DIALLEL ANALYSIS OF AGRONOMIC TRAITS IN RICE (*ORYZA SATIVA* L.)[1]

CHENG-CHANG LI[2] and TE-TZU CHANG[3]

(Accepted June 20, 1970)

Abstract

A diallel set consisting of p^2 combinations [p parents, $\frac{1}{2}p(p-1)$ reciprocal F_1 hybrids, $\frac{1}{2}p(p-1)$ F_1 hybrids, and $\frac{1}{2}p(p-1)$ F_2 hybrids] among four rice cultivars of extremely diverse phenotypes were grown in replicated trials in years. The study was aimed at elucidating the genetic system underlying the inheritance of six quantitative traits: seeding-to-heading period, plant height, number of panicles per plant, panicle length, panicle weight, and number of spikelets per panicle.

Diallel analysis showed that much of the genetic variation of each of the six traits was due to additive effect. Dominance effect also was a significant source in all the traits. Indirect evidence indicated that gene interaction played a negligible role.

No evidence of maternal effect was found. The effect of genotype environment interaction was relatively small in the F_1 hybrids and was only expressed for panicle length.

For those loci which showed dominance there was overdominance for panicle weight and partial dominance for the other five traits. Generally dominance was toward earlier maturity, taller plant stature, higher panicle numer, longer panicles, higher panicle weight, and larger number of spikelets per panicle. On the average, the positive and negative genes in the parents were unequally distributed, the dominant alleles exceeding the recessive alleles for seeding-to-heading period, plant height, panicle length, and panicle weight and the recessive alleles exceeding the dominant alleles for panicle number and spikelet number. The parents carrying dominant genes also differed in level of dominance.

Heritability estimates were generally high in the F_2 populations, substantiating the postulate that a major portion of the phenotypic variability was

---

1. Research supported in part by grant GB 2417 from U. S. National Science Foundation.
2. Former research fellow of International Rice Research Institute and presently lecturer of Chung-Hsing University, Taichung, Taiwan.
3. Geneticist of International Rice Research Institute, Los Baños, Laguna, Philippines.

controlled by additive gene action. The heritability estimates were high for seeding-to-heading period, moderately high for plant height, panicle weight, and panicle length, and moderately low for panicle number and spikelet number.

Data obtained from F_2 populations largely confirmed the findings obtained in the two F_1 populations. Transgressive segregation was noted in several populations. Environmental effect seemed to influence the F_2 plants grown in bulk populations slightly more than the F_1 plants.

Introduction

Significant advances have been made in rice improvement by conventional methods of hybridization and selection. Much of the recent success in improving indica rices of tropical areas was the direct outcome of recombining semi-dwarf stature and stiff culms, erect and short leaves, relatively early maturity and low sensitivity to photoperiod, a large panicle number, and an adequate number of well-developed grains on the panicles. Genetic information about these economically significant quantitative traits was limited, however, to a few studies where either a few major genes or polygenic genes were considered to account for the continuous variation found in the segregating generations of single crosses. Little is known about the genetic system underlying the complex variation of agronomic traits in progenies of crosses involving diverse parents.

Diallel analysis is an effective way to examine the system of genes involved in the control of a quantitative trait. This study was designed to investigate several agronomic traits related to a high yield potential. In the study three of the parents represented extreme differences commonly found in tropical cultivars developed either by pedigree selection or through conventional hybridization programs. The fourth parent was bred for direct-seeding culture in the temperate zone. Moreover, the parents were selected to exclude the monogenic control of semi-dwarf stature and the oligogenic control of heading date due to photoperiod sensitivity. The F_2 progeny were included to provide supplementary information to that derived from F_1 hybrids.

Materials and Methods

All possible cross-combinations, including the reciprocals, were made among four relatively early maturing, essentially photoperiod-insensitive and cross-fertile, pure-line cultivars: Sigadis (from Indonesia), H-4 (from Ceylon), Dawn (from U. S. A.), and Sukhwel-20 (from India). The four parents and one set of F_1 hybrids (p^2 combinations) were culture and transplanted in flooded seedbeds at Los Baños, Philippines, in the dry season (January to

May) of 1966 in a randomized complete block design with four replications. Each block consisted of 16 two-row plots. Each plot included 16 plants spaced 40×30 cm. Fertilizers were applied at the rate of 60–30–30 kg/ha. Date of heading, plant height, panicle number, mean weight of panicles, mean length of panicles, number of spikelets, and number of fully developed grains on each panicle were recorded for each plant.

A second planting of the half-diallel set was made in the dry season of 1967. Twenty F_1 and 60 parent plants were grown in rows of 10 plants each, replicated twice. For each cross, 560 F_2 plants were grown in replicated plots of 28 rows each. The four traits measured in 1967 were date of heading, plant height, panicle number, and panicle length.

Analysis of data was based on the diallel-cross techniques of Hayman (1954a, 1954b, 1958), Jinks (1954), and Jones (1965). For these experiments, the following assumptions were made: (1) parental homozygosity, (2) normal diploid segregations, (3) no maternal effect, (4) no multiple alleles, (5) no linkage, and (6) no non-allelic gene interaction (epistasis).

The four parents were a selected sample of rice cultivars and constituted the entire population about which inferences were made.

