DIALLEL ANALYSIS OF VARIETAL DIFFERENTIATION IN A RICE VARIETY

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Synopsis. The pattern of intra-variety differentiation were studied by diallel cross analysis with seven local strains of a rice variety "Taichung 65".

Genetic differences between strains were corroborated in several agronomic characters, though they were small in magnitude. In grain yield, the strains which had been cultivated over an extended period in Japan, appeared to have accumulated alleles showing dominance in positive direction here in Japan.

Introduction

A variety of self-pollinated crop-plants, though usually it is considered to be unique, contains different genotypes. This may be especially true for so-called polygenic characters, in which differentiation cannot be easily detected. Therefore, problems arise, as to the magnitude, direction and limits of genetic differentiation within a variety.

The present experiment was undertaken to investigate the pattern of genetic differentiation in a rice variety. Strains of "Taichung 65" were used, as this variety is one of the varieties which have been grown widely and for an extended period.

Materials and Methods

"Taichung 65" is a rice variety selected from a cross between "Kameji" and "Shinriki" at the Taichung Agricultural Experimental Station, Taiwan. The crossing was made in 1923. It is a japonica variety relatively insensitive to day-length and temperature.

Seven local strains, obtained from three different countries separately, were used for this experiment (Table 1). The strain A had been grown annually at this Institution until 1955, and the strain C had been maintained at the original breeding station. Though the conditions of their maintenance in different institutions remain unknown, the seeds obtained were usually kept in a low-temperature

and low-humidity room. In the seed raising they were grown in four rows of 12 to 15 single plants (one plant per hill) and seeds were harvested from the two middle rows.

Table 1. List of strains of Taichung 65 used

Strain	Location	Year of acquisition
A	Taiwan (Taichung)	1936
B	Japan (Miyazaki-ken)	1955
C	Taiwan (Taichung)	1956
D	U. S. A.	1958
E	Taiwan	1959
F	Japan (Amami Island)	1959
G	Japan (Mie-ken)	1960

In 1963, diallel crosses of the seven strains resulted in 42 F_1 's and seven selfed families. In 1964, the seeds were sown in a nursery bed on April 30 and seedlings were transplanted on June 10 with the standard mixture of fertilizers and standard spacing. The randomized complete-block design with three replications was followed. Each plot contained twelve plants. Grain yield, culm length, panicle length, panicle number per plant, and heading date were recorded from ten plants in the middle portion. The weight of 1000 grains was measured for one block only. The method of diallel analysis by JINKS (1954) and HAYMAN (1954, 1958) was used for analysis of data.

Results

Mean values of the parents and arrays con-

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Table 2. Mean values for each parent and its array

Strain	Grain yield (g)	Number of panicles	Panicle length (cm)	Weight of 1000 grains (g)	Culm length (cm)	Growth duration (day)
A	258	9.6	22.67	24.5	100.8	115.7
	280	10.3	22.66	24.3	103.2	117.0
B	334	11.8	22.63	25.1	105.9	115.6
	311	11.1	22.63	24.9	105.6	116.8
C	290	11.1	22.60	25.3	106.6	117.0
	279	10.3	22.59	24.6	105.1	118.5
D	261	9.5	22.10	25.1	103.6	117.2
	267	10.0	22.59	24.5	104.3	118.6
E	246	9.5	21.53	23.8	102.3	117.4
	267	10.0	22.28	24.2	104.1	118.0
F	231	8.6	22.17	24.4	102.2	117.5
	263	9.9	22.69	24.7	104.1	117.5
G	250	8.4	22.20	24.3	104.4	121.9
	262	9.4	22.71	24.4	105.2	119.5

Upper figure : parent

Lower figure : array

Table 3. Analysis of variance for grain yield

Item	D. F.	M. S.
(a) Parental strains	6	168.59**
(b) Genetic interaction	21	13.17
(c) Av. maternal effects	6	88.83**
(d) Reciprocal effects	15	20.79
Blocks	2	149.01**
Error	96	16.23

