

GENOTYPIC CORRELATION, HETEROSIS, INBREEDING  
DEPRESSION AND TRANSGRESSIVE SEGREGATION  
OF AGRONOMIC TRAITS IN A DIALLEL CROSS  
OF RICE (*ORYZA SATIVA* L.) CULTIVARS

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**Abstract**

Progenies from a four-parent diallel cross were studied to estimate genotypic correlation between selected agronomic traits and to assess the extent of heterosis and of inbreeding depression. Plant height and the period from seeding to heading showed positive association in the  $F_2$  populations. Plant height and panicle length also showed positive correlation. The relationships between plant height and panicle number, seeding-to-heading period and panicle number, and between the seeding-to-heading period and panicle length were variable from one cross to another and the correlation coefficients were generally low.

Compared with their parents over two seasons  $F_1$  hybrids were superior to the midparent values in plant height, panicle number, panicle length, and grain yield per plant. But true heterosis (heterobeltiosis) over the high parent was not observed. The hybrids were inferior to the high parent in all the traits related to grain yield components. Inbreeding depression in the  $F_2$  was not indicated for any of the component traits of grain yield.

The lack of heterobeltiosis and of inbreeding depression could be attributed to primarily additive effect of genes controlling the yield component traits. Non-allelic interaction was detected for plant height and panicle number, but it was low. Spikelet sterility in three cross contributed to the lack of heterosis in grain yield. Hybrid sterility could also restrict the full range of recombinations attainable in the  $F_2$  populations concerned.

Transgressive  $F_2$  segregates having extreme earliness, high panicle number, and long panicles were carried into the  $F_3$  and  $F_4$  generations. The segregates lost their superiority largely in the  $F_4$  generation.

**Introduction**

Recent advances in tropical rice breeding resulted from conventional hybridization efforts which recombined the short stature, erect and relatively short leaves, early maturity and insensitivity to photoperiod, tillering ability

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and early growth vigor of Taiwan's semidwarfs with the vegetative growth vigor, disease and insect resistance, grain dormancy, and grain quality of the tall, late, tropical cultivars. Among these traits, the simply inherited and highly heritable nature of semidwarfism, the basic vegetative phase of the growth duration, and photoperiod response have been thoroughly studied (Chang *et al.*, 1965; Aquino and Jennings, 1966; Heu, Chang and Beachell, 1968; Chang, Li and Vergara, 1969). Li and Chang (1970) recently studied the system of genes controlling agronomically significant quantitative traits such as plant height, heading date, panicle number, panicle weight, and number of spikelets per panicle in non-dwarf cultivars through the diallel analysis method.

Sufficient data were collected from hybrid progenies of the four-parent diallel cross involving extremely diverse parents (Li and Chang, 1970) to provide information on the genotypic correlation between traits and to assess the magnitude of  $F_1$  heterosis and of  $F_2$  inbreeding depression. The breeding behavior of  $F_2$  plants that showed transgressive segregation was followed in three crosses by progeny testing. This paper presents information on these aspects in the self-pollinated rice crop.

#### Materials and Methods

Four extremely different varieties—Sigadis (from Indonesia), H-4 (from Ceylon), Dawn (from U.S.A.), and Sukhwel-20 (from India)—were selected from relatively early maturing, essentially photoperiod-insensitive, and relatively cross-fertile cultivars. The parents and one set of reciprocal  $F_1$  hybrids were grown in a flooded bed at Los Baños, Philippines in the 1966 dry season (January to May) in a randomized complete block with four replications. Each plot included 16 plants spaced  $40 \times 30$  cm. Fertilizers were applied at 60-30-30 kg/ha. Information was obtained on date of heading of the first emerging panicle, plant height, panicle number, mean weight of three panicles per plant, mean length of three panicles, number of spikelets and of fully developed grains on each panicle, and grain yield per plant.

A half-diallel set was grown in the dry season of 1967. The planting consisted of the four parents, six non-reciprocal  $F_1$  populations, and six  $F_2$  populations, replicated twice. The plots contained 30 parent plants, 10  $F_1$  plants, and 280  $F_2$  plants. Data were taken on heading date, plant height, panicle number, and panicle length.

Large  $F_2$  populations of 3,000 plants each from two crosses that had earlier indicated transgression were planted in the 1968 wet season to isolate transgressive segregates. Plants that either produced more tillers than the high parent, or gave longer panicles than the high parent, or exerted panicles earlier than the early-maturing parent were harvested and grown as a line of

21 plants each. Data were taken on 10 randomly sampled plants per line. From  $F_3$  lines that surpassed the extreme parent in one of the mentioned characters, seeds sampled from the recorded plants were grown as  $F_4$  lines in the 1969 wet season. Data were again taken from 10 plants in each line.