Results

The mean values of the parents and F_1 hybrids obtained in two plantings are in Table 1 and 2. The parents differed appreciably in each of the six quantitative traits studied. The maximum differences among parents were:

Crop season	Seeding to heading	Plant ht.	Panicle length	Panicle No.	Panicle wt.	No. of spikelets/ panicle
1966	33 days	75 cm.	11 cm.	26	5.5 g.	152
1967	30 days	62 cm.	11 cm.	20	—	—

The differences were highly significant for each of the six quantitative traits when the parents and their progenies were compared in each of the 2 years, thus meeting the prerequisite for further analsis. The reciprocal F_1 hybrids did not differ significantly in any of the six traits obtained in 1966. The variance of each arry (V_r) and the covariance between the parents and their F_1 progenies in each array (W_r) were computed. Homogeneity tests for (W_r—V_r), which showed conformity to Hayman's postulates (1954a), preceded the estimation of various genetic components.

Experiments Involving F_1 Hybrids and Parents

The analyses of variance of the complete diallel and of the half-diallel tables showed that $\underset{\sim}{a}$ values were highly significant for all six traits tested

Table 1. *Mean values of parents (underlined) and F_1 hybrids in a four-parent diallel cross (1966 dry season)*

Character	Female array	Male array			
		Sigadis	Dawn	H-4	Sukhwel-20
Seeding-to-heading period (days)	Sigadis	**101**	79	84	75
	Dawn	77	**82**	79	71
	H-4	83	80	**93**	71
	Sukhwel-20	75	72	70	**68**
Plant height (cm)	Sigadis	**189**	201	189	160
	Dawn	200	**155**	197	168
	H-4	188	197	**181**	152
	Sukhwel-20	159	160	151	**114**
Panicle length (cm)	Sigadis	**34**	32	33	28
	Dawn	32	**29**	31	29
	H-4	32	32	**32**	28
	Sukhwel-20	28	29	27	**23**
Panicle number (per plant)	Sigadis	**19**	17	22	32
	Dawn	18	**8**	15	27
	H-4	23	17	**20**	30
	Sukhwel-20	30	24	32	**34**
Panicle weight (g)	Sigadis	**7.64**	4.03	7.32	4.77
	Dawn	3.98	**5.95**	4.76	3.96
	H-4	7.78	4.74	**7.44**	4.74
	Sukhwel-20	4.61	4.78	4.03	**2.11**
Spikelet number (per panicle)	Sigadis	**280**	238	273	189
	Dawn	252	**296**	300	185
	H-4	281	319	**256**	206
	Sukhwel-20	208	206	188	**144**

(Table 3) and the D component was highly significant in nearly all cases (Table 4), indicating that the additive effects were largely due to genetic variation among the parents. The very high levels of significance of $\underline{a}$ and the high levels of D in six traits indicate that additive gene action played a primary role in these crosses.

The analyses also showed that the $\underline{b}$ values were highly significant in all six traits (Table 3), indicating the role of dominance at some of the loci. Among the components of $\underline{b}$, $\underline{b}_1$ values were consistently significant at the 0.1 percent level in all traits except spikelet number, suggesting that the dominance was largely iso-directional. Unequal distribution of dominant genes among

Table 2. *Mean values of parents (underlined), F_1 hybrids and F_2 populations (in parentheses) in the half-diallel set (1967 dry season)*

Character	Female array	Male array			
		Sigadis	Dawa	H-4	Sukhwel-20
Seeding-to-heading period (days)	Sigadis	**110**	90	92	95
	Dawn	(96)	**92**	87	80
	H-4	(98)	(94)	**99**	83
	Sukhwel-20	(89)	(83)	(86)	**81**
Plant height (cm)	Sigadis	**165**	172	166	143
	Dawn	(168)	**142**	170	144
	H-4	(163)	(167)	**160**	144
	Sukhwel-20	(145)	(139)	(141)	**103**
Panicle length (cm)	Sigadis	**31**	29	30	28
	Dawn	(30)	**27**	29	26
	H-4	(30)	(29)	**30**	27
	Sukhwel-20	(26)	(25)	(25)	**20**
Panicle number per plant	Sigadis	**15**	15	17	23
	Dawn	(13)	**6**	13	19
	H-4	(17)	(14)	**15**	22
	Sukhwel-20	(21)	(18)	(23)	**26**

Table 3. *Levels of significance from the analyses of variance of the F_1 diallel sets (1966 and 1967)*

S. V. / Trait	a		b		b_1		b_2		b_3		c	d
	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967
Seeding-to-heading period	***	***	***	***	***	***	***	*	***	—	—	—
Plant height	***	***	***	***	***	***	***	*	—	—	—	—
Panicle number	***	***	***	***	***	***	—	*	—	—	—	—
Panicle length	***	***	***	***	***	***	***	*	*	—	—	—
Panicle weight	***		***		***		***		***		—	—
Spikelet number per panicle	***		***		—		—		***		—	—

—=Probability >.05
*=Probability .05-.01
**=Probability .01-.001
***=Probability <.001
Blank=No data

parents was indicated by the highly significant values of $\underline{b}_2$ for seeding-to-heading period, for plant height, and panicle length in both seasons, for panicle weight in the 1966 season, and for panicle number in the 1967 season. The highly significant values of $\underline{b}_3$ for seeding period, panicle weight, and spikelet number, and the significant value for panicle length in the 1966 complete-diallel set implied that the residual dominance effect might have been caused by dominance×additive effects or dominance×dominance effects. However, in the half-diallel set grown in 1967, the $\underline{b}_3$ values were below the 5-percent significance level for all four traits examined.

The presence of the dominance effect was substantiated by the significant values of the H_1 component (Table 4) for seeding-to-heading period, plant height, panicle number, and panicle length (in 1967 season only). The asymmetry of dominant genes with respect to positive and negative effects on seeding-to-heading period, panicle number, plant height, and panicle length (1967 season only) was indicated by the significant H_2 component. Significant and positive F values, suggesting an excess of dominant alleles, were obtained for panicle number, panicle length, and plant height (1967 season only). Negative and significant F values were found for panicle number (1966 season only), indicating an excess of recessive alleles. The ratios of K_D/K_R (Table 5) for the above traits generally agreed with the F values.