** $P < 0.01$

Table 4. Factorial analysis of grain yield

Source of variation	D. F.	M. S.
Maternal strains (M)	6	194.77*
Paternal strains (P)	6	62.65
(M) × (P)	36	16.34
Blocks (B)	2	149.01**
(B) × (M)	12	40.46**
(B) × (P)	12	21.86*
(B) × (M) × (P)	72	11.25

* $P < 0.05$ ** $P < 0.01$

taining a parent in common, are given in Table 2, and the results of analysis of variance (HAYMAN, 1954a) are presented in Table 3, 5 and 6, where effects were tested against error mean square. Differences in all observed characters except for panicle length were statistically significant.

The observed characters are separately dealt with in the following description.

(i) **Grain yield** The variation between the mean effects of each parental strains; and

average maternal effects of each parental strains were found significant. Since maternal effects were found and there was a possibility of block-genotype interaction, the factorial analysis was used for testing genic variances (WEARDEN, 1964). The analysis is shown in Table 4. Genic variance is generally tested for significance by the ratio, parental mean square/error mean square in the fixed sample model, but in Table 4 the effects were tested against each block-array interaction, since the interactions were found significant. In this test, the parental mean square failed just to be

significant, indicating that the genic differences between the strains were small. However, these analyses indicate some genetic differences between strains. Further analysis of these data was made by the graphical analysis by JINKS (1954) and HAYMAN (1954b).

The variance of the progeny of the r th parent (V_r), the covariance between the parents and their progeny in the r th array (W_r), and the covariance between the array means and the r th array (W_r') were calculated from the diallel table of reciprocal means. Since the analysis of the variance of $W_r - V_r$ showed no significant differences either between strains, or blocks, the statistics from the pooled data over blocks are given in the following.

W_r/V_r graph is shown in Fig. 1. The regression of W_r/V_r is significant and does not deviate significantly from the unit. The regression line with unit slope through the mean point of W_r and V_r lies close to the point of origin, indicating almost complete dominance. In W_r/V_r graph, points with lower values of V_r and W_r correspond to dominant parents and points with higher values to the recessive parents. The distribution of the points in Fig. 1 indicates that there were genic differences between strains and that C and F were parents with more recessive alleles while A, B, and D were relatively dominant parents.

One of the supposedly dominant strain, A, was early introduced in Japan in 1936, and

Fig. 1. W_r/V_r (a) and W_r'/W_r (b) graph for grain yield. A broken line in the W_r/V_r graph is line of unit slope through the mean point. The line in the W_r'/W_r graph has a slope of 0.5 and passes through the mean point. $b_{W_r/V_r}=0.839\pm0.229$; $b_{W_r'/W_r}=0.524\pm0.065$

the other dominant strain, B, is thought to have been cultivated in Japan relatively longer than others except for A, whereas the two recessive strains, C and F, were obtained recently from Taichung (the original breeding station) and Amami Island, in the southwest end of Japan.

The gene distributions in the strains may give another aspect of the interrelationship between the strains. The gene distributions in the parents reflected in Fig. 1, W_r'/W_r graph. When the gene distributions in the parents are symmetrical the graph is a straight line of slope $1/2$ through the mean point of W_r and W_r' and with the asymmetry the points are scattered about a line of slope $1/2$, indicating that the most common genotypes correspond to points above the line and uncommon genotypes below the line (HAYMAN, 1958).

As shown in Fig. 1, the regression coefficient of W_r'/W_r does not differ from the expected value, and any points do not deviate far from the line. This indicates that the gene distributions in these strains were symmetrical and that any strains had neither more common, nor rare genotypes in them. Therefore, it may be that this variety had initially some genic variation and the different strains accumulated a number of different alleles by the action of natural selection.