Genotypic correlation coefficients were calculated from the  $F_2$  and non-segregating  $F_1$ ,  $P_1$ , and  $P_2$  populations, based on phenotypic variances and covariances by the method outlined by Weber and Moorthy (1952).

Superiority of  $F_1$  hybrids was estimated on the basis of heterosis—mean increase of  $F_1$  hybrids over the midparent value (MP) of parents (Matzinger, Mann and Cockerham, 1962)—and on heterobeltiosis—mean increase of  $F_1$  hybrids over the high parent (HP) (Fonseca and Patterson, 1968). Average inbreeding depression was measured by the mean difference between the  $F_1$  and  $F_2$  populations.

Non-allelic interaction was estimated by the deviation of the mean  $F_1$  hybrids and MP from the  $F_2$  mean expressed as percentage of the MP:  $100 \times [F_2 - \frac{1}{2}(F_1 + MP)] / MP$  (Jinks, 1955).

## Results and Discussion

### *Genotypic Correlation in $F_2$ Populations*

The phenotypic and genotypic correlation coefficients between pairs of traits in the  $F_2$  populations of six crosses are in Table 1. Plant height and the period from seeding to heading produced highly significant and positive phenotypic coefficients ( $r_{ph}$ ) in all crosses. The positive association between plant height and growth duration agrees with previous findings in studies of a large group of pureline cultivars (Vergara *et al.*, 1966; Guevarra and Chang, 1965) although such an association may not apply to the progenies of a tall  $\times$  semidwarf cross (Chang *et al.*, 1965; Heu, Chang and Beachell, 1968; Chang and Tagumpay, 1970). The genotypic correlation values ( $r_g$ ) in this study were rather low, however, ranging from 0.173 to 0.466, because dominance for plant height was toward tallness while dominance for the heading date was toward earliness (Li and Chang, 1970).

The correlation coefficients for plant height and panicle number varied from cross to cross and showed no consistent trend. In such a segregating population, the competition between tall and short plants might affect the expression of panicle number because mutual shading would prevent the late tillers of short plants from developing into panicles.

The association between the seeding-to-heading period and panicle number was variable and the correlation coefficients were rather low. Four crosses produced negative coefficients, of which only one was significant.

Plant height and panicle length were positively correlated in all crosses

**Table 1.** Phenotypic and genotypic correlations between all pairs of four traits in  $F_2$  plants of six crosses

phenotypic correlation coefficients are on right of the diagonal;  
the genotypic correlation coefficients, on the left

Trait	Cross	Plant height	Days to head	Panicle number	Panicle length
Plant height	Sigadis × H-4		0.242**	-0.180**	0.453**
	Sigadis × Dawn		0.201**	0.123**	0.537**
	Sigadis × Sukhwel		0.433**	0.033n. s.	0.452**
	H-4 × Dawn		0.196**	0.007n. s.	0.534**
	H-4 × Sukhwel		0.406**	-0.106n. s.	0.529**
	Dawn × Sukhwel		0.189**	-0.002n. s.	0.311**
Days to head	Sigadis × H-4	0.308		0.029n. s.	0.397**
	Sigadis × Dawn	0.207		-0.065n. s.	0.301**
	Sigadis × Sukhwel	0.490		0.070n. s.	0.277**
	H-4 × Dawn	0.220		-0.026n. s.	0.323**
	H-4 × Sukhwel	0.466		-0.079n. s.	0.075n. s.
	Dawn × Sukhwel	0.173		-0.096*	-0.170**
Panicle number	Sigadis × H-4	-0.410	0.049		-0.058n. s.
	Sigadis × Dawn	0.139	-0.088		0.009n. s.
	Sigadis × Sukhwel	0.020	0.187		0.018n. s.
	H-4 × Dawn	-0.028	-0.031		-0.043n. s.
	H-4 × Sukhwel	-0.231	-0.099		-0.045n. s.
	Dawn × Sukhwel	-0.064	-0.122		-0.020n. s.
Panicle length	Sigadis × H-4	0.429	0.520	-0.119	
	Sigadis × Dawn	0.604	0.378	0.016	
	Sigadis × Sukhwel	0.490	0.318	0.020	
	H-4 × Dawn	0.657	0.437	-0.114	
	H-4 × Sukhwel	0.722	0.109	-0.262	
	Dawn × Sukhwel	0.392	-0.209	-0.057	

\*, \*\* Significant at 5% and 1% levels.

n. s. Non-significant.