Ratios computed from the above genetic components provide information on the degree, order, and direction of dominance in the inheritance of the traits. Incomplete or partial dominance was indicated for the seeding-to-heading period, plant height, panicle length, panicle number, and spikelet number, since the $(H_1/D)^{\frac{1}{2}}$ estimates were smaller than one (Table 5). The ratio exceeded one for panicle weight, suggesting overdominance. Regression coefficients of the parent-progeny covariances (W_r) on variances of the arrays (V_r) approached the theoretical slops of 1.0 in five traits, and the slope of the regression lines lay significantly above the point of origin, indicating partial mean dominance over all loci (Table 5). In the case of panicle weight, since the significance of the regression coefficient of W_r on V_r and the correlation coefficient between parental measurement (Y_r) and the order of dominance (W_r+V_r) were below the 5-percent level of significance, the overdominance indicated by $(H_1/D)^{\frac{1}{2}}$ could be confounded with complementary gene action (Allard 1956, Johnson 1963).

The proportion of $H_2/4H_1$ (Table 5) estimates the average frequency in the parents of positive (u) versus negative (v) alleles of genes that exhibit dominance. All ratios for the six traits in both seasons were less than 0.25, indicating unequal proportions of dominant and recessive alleles. Similarly, most of the K_D/K_R ratios also exceeded one. The estimates generally agreed

Table 4. *Genetic components in the F_1 diallel sets (1966 and 1967) and their levels of significance*

Trait	D		H_1		H_2		F		h^2		E	
	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967
Seeding-to-heading period	209**	75**	131*	48*	123*	46**	82#	28#	391**	187**	0.34	1.02
Plant height	1,153**	392**	720**	142**	576**	126**	120#	62*	1,138**	443*	3.75	9.13
Panicle number	112**	35**	17*	4*	16*	4*	-16*	7*	52**	16**	1.36	0.40
Panicle length	33**	13**	7#	4*	5#	3**	13*	7**	9*	4**	0.58	0.21*
Panicle weight	7**		5		5		3		11**		0.05	
Spikelet number per panicle	4,944**		1,853		1,671		-366		68		128	

Different from zero at P=.10-.05
* Different from zero at P=.05-.01
** Different from zero at P=<.01

Table 5. *Ratios between genetic components and their levels of significance in the F_1 population*

Trait	$(H_1/D)^{\frac{1}{2}}$		$H_2/4H_1$		h^2/H_2		K_D/K_R		r between Y_r & (W_r+V_r)		b of W_r/V_r	
	1966	1967	1966	1967	1966	1967	1966	1967	1966	1967	1966	1667
Seeding-to-heading period	0.79	0.80	0.24	0.24	3.17	4.10	1.62	1.62	.859**	.887**	.897**	.856**
Plant height	0.79	0.60	0.20	0.22	1.98	3.50	1.14	1.30	-.763**	-.952**	.833**	.956**
Panicle number	0.38	0.34	0.24	0.23	3.26	4.11	0.69	1.78	-.938**	-.811**	1.043**	.940**
Panicle length	0.46	0.53	0.19	0.18	1.62	1.48	2.43	3.26	-.638*	-.887**	.875*	1.011**
Panicle weight	1.18		0.20		2.86		1.69		.295		.843	
Spikelet number per panicle	0.61		0.23		0.39		0.70		.679*		.640**	

* =Probability .05-.01

** =Probability <.01

with the information obtained from H_2 concerning the unequal distribution of positive and negative alleles in the parents.

The ratio h^2/H_2 (Table 5) provides an estimate of the number of groups of genes which exhibit some degree of dominance. Three to four groups might affect in panicle number and seeding-to-heading period. Panicle weight might be affected by three groups, plant height by two to four groups, and panicle length by two groups. For spikelet number, no difference in major gene groups was greater than one.

The graph of standardized deviations (Fig. 1) for parental measurement and the order of dominance showed that the postive (fo lateness) and negative (for earliness) genes were nearly equal in frequency but different in the magnitude of their individual effects in controlling the period from seeding to heading. However, dominance at all loci was negative for earliness. The order of dominance among the parents for heading duration was Sukhwel-20>Dawn>H-4>Sigadis.

For plant height, positive dominant genes exceeded the recessive genes, and partial dominance was positive for tallness over all loci. The tall Sigadis and H-4 appeared to carry most of the dominant alleles, while the short Sukhwel-20 had most of the recessive alleles, and the intermediate Dawn probably carried a nearly equal proportion of dominant and recessive genes. All four-parent arrays showed shifts between years with respect to parental order of dominance (Figure 1), probably because of genotype-environment interaction. However, the parental order of dominance remained Sigadis> H-4>Dawn>Sukhwel-20.

The dominance effect for panicle number indicated that positive genes of unequal strength controlled the high panicle count. The order of dominance in parental arrays was Sukhwel-20>H-4>Sigadis>Dawn in 1966 and Sukhwel-20>Sigadis>H-4>Dawn in 1967. In the Sigadis array, this trait shifted appreciably on the (W_r+V_r) axis between the two seasons, indicating interaction with environment.

For panicle length, partial dominance was positive for longer panicles. The parental order of dominance was Dawn>H-4>Sigadis>Sukhwel-20 in 1966. It was modified in 1967 into H-4>Dawn>Sigadis>Sukhwel-20. There were more dominant alleles than recessive alleles.