The correlation between grain yield of parental strains and the order of dominance, W_r+V_r , was not significant, and dominance

Fig. 2. Relationship between dominance and grain yield of parental strains. $r=0.118$

acted both in positive and negative direction. Therefore, information on the limits of intra-varietal differentiation from genes exhibiting dominance can not be given in general. However, Fig. 2 shows that there are two groups, one containing A, B, E, F, and G, and the other of B and C. Since the correlations within the groups are negative, it seems that dominance acted in positive direction within the group, and the dominant strains, A, B, and D had higher grain yield than others in their groups.

The above-mentioned results of analysis depend on the genic differences, while maternal effects appeared to be significant. Therefore, it is desirable in this experiment to study the maternal effects for more precise evaluation of the inter-relationship between

the strains, though the maternal effects in crop-plants are rare and they are not important. The male array covariance, the covariance between the progeny of the male parent and their non-recurrent parents, is graphically compared with the female array covariance, the covariance between the progeny of the female parent and their non-recurrent parent (DURRANT and TYSON, 1964). If there are no reciprocal differences, the points should lie on a straight line of the unit slope, passing through the origin, and any differences will put the points above or below the line. As shown in Fig. 3, the points are rather perpendicular to the abscissa, indicating nucleus-cytoplasm interaction. The progeny of the female parent A had strong maternal effects and showed negative dominance in the cross with strain B. Strain D, also, gave its maternal influences to the progeny but to a lesser degree. Strain C showed just opposite to the formers. These results indicate that the stronger the maternal effects a strain had, the more dominant it was classified. Therefore, it may be that the genic effects, causing the differences between these strains, were small and they were easily confounded by the

Fig. 3. Male/female array covariance graph for grain yield. A broken line is the line of unit slope through the origin.

cytoplasmic effects.

(ii) **Characters composing grain yield (number of panicle, panicle length and weight of 1000 grains)** Table 5 shows that items (a) and (c) of panicle number are significant, but there is no significant dominance. The test of significance for genic variance by the ratio (a)/(c) indicated that there were no significant genic differences between the strains. Therefore, differences found might depend mainly on the maternal effects. Male/female array covariance graph is shown in Fig. 4, where the points tend to fall on a line of a negative slope. The strain A and B displayed relatively strong maternal effects in their progeny, whereas strain C had the opposite effects to the formers. The results of maternal effects in panicle number are slightly different from those in grain yield, but it seems that the maternal effects in yield resulted partially from the effects in panicle number.

No significant differences in panicle length were detected as reflected in Table 2 and 5.

Table 5. Analysis of variance

Item	D. F.	M. S.		
		Number of panicle	Panicle length	Weight of 1000 grains
(a) Parental strains	6	11.61**	1.478	0.910**
(b) Genetic interaction	21	2.00	0.978	0.172
(c) Av. maternal effects	6	11.71**	0.828	0.202
(d) Reciprocal effects	15	2.06	0.428	0.162
Blocks	2	11.90**	8.205	—
Error	96	2.24	3.426	—

* $P < 0.05$ ** $P < 0.01$

Table 6. Analysis of variance

Item	D. F.	M. S.	
		Culm length	Growth duration
(a) Parental strains	6	31.32**	38.47**
(b) Genetic interaction	21	5.31	2.87
(c) Av. maternal effects	6	3.01	15.62
(d) Reciprocal effects	15	11.30	2.30
Blocks	2	290.83**	66.04**
Error	96	6.72	2.04

* $P < 0.05$ ** $P < 0.01$

Fig. 4. Male/female array covariance graph for number of panicles. A broken line is the line of unit slope through the origin. $b = -1.089 \pm 0.575$

The panicle length had no significant bearing on the differences between the strains.

