4	- 6.7	31.9	-12.2
	Up.	+1.2	10.7	-4.2	+ 1.7	24.8	-13.0
"Red-rice" (Upland)	Low.	+7.4	+ 9.1	21.1	+ 5.8	+ 7.3	44.6
	Up.	+7.9	+ 2.5	28.4	+12.9	+ 2.4	50.8

(1955, at MISIMA)

definite tendency was found for competitive ability to be increased or decreased in lowland or upland conditions, though in singly-planted plots, upland ones were apparently adaptive to upland condition.

5. Competition against weeds.

Five representative rice varieties grown in Formosa, Taichung No. 65, Taichung No. 150, Pei-ku, Pei-mi-fen and O-chiam, the former two being of the Horai or the Temperate-Insular type, and the latter three being of the Formosan native or the Continental type, were tested in cleanly weeded and non-weeded conditions. The plots were arranged according to the split plot design (sub-plots representing varieties) with three replications, and the same design of experiment was repeated in the first and second crop seasons. The standard dosage of fertilizers (8g·N/m²) was applied in both seasons. Measurements were taken for panicle number, grain number per panicle and other agronomic characters. The records for weeded plots, and the increments or decrements for non-weeded plots as compared with the former, are given in Table 9.

Table 9. Test of varieties in weeded and non-weeded conditions (Showing the records for weeded plots and their increments or decrements for non-weeded plots as compared with the former).

Crop	Variety	Panicle number		Grain number per panicle		% of seed setting		Grain yield (kg/ha)	
		W.	Non-W.	W.	Non-W.	W.	Non-W.	W.	Non-W.
1st	Taichung No. 65	20.5	- 4.6	73.0	- 3.4	89	+ 5	548	-236
	Taichung No. 150	22.3	- 8.6	81.5	-14.3	87	+ 4	609	-214
	Pei-mi-fen	23.2	- 3.8	76.6	- 4.9	91	+ 2	473	+ 29
	O-chiam	24.2	- 1.4	68.5	- 7.9	97	- 1	521	- 24
2nd	Taichung No. 65	17.9	-11.9	63.8	-22.2	79	+ 1	340	-269
	Taichung No. 150	17.4	-10.5	67.6	-21.0	82	+ 1	329	-275
	Pei-mi-fen	18.8	- 8.5	76.4	-14.1	55	+13	116	- 54
	O-chiam	19.4	- 6.9	66.6	+ 1.6	74	+ 1	179	- 63
	Pei-ku	17.0	- 4.2	78.2	- 6.2	48	+20	127	- 15

W. ... Weeded, Non-W. ... Non-weeded. (1948, at TAICHUNG)

In the case of non-weeded field, weeds grew vigorously among the rice plants in both the first and second crops. The data in Table 9 show that in non-weeded condition, varieties of the Horai or Temperate-Insular type had a larger drop in panicle number, grain number per panicle and yield than those of the Continental type, and that this tendency was more pronounced in the second crop season (under higher temperatures) than in the first crop season. The results of variance analysis showed that these inter-varietal differences were highly significant. The data in Table 9 thus seem to suggest that the Continental or Indica varieties are adaptable to less intensive cultivation such as non-weeding than the Insular or Japonica varieties. It seems that their resistance

against weeds comes from their generally high competitive ability which we have found first against other rice varieties. It is interesting to note, however, that in the second crop experiment, Pei-mi-fen and Pei-ku indicated a low fertility in weeded plots and higher one in non-weeded plots. The reduction of panicle number or grain number per panicle due to weeds might have improved the fertility in those varieties.

Discussion

The data of a crossing experiment presented in this paper show that competitive ability might be controlled by Mendelian genes. Then, its variations might be attributed to mutations of those genes. In hybrid populations, however, genes which endow their carriers with a high competitive ability might increase from generation to generation. It then follows that so far as the genetic variability for this character persists in a population, the competitive ability of the population as a whole would be promoted year after year. Accordingly, a large population in which hybridization occurs frequently may have a higher competitive ability than small isolated ones.