Considering panicle weight, dominance was positive for heavier panicles in the array involving Dawn. In the array involving Sukhwel-20, the negative effect of weakly dominant genes controlled light panicles. However, the mean degree of dominance was largely heavier panicles. The parental order of dominance was Dawn>Sukhwel-20>H-4>Sigadis.

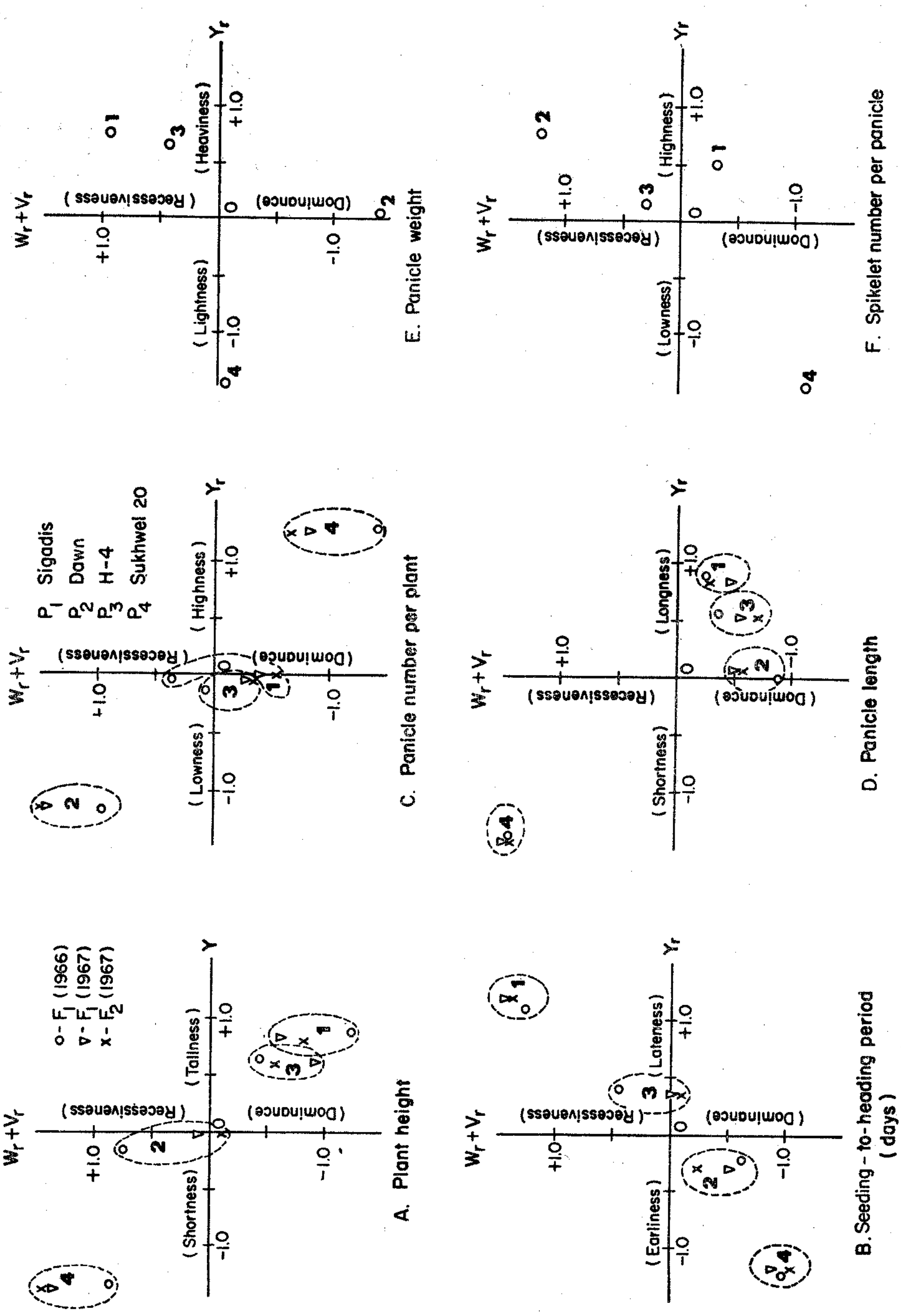

Fig. 1. Y_r and W_r+V_r graph in 4-parent diallel cross, showing parental measurements and parental order of dominance.

For the number of spikelets on each panicle, the asymmetry of the positive and negative effects of the dominat genes was indicated by the widely dispersed distribution on the (W_r+V_r) axis of the three arrays involving parents with high spikelet number. Thus, Sigadis was positively dominant for high spikelet number, while Sukhwel-20 had a negative effect. There seemed to be more recessive alleles than dominant ones.

The environmental component E (Table 4) was significant only for panicle length in the 1967 season.

The relative position of the four parents with respect to parental performance and the recessiveness-dominance indicator (W_r+V_r) are presented in Figure 1. Dominance for early heading and high panicle number was most pronounced in Sukhwel-20. Recessive genes for low panicle number and low spikelt number were most pronounced in Dawn. Similarly, recessiveness for short culm, short panicles, and light panicles was well expressed by sukhwel-20.

Experiment Involving F_2 progenies and Parents

The analyses of variance of the F_2 data obtained in 1967 again showed that the additive effect was highly significant in all four traits studied (Table 6). The highly significant values of the D component verified the preponderant role of additive gene action. The significant $\underline{b}$ values indicated that dominance at some loci was operating in each of the traits measured. The H_1 component showed that the dominance effect was significant at the 5-percent level for seeding-to-heading period and panicle length. The asymmetry of dominant genes was indicated by the significant H_2 components in each of these two traits. On the other hand, the highly significant values of the h^2 component suggested that dominance effect was iso-directional over all loci for the four traits.