Weight of 1000 grains was measured only in one block. The variation between the mean effects of each parental strains was found significant. Fig. 5 indicates a failure of the hypothesis required, but the omission of strain D from the diallel table passably satisfied the hypothesis. As shown in Fig. 5(b), the regression coefficient does not deviate significantly from the unit, though it is still less than the unit. The order of dominance of the parental strains is G, E, A, E, B and C, where the differences in the degree of dominance among the former three are small. Strain B had the order quite different from that in grain yield and was relatively recessive in these strains. The correlation coefficient of $W_r + V_r$ onto the weight of 1000 grains of parental strains is positive and significant ($r = +.849$). Therefore, dominant alleles acted mostly in negative direction, that is, the small grain was dominant to the large one. Fig. 6 shown that the points are scattered about a line of slope 1/2, indicating an asymmetry of gene distributions in the parents. Since strain B is the furthest above the line, it seems to contain the most common genotype in these strains. The most common genotype in these

Fig. 5. W_r/V_r graphs for weight of 1000 grains. A broken line in the graph (b) is the line of unit slope through the mean point. $b_{(a)} = 0.38 \pm 0.222$; $b_{(b)} = 0.624 \pm 0.218$

strains is assumed to be the nearest genotype to the original variety. Therefore, it is highly probable that the original variety had rather recessive genotype on seed size, and that more dominant strains than the original was differentiated.

(iii) **Other characters (culm length and growth duration)** Table 6 shown the analysis of variance of culm length and growth duration. Genetic differences between the strains were detected in both of the characters, and in growth duration maternal effects were found. Differences between the strains in culm

Fig. 6. Wr'/Wr graph for weight of 1000 grains. A broken line in the graph has a slope of 0.5 and passes through the mean point. $b=0.428 \pm 0.134$

length were small (within 5% of the total mean) but consistent, while interaction between blocks and strains was found significant in growth duration.

Wr/Vr graph of culm length is shown in Fig. 7 (a), the regression coefficient does not deviate significantly from the unit, though A, C, and F fall off the line of unit slope. The order of dominance of parental strains is D, G, B, E, C, A and F, differing quite from that in grain yield. Dominance acted in both directions and the most dominant strain D had the intermediate culm length in these strains. Strain C seems to be a rare genotype in these strains, as shown in Fig. 7 (b). However, no specific relation was found between the order of dominance of the strains and the place where strains were obtained. Hence it appears that some initial heterogeneity of the original variety

Fig. 7. Graphs for culm length (a and b) and growth duration (c and d). A broken line in the graph has a slope of an expected values through the mean point. $b_{(a)}=0.820 \pm 0.166$; $b_{(b)}=0.427 \pm 0.218$; $b_{(c)}=0.848 \pm 0.362$; $b_{(d)}=0.340 \pm 0.209$

made it possible to differentiate the strains at random in the process of seed propagation and distribution with the aid of a high heritability usually shown in this character.

In growth duration, only strains B and G had the different orders of dominance from others, as shown in Fig. 7 (c), and strain A, one of the intermediate parents in the order of dominance, appeared to contain the most common genotypes in these strains (Fig. 7(d)). The maximum phenotypic difference between the parental strains was 6.5 days, and it was reduced to 1.9 days with the omission of strain G which had the largest growth duration in the strains. Though strain G was different from other strains, it was differentiated probably from the original variety, since its genotype showed no rarity in these strains (Fig. 7(d)).

Discussion

The present study proved some statistically significant differences in agronomic characters between local strains of Taichung 65, though genic variation seemed to be small in magnitude. The differences in grain yield and yield-component characters appeared to be mainly due to nucleus-cytoplasm interaction. The differences in culm length and growth duration seemed to be genic, probably because these characters are relatively stable and can be easily selected in seed multiplication farms.

Considering grain yield, heterogeneity of this variety might not be large, though more variations were found in other characters. The accuracy of the experiment to detect minor differences in yield might be responsible for ambiguous results ($cv = 14.6\%$), but it is highly probable that grain yield generally has a low heritability and selection is not effective when genetic variation is small. This view is supported by the results of other researchers. KANDA et al. (1952) found no varietal differentiation in two local strains of a rice variety "Rikuu 132". GOTOH (1956) reported that the local strains of a barley variety "Hakata 2" did not differ in grain yield in spite of the presence of distinct differences in ear length. Though the genic differences between the strains were small, the inter-relationship between the strains could be

fairly well described by the analysis of diallel crosses.