( $r_g$ : 0.392 to 0.722). This association agrees with the previous findings of Syakudo *et al.* (1952) and Chang *et al.* (1965). Nei (1960) also noted a positive correlation between culm length and panicle length in the  $F_2$  lines.

Panicle length showed a positive and significant association with the seeding-to-heading period in four crosses, a negative association for one cross, and a non-significant correlation in another. The coefficients were relatively low however. Nei (1960) found a positive correlation between the two traits in the  $F_4$ , but a negative correlation in the  $F_2$  lines.

Panicle length and panicle number did not appear to be strongly associated.

The  $F_2$  populations involving Dawn produced some partially sterile plants. The sterility found in those crosses involving Dawn could have affected the pattern of genotypic correlations.

#### *Heterosis and Inbreeding Depression*

The data on the reciprocal  $F_1$  hybrids (1966 experiment) were combined for each cross combination since the reciprocal hybrids were not significantly different (Li and Chang, 1970). Comparison of parents and  $F_1$  populations in each of the two seasons indicated similar differences for estimates of heterosis and heterobeltiosis (Table 2). The  $F_1$  means exceeded the average midparent values in plant height, panicle number, panicle length, and grain yield per plant. In seeding-to-heading period, panicle weight, and spikelet fertility, they were inferior to the midparent values. The  $F_1$  hybrids were inferior at the 1-percent level of significance to the high parent in all traits studied except plant height. Among the  $F_1$  populations grown in 1966, the highest  $F_1$  mean for grain yield (105.7 g/plant) was obtained from the H-4 array, but it was lower than the yield of the two high parents (120.6 g. for Sigadis and 121.1 g. for H-4) (Figure 1).

**Table 2.** Average percent of  $F_1$  performance over midparent and high parent values and percent  $F_2$  depression from  $F_1$  for eight agronomic traits

Trait	$F_1$ -MP MP		$F_1$ -High parent High parent		$F_1$ - $F_2$ $F_1$
	1966	1967	1966	1967	1967
Days to heading	-11.15**	- 9.48**	-19.76**	-16.37**	-5.43**
Plant height	10.83**	10.23**	- 2.06n. s.	- 1.77n. s.	1.64n. s.
Panicle number/plant	18.31**	20.25**	-10.17**	- 9.56*	3.31n. s.
Panicle length	5.73**	5.67*	- 6.13**	- 5.75**	2.24n. s.
Panicle weight	-13.81**		-32.06**		
Spikelet number	- 2.34n. s.		-17.23**		
Grain yield	8.05**		- 5.06**		
Spikelet fertility (%)	-17.16**		-20.62**		

\*, \*\* Significant differences from zero at 5% and 1% levels.

n. s. Non-significant.

Reports in rice literature consistently show  $F_1$  superiority expressed in plant height, tiller or panicle number, and in several cases, panicle length. The heterobeltiosis in these traits associated with vegetative vigor may be interpreted as "luxuriance" or competitive advantage in a mixed stand (Ramiah and Ramasamy, 1941; Jennings and Herrera, 1968; Kawano, Kurosawa and