Table 6. *Genetic components and their ratios in the F_2 progeny (1967 data)*

Components Trait	D	H_1	H_2	h^2	E	$(H_1/D)^{\frac{1}{2}}$	$H^2/4H_1$	b^2/H_2
Seeding-to-heading period	**	*	*	**	—	0.42	0.23	3.62
Plant height	**	#	#	**	*	0.39	0.25	4.80
Panicle number	**	#	—	**	—	0.32	0.21	3.18
Panicle length	**	*	*	**	**	0.26	0.15	3.23

—=Probability $>.01$
#=Probability .10-.05
*=Probability .05-.01
**=Probability $<.01$

When the H_1 component in the F_2 generation was multiplied by 4, the adjusted estimates for the four traits ranged between 0.52 and 0.84, indicating

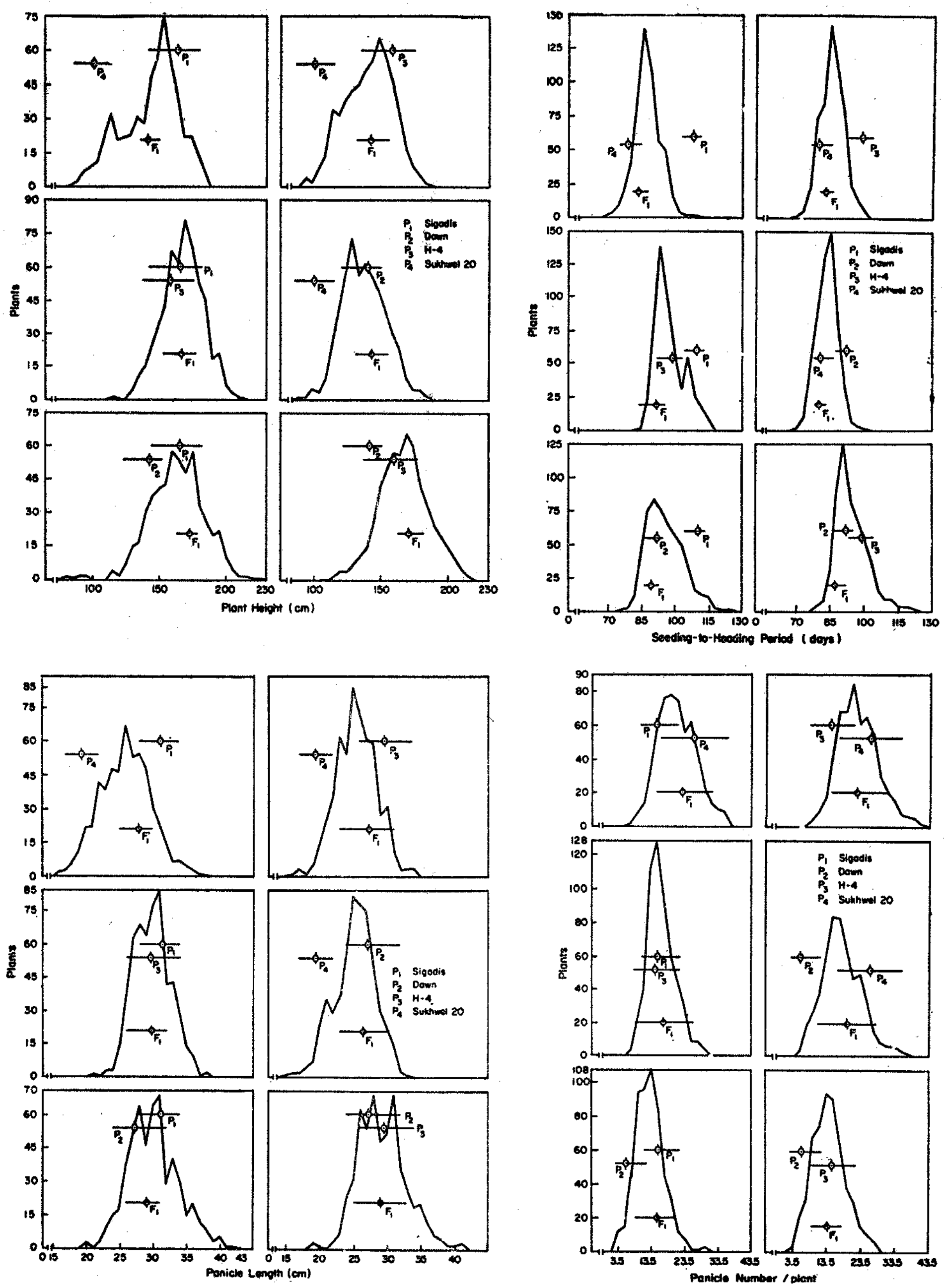

Fig. 2. Distribution and means of parents, F_1 and plants by plant height, panicle length, seeding-to-heading period, and panicle number in the six crosses. Solid horizontal lines indicate the range of parents and F_1 hybrids about the means (dotted circles). 1967 dry season.

a level equivalent to partial dominanc in the F_1 generation (Johnson and Aksel 1959).

The ratio between genetic components H_1 and D indicated partial dominance and varying degrees of asymmetry in the distribution of dominant genes for each of the traits concerned.

The estimated number of gene groups operating in the F_2 populations was four for seeding-to-heading period, five for plant height, three for panicle number and two for panicle length.