In the discussion of the pattern of intra-varietal differentiation, it is desirable to know the original genotype of the variety at the time of release, but the original variety was not available in this experiment. However, it can be assumed that strain which has the nearest genotype to that of the original variety is I) one which contains the most common genotypes in the strains, because no two strains were obtained at the same time from the same place, and/or II) one which has been maintained at the well-adapted area, or at the original breeding station. As far as grain yield is concerned, the assumption I was not applicable, because the gene distributions in the strains were found symmetry, but by the assumption II the original genotype was supposed rather recessive and the direction of the differentiation was dominant, that is, different strains accumulated different numbers of dominant alleles in accordance with their periods of cultivation in Japan. The original genotype of grain size was supposed recessive by the assumption I and II, and the direction of differentiation was concluded dominant, that is, the grain size of differentiated strains smaller than the original.

Though the mean direction of dominance in grain size was negative, dominant genes in grain yield seemed to act both in positive and negative direction, but as mentioned before, with some restriction dominance was supposed rather in positive direction. The fact that the strains with more dominant alleles on grain yield did not always have the higher yield may be partly explained by considering yield-component characters. Since the phenotypic expression of grain size is more stable than that of grain number, it is probable that in a strain with dominant alleles the decrease in grain size is not compensated phenotypically with the increase in grain number so that grain yield of such strain happens to decrease. However, as the results showed, more dominant strain A, B and D had grain yield at least equal to, or more than the recessive strain C. Therefore, it may be that the strains maintained or improved their performances in grain yield by accumu-

lating alleles showing dominance where they had been cultivated.

Differentiations in culm length and growth

duration were found rather at random and their differentiation seemed to be brought by random drift.

Summary

Investigations of intra-varietal differentiation in a rice variety "Taichung 65" by diallel analysis resulted in the following conclusions:

1. Significant genetic variations between seven strains were found in grain yield, panicle number per plant, weight of 1000 grains, culm length and growth duration, but not in panicle length.

2. The inter-relationship between the strains could be fairly well described by the analysis of diallel crosses. Genetic variations were almost additive, but in the weight of 1000 grains non-allelic interaction was found.

3. Variations in grain yield and its component characters were small and appeared to be mainly due to nucleus-cytoplasm interaction. The range of parental strain means in culm length and growth duration was within 5% of the total mean value.

4. In grain yield and its component characters, the strains seemed to have accumulated different numbers of alleles showing dominance in accordance with their periods of cultivation in Japan, while the directions of the differentiation in culm length and growth duration seemed to be at random.

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ダイアレル分析による稲の品種内分化の解析

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稲品種「台中65号」の7つの地方系統を用いて、系統間差異の程度と分化の方向を検討した。収量・粒重・稈長・穂長・生育日数について調査を行ない、ダイアレル分析法 (JINKS; 1954, HAYMAN 1954, 1958) によって解析した。

穂長以外の形質では、系統間の遺伝的変異が認められた。これらの変異は相加的であつて、エピスタシスが認められたのは粒重だけであつた。

収量と穂数では、核と細胞質の交互作用が系統間変異

を拡大することが想像された。収量と粒重では、優性遺伝子の作用が、ほぼ一定方向であつた。これらの形質では、原品種が比較的多く劣性遺伝子を持っていたと推察された。また、日本での栽培期間の長い系統ほど優性遺伝子を多く持っていた。これらのことから、分化は優性遺伝子を集積する方向にあつたと推察された。

稈長では優性遺伝子の作用は一定方向でなく、分化の方向も任意であつた。生育日数では、一つの系統をのぞいて系統間に差がなかつた。