Needless to say, we must take it for granted that the above-mentioned view can only be applied for the competitive ability between genotypes of the same species. Theoretically, the competitive ability of a genotype may be apportioned into a general and a specific one. The former means the average ability in competition with various genotypes of the same and different species with similar growing habits and the latter means the competitive ability of a genotype in relation to a particular one. Though no adequate experimental datum is available, it may be assumed that a plant which shows a high competitive ability in relation to a certain tester strain in an experiment, can generally be a good competitor against other similar plants. This assumption may hold good if in a group of genotypes or species, the means by which they compete with each other do not differ so much among themselves. If so, a population in which an amount of genetic variability is continuously supplied by hybridization may be furnished with a high competitive ability and may be at a selective advantage.

The present study shows that varieties of the Indica or the Continental type generally have higher competitive abilities than those of the Japonica or the Insular type. According to the above-mentioned view, this fact seems to indicate that the Indica varieties have developed from large intermingled populations, while the Japonica varieties have been in relatively isolated populations. For more detailed discussions, however, the role of competition in natural selection should be understood more thoroughly.

From the agronomic view-point, varieties with a high competitive ability may be desired, since they may be strong against weeds and other off-types. It was found that the competitive ability was not correlated with most agronomic characters. It may then be pointed out that an improvement in competitive ability can easily be achieved if hybrid populations are grown in bulk for several generations.

Summary

This paper deals with the results of various competition experiments with rice. The results are summarized below:-

1. Varieties of the Indica or the Continental type generally have higher competitive abilities than those of the Japonica or the Insular type.
2. Among lines derived from hybrids between distantly related varieties, those from

bulk propagation of hybrid populations tended to have a higher competitive ability than those from pedigree propagation. This indicates that genotypes with high competitive ability increase in hybrid populations.

3. Among hybrid-derived lines, the competitive ability showed no significant correlation with various agronomic characters. However, the characters differentiating the Indica and Japonica types were found to be correlated with competitive ability in the way that lines resembling in a character the Indica type tended to have a higher competitive ability than those resembling the Japonica type. This may be explained by the tendency generally recognizable toward restriction of character recombination in hybrids between distantly related rice varieties.

4. The inheritance of competitive ability in an intervarietal cross was investigated by using Mather's method of partitioning variance components. The results indicate that competitive ability might be controlled by Mendelian genes.

5. An Indica and a Japonica variety were mix-propagated for three generations under different growing conditions. It was found that the competitive ability of one variety to the other might become higher under conditions rather unfavorable to it.

6. Varieties of the Indica or Continental type showed higher competitive ability or resistance against weeds than those of the Japonica or Insular type.

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栽培稲の系統発生的分化第19報 稲品種間の競争力の変異

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本論文は稲を用いた種々の競争実験の結果を報告するものであるが、以下の事実が指摘された。

1. インド型または大陸型の品種は一般に日本型または島型のものより強い競争力をもっている。

2. 遠縁品種間の交雑から得られた系統の間では、雑種集団の集団的繁殖によるものは系統的繁殖によるものより強い競争力をもつ傾向があつた。このことは雑種集団の中で競争力の強い遺伝子型が増加することを示す。

3. 雑種に由来する系統の間で競争力は種々の生産形質と殆ど相関を示さなかつた。しかしインド型と日本型を分化させる形質は競争力に相関し、ある形質においてインド型に似る系統は日本型に似る系統より高い競争力

をもつ傾向があつた。このことは遠縁の稲品種間雑種において一般的に認められる形質組換えの制限される傾向によつて説明される。

4. 品種間雑種における競争力の遺伝を MATHER の分散成分分割法で調査した。その結果は競争力がメンデル遺伝子に支配されることを示した。

5. インド型と日本型の各品種の混合集団を世代種々の条件の下に繁殖した。それら品種の一方の他方に対する競争力はその品種にとつてむしろ不利な条件の下に高くなることを見出された。

6. インド型または大陸型の品種は日本型または島型のものより雑草に対して強い競争力を示した。(摘要)