Following the method of Weber and Moorthy (1952), the heritability estimates based on F_2 phenotypic variance and an environmental variance calculated from parental and F_1 values were high in the six crosses for sowing-to-heading period (87–96%), moderately high for plant hight (65–92%) and panicle length (61–84%), and moderately low for panicle number (39–55%). In the absence of F_2 data, the hertability estimates for panicle weight and spikelet number were computed from F_1 data by the formula of Crumpacker and Allard (1962). The mean values were moderately high for panicle weight (76%) and moderately low for spikelet number (56%). Some of the variability in heritability estimates among crosses could be ascribed to crosses involving Dawn which showed varying degrees of spikelet sterility.

The distribution of the F_2 plants for each of the four traits was continuous and mostly unimodal (Fig. 2). For panicle length, transgressive segregation occurred in five crosses especially at the upper end of the distribution. A small degree of non-isodirectional allelic distribution was detected among the genes controlling heading date and those affecting panicle number. The moderately skewed or bimodal distribution in several instances could have been affected by the unequal frequency of dominant and recessive alleles in the parents or by the lack of isodirectional distribution, or by both.

Discussion

Analyses of our diallel tables indicate that both additivity and dominance are involved in the inheritance of the six traits. The predominance of additive gene effect is amply demonstrated by the highly significant $\underline{a}$ and D values. The effect of dominance at some of the loci is also obvious from the highly significant values of $\underline{b}$ in all cases and the significant estimates of H_1 and h^2 components in most of the populations. The additive effect however, appears much greater than the dominance effect, as indicated by the large differences between the D and H_1 components (Table 4), except for panicle weight (in 1966) which could have been affected by spikelet sterility in crosses involving Dawn. The epistatic fraction appears negligible.

This picture agrees with results generally obtained in self-pollinated plant species (Matzinger 1963), particularly wheat (Whitehouse *et al.* 1958, Crumpacker and Allard 1962, Kronstad and Foote 1964; Jackson *et al.* 1968). But the reletive magnitude of the dominance effects in this series of rice crosses exceeds those of similar agronomic traits reported from other self-pollinated crops such as wheat (Crumpacker and Allard 1962, Kronstad and Foote 1964), barley (Johnson and Aksel 1959, Aksel and Johnson 1961, Johnson and Aksel 1964) and tobacco (Jinks 1954, Povilaitis 1966). Since three parents in our study (H-4, Sigadis, and Sukhwel-20) are rather primitive varieties and represent extreme types, they are likely to carry more dominant loci than the elite cultivars used in the experiments on barley, wheat, and tobacco.

Our findings generally agree with those obtained by Wu (1968) in a 5-parent diallel set of rice crosses, except that he obtained larger estimates of H_1 than of D for spikelet number per panicle and number of primary branches on the panicle.

Our results on heading date are similar to those obtained by Heu and Chae (1968) in their short-day planting of a seven-parent, half-diallel set at IRRI (Los Baños). But their data on growth duration involved the interaction of prevailing environmental factors with the photoperiod or the thermosensitivity of four of the parents, or with both.

The role of the effect of dominance at some loci in this study appears sufficiently interesting to warrant further evaluation. Averaged over all genes, incomplete dominance was indicated in all traits, except panicle weight for which the $(H_1/D)^{\frac{1}{2}}$ value fell within the overdominance range. The non-significant regression value of W_r on V_r for panicle weight was 0.843, indicating the probable presence of non-additive interaction due to complementary gene action. In his diallel cross of waxy rice cultivars, Wu (1968) obtained overdominance for heading date, number of spikelets per panicle, and number of primary branches on the panicle. He also attributed the inflated $(H_1/D)^{\frac{1}{2}}$ values to complementary gene action. We expected to detect overdominance in our experiments because we included extremely different parents, but this expectation was not fulfilled.

A comparison of the 1966 F_1 data with those of 1967 indicates that the additive effects were quite stable and agreed with the findings in wheat by Crumpacker and Allard (1962). On the other hand, some of the parents did not maintain the same dominance relationship with respect to plant height and panicle length in the two seasons, indicating interaction with environment. But the shift in the parental level of dominance probably balanced one another, since the mean dominance relationship over all arrays was not altered.

The unstable nature of the dominance effect also noted in an earlier study on tobacco by Allard (1956).

The asymmetry in the distribution of dominant and recessive genes in the parents was more pronounced for panicle number, panicle length, and spikelet number. The F values suggest an excess of dominant alleles for plant height and panicle length and a preponderance of recessive alleles for panicle number (in 1966). The K_D/K_R ratios show an excess of dominant alleles for the period from seeding to heading, plant height, panicle weight, and, particularly, panicle length. Recessive alleles exceeded the dominant ones in the case of spikelet number. Panicle number varied markedly in the K_D/K_R ratio between the two seasons. However, the excess of dominant alleles for panicle weight was not supported by the non-significant correlation coefficient between Y_r and W_r+V_r), probably because of complementary gene action (Allard 1956, Johnson and Aksel 1959) or transgressive segregation (Johnson and Eunus 1964).

The F_1 hybrids of different crosses showed good consistency in direction of dominance in the two seasons. For seeding-to-heading period the average dominance of all loci was for earliness. The dominance effects for all five other traits ware positive for higher counts or heavier measurements. Wu (1968) arrived at the same conclusion. Mohamed and Hanna (1965) and Heu *et al.* (1968) also reported that long panicles were partially dominant to short ones and that the two "effective factor pairs" controlling panicle length were unequal in dominance. The results for maturity agree with our earlier findings (Chang *et al.* 1969) in which a short basic vegetative phase was dominant to a long one and the earliness genes (*Ef*) for short basic vegetative phase showed varying degrees of dominance and cumulative effect.

Maternal effects and variation in reciprocal crosses were not found in the F_1 populations grown in 1966.

Hertiability estimates in this study show that a major part of the total phenotypic variability in this diallel set is genetically controlled by additive or additive×additive variance, or by both. The estimates were rated high for the seeding-to-heading period, moderately high for plant height, panicle length, and spikelet number per panicle, and moderately low for panicle number and panicle weight. Wu (1968) also obtained a high heritability estimate for plant height, but low estimates for panicle branches and heading dates.

Various estimates of genetic components and their ratios obtained from the F_2 progenies generally substantiated those derived from the F_1 hybrids. Additive effects for all traits again were from highly significant to significant. The dominance effect was reduced in significance, as expected from the F_2 generations self-pollinated species where linkage of some loci (Hayman 1958) or gene interaction (Johnson and Aksel 1959) might be involved.

Nevertheless, the dominance effect over all loci (h^2) was pronounced in all traits. Moreover, the mean dominance, the relative distribution of positive and negative alleles, the direction of dominance effect, the number of loci showing dominance, and heritability estimates agreed closely with those obtained in the F_1 generation. Johnson and Aksel (1959) pointed out that the proportion of positive alleles to negative ones at loci exhibiting dominance is not affected by the advance in generation as long as dominance in a segregating population can be detected.

The sum of W_r+V_r has been suggested as a measure of genetic diversity among parents and could be used to indicate the magnitude of variances to be expected in segregating generations (Crumpacker and Allard 1962). The application of the (W_r+V_r) values obtained in the F_1 set of this study, however, failed to confirm the maximum range of distribution indicated by the F_2 populations.

The environment component of variation (E) appears significant only for panicle length (1967 F_1 and F_2), and plant height (1967 F_2). These traits are more susceptible to environmental influence whose effect is more clearly seen in the F_2 plants among which competition is more pronounced in segregating progenies of different height, maturity, and tillering ability.

The six traits have so far been treated as independent of one another. In previous investigations, plant height and panicle length were reported to be positively correlated (Chang *et al.* 1965; Mohamed and Hanna 1965), while panicle number and panicle weight were negatively correlated (Nei 1960). Likewise, the contribution of these traits to grain yield may be quite different from the rather simple genetic system found in each trait. The complexity of predicting and analyzing yielding ability, based on diallel analysis of individual yield components which involves interaction both among genes and between component traits is illustrated by the analysis of wheat grain yield in a four-parent diallel set (Whitehouse *et al.* 1958).

As mentioned earlier, parents chosen for this study, confine it to the restricted model (I) of Hayman (1960) from which only certain inferences about the parents can be drawn. The three tropical parents (Sigadis, H-4, and Sukwel-20) in this study, however, are largely representative of the photoperiod-insensitive cultivars grown in the tropics and Dawn could represent the directly sown cultivars of the North and South America. Since the four parents are unrelated, some information obtained from this diallel set may be extended to many varietal types grown in the tropics, if the correlated effects of the short stature gene in Taiwan's semi-dwarfs or of the photoperiod-sensitive gene (or genes) in tropical indicas on height, panicle number, and length are not involved. Interestingly our findings and those of Wu (1968) agree closely for plant height, panicle number, panicle length, and spikelet number per panicle, although the parents used in the two studies are unrelated.

水稻農藝性狀之完全互交法分析

李成章 張德慈

利用完全互交法（Diallel cross method），選揀具有極大表現型差異之四個水稻栽培種，試驗包括 p^2 組合 [p 個親本，$\frac{1}{2}p$（p-1）之 F_1 雜種，$\frac{1}{2}p$（p-1）反交之 F_1 雜種與 $\frac{1}{2}p$（p-1）之 F_2 雜種] 之材料，種植二季，用以研究六個數量性狀（自下種至抽穗日數、株高、每株穗數、穗長、穗重與每穗小穗數）之遺傳體系。今將本試驗結果總括如下：

由完全互交法之分析，各性狀顯示四親本間具有顯著之遺傳變異，此種變異大半係由因子之相加性效應（additive effect）與因子之顯性效應（dominance effect）所致。但在每一性狀內間接表指因子間具有微小之交感作用。

在此六種性狀中未見母系作用（maternal effect）之徵象。穗長略具有遺傳因子與環境之交感作用，其他五種性狀之 F_1 則均呈微小之作用，換言之，該五種性狀之因子相加性作用與顯性作用 [指六個親本之顯性秩序（order of dominance）與顯性方向（direction of dominance)] 在不同季節下祇表現微小之變異現象。

在控制六種不同性狀之因子座（loci）間，一穗穗重呈超顯性（overdominance），而其他五種性狀內則呈部分顯性（partial dominance）之現象。在 F_1 與 F_2 雜種中，早熟性對晚熟性呈顯性，植株高者對矮者爲顯性，穗數多者對少者爲顯性，穗長長者對短者爲顯性，穗重重者對輕者爲顯性，一穗小穗數多者對少者亦爲顯性。在具有顯性之因子間，顯性作用不論在方向與等級上，其正負因子（positive and negative gene）作用均呈不相等之分佈現象，在抽穗期、株高、穗長與穗重等性狀中，其顯性對性因子（dominant alleles）超過隱性對性因子（recessive alleles），但在一穗粒數與穗數兩性狀間則有隱性對性因子超越顯性對性因子之顯示。而且各親本所帶之顯性因子其顯性作用程度亦有所不同。

根據 F_2 估值之高度遺傳率（heritability）下證實各性狀表現型變異性之主要部分係由因子相加性作用（additive gene action）所致。抽穗期之遺傳率最高，株高、穗重與穗長次之，穗數與一穗小穗數則較低之現象。

由 F_2 所得之遺傳資料表示兩個不同年代之 F_1所得之遺傳體系（genetic system）分析大致相同。超越分雜（transgressive segregation）之現象亦于數個羣體中發現之。環境效應在 F_2 集團族羣中似乎較 F_1 植株爲高

References

ALLARD, R. W. 1956. The analysis of genetic-environmental interaction by means of diallel crosses. Genetics **41**: 305-318.

AKSEL, R. and JOHNSON, L. P. V. 1961. Genetic studies on sowing-to-heading and heading-to-ripening periods in barley and their relation to yield and yield components. Canad. J. Genet. Cytol. **3**: 242-250.

CHANG, T. T., LI, C. C. and VERGARA, B. S. 1969. Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod-sensitive phase. Euphytica **18**: 78-91.

CHANG, T. T.. MORISHIMA, H., HUANG C. S., TAGUMPAY, 0, and TATENO, K. 1965. Genetic analysis of plant height, maturity and other quantitative traits in the cross of Peta ×I-geo-tze. J. Agr. Assoc. China **51**: 1-8.

CRUMPACKER, D. W. and ALLARD, R. W. 1962. A diallel cross analysis of heading date in wheat. Hilgardia **32**: 274-318.

HAYMAN, B. I. 1954a. The theory and analysis of diallel crosses. Genetics **39**: 789-809.

HAYMAN, B. I. 1954b. The analysis of variance of diallel tables. Biometrics **10**: 235-244.

HAYMAN, B. I. 1958. The therry and analysis of diallel crosses. II. Genetics **43**: 63-85.

HAYMAN, B. I. 1960. The theory and analysis of diallel crosses. III. Genetics **45**; 155-172.

HEU, M. H. and Y. CHAE. 1968. Studies on the practical utilization of traopical rice varieties as breeding materials in Korea. 1. Studies on growth duration in remote cross breeding of cultivate rice. Res. Rept. Office Rural Develop. (Korea) **11**: 43-52.

HEU, M. H., CHANG, T. T. and BEACHELL, H. M. 1968. The inheritance of culm length, panicle length, duration to heading and bacterial leaf blight reaction in a rice cross: Sigadis×Taichung (Native) 1. Jap. J. Breed. **18**: 7-11.

JACKSON, B. R., DIRKS, V. S. and SNYDER, L. A. 1968. Quantitative inheritance in crosses among four tetraploid wheats. Canad. J. Genet. Cytol. **10**: 33-43.

JINKS, J. L. 1954. The analysis of continuous variation in a diallel cross of *Nicotiana rustica* varieties. Genetics **39**: 767-788.

JOHNSON, L. P. V. 1963. Application of the diallel-cross techniques to plant breeding. Statistical Genetics and Plant Breeding, p. 561-569. Nat. Acad. Sci-Nat. Res. Council, Washington, D. C.

JOHNSON, L. P. V. and AKSEL, R. 1959. Inheritance of yielding capacity in a fifteen-parent diallel cross of barley. Canad. J. Genet. Cytol. **1**: 208-265.

JOHNSON, L. P. V. and AKSEL. R. 1964. The inheritance of malting quality and agronomic characters in a diallel cross of barley. Canad. J. Genet. Cytol. **6**: 178-200.

JOHNSON, L. P. V. and A. M. EUNUS. 1964. Inheritance of earliness in a six-parent diallel cross of barley. Advancing Frontiers of Plant Sciences (New Delhi) **4**: 111-118.

JONES, R. M. 1965. Analysis of variance of the half diallel table. Heredity **20**: 117-121.

KRONSTAD, W. E. and FOOTE, W. H. 1964. General and specific combining ability in winter wheat (*Triticum aestivum* Vil., Host.). Crop Sci. **4**: 616-619.

MATZINGER, D. F. 1963. Experimental estimates of genetic parameters and their applications in self-fertizing plants. Statistical Genetics and Plant Breeding, p. 253-276. National Acad. Sci.-Nat. Res. Council, Washingto, D. C.

MOHAMED, A. H. and HANNA, A. S. 1965. Inheritance of quantitative characters in rice. II. Inheritance of panicle length. Canad. J. Genet. Cytol. **7**: 406-417.

NEI, M. 1960. Studies on the application of biometrical genetics to plant breeding. Mem. Coll. Agr. Kyoto Univ. **82**: 1-100.

POVILAITIS, B. 1966. Diallel cross analysis of quantitative characters in tobacco. Canad. J. Genet. Cytol. **8**: 336-346.

WEBER, C. R. and MOORTHY, B. R. 1952. Heritable and non-heritable relationships and variability of oil content and agronomic characters in the F_2 generation of soybean crosses. Agron. J. **44**: 202-209.

WEHRHAHN, C. and ALLARD. R. W. 1965. The detection and measurement of the effects of individual genes involved in the inheritance of a quantitative character in wheat. Genetics **51**: 109-119.

WHITEHOUSE, R. N. H., THOMPSON, J. B., and DO VALLE RIBEIRO, M. A. M. 1958. Studies on the breeding of self-pollinating cereals. 2. The use of a diallel cross in yield prediction. Euphytica **7**: 147-169.

WU, H. P. 1968. Studies on the quantitative inheritance of *Oryza sativa* L. 1. and 2. Bot. Bull. Acad. Sinica **9**: 1-9, 124-138.