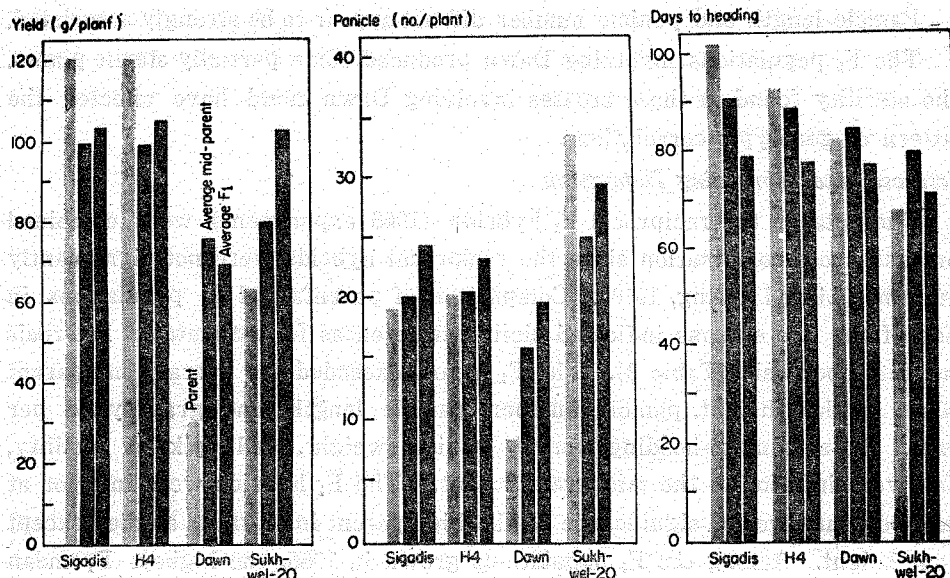


Fig. 1. Parent, midparent, and F<sub>1</sub> means for yield, panicle number, and number of days from seeding to heading obtained from six rice crosses.

Takahashi, 1969). The F<sub>1</sub> hybrids flowered earlier than the midparental values, consistent with the interpretation based on dominant anisomeric genes controlling the basic vegetative phase (Chang, Li and Vergara, 1969). For grain yield, only a few experiments in previous studies involved an adequate sample size to provide valid comparisons. In a large number of hybrids, the F<sub>1</sub> yield was below the midparent value (Jones, 1926; Kadam, Patil and Patankar, 1937; Jennings, 1967; Karunakaran, 1968). In experiments where some of the F<sub>1</sub> hybrids were reported to be superior in yield, the difference between the parents and the hybrids was generally about 10 percent (Jones, 1926; Madhusudhana Rao, 1965; Lee *et al.*, 1968). Only rarely did the F<sub>1</sub> hybrids exceed the high parent by a greater margin (Hsu *et al.*, 1969; Chang, Lin and Yang, 1971; Chang and Lin, 1972). In crosses among japonicas, rice breeders in California reported yield increases from 122 to 210 percent over the better parent in eight out of 19 hybrids, mainly because of increase in panicle number and number of seeds per panicle. But the yield differences may not be the same under commercial cultural practices (Carnahan, Erickson, Tseng and Rutger, 1972).

The failure of our hybrids to show heterobeltiosis in grain yield could be partly attributed to spikelet sterility in crosses associated with Dawn. In the three crosses involving Dawn, the F<sub>1</sub> spikelet fertility ranged from 38 to 82 percent with a mean of 54 percent. In other crosses, it ranged from 84 to 90 percent. When the crosses involving Dawn were excluded, the three remaining crosses showed a 19.8 percent increase in yield over the midparent value and

the difference was significant at the 1-percent level. Compared with the high parent, however, only the  $F_1$  plants from Sigadis $\times$ H-4 produced a mean yield of 133.5 g which exceeded that of the high parent. But the difference is non-significant.

The average performance of the  $F_1$  hybrids was slightly better than that of the  $F_2$  population means for plant height, panicle number, and panicle length but the differences were non-significant (Table 2). For the seeding-to-heading period, the  $F_1$  means were definitely shorter than the  $F_2$  means. The differences ranging from 1.7 to 5.5 percent indicate negligible inbreeding depression.

Three studies on inbreeding depression in the  $F_2$  presented divergent findings. Misro and Sastri (1962) reported  $F_2$  heterosis in plant height and growth duration in a group of wide crosses, and observed inbreeding depression only in panicle number. Lee *et al.* (1968) found that in one group of nine crosses, the  $F_2$  means were superior to the related high parents in panicle number but inferior in number of grains per panicle, 100-grain weight, and spikelet fertility. In another set of four-parent diallel cross, the  $F_2$  populations of crosses in three arrays were superior to the  $F_1$  hybrids. Chang and Lin (1972) reported a 6-percent average decrease in yield for means of  $F_1$  and  $F_2$  populations in 21 crosses. Because the size of  $F_2$  populations in the mentioned studies was limited, it was difficult to assess the true extent of inbreeding depression.

The role of non-allelic interaction in affecting heterosis and inbreeding depression was assessed on the basis of the parental,  $F_1$ , and  $F_2$  data of the 1967 experiment. Although additive and dominance effects were the predominant components of genetic variation (Li and Chang, 1970), the  $F_2$  means were not identical to the respective midparent values or  $F_1$  means. An analysis of variance of epistatic effect based on the midparent value,  $F_1$  means, and  $F_2$  means indicated a detectable interaction effect for plant height, panicle length, and especially panicle number (Table 3). Among the four parental arrays, the Dawn array showed the greatest expression of epistasis. However, the over-all extent of interaction did not appear large, as indicated by the relatively low heterosis or inbreeding depression (Jinks and Jones, 1958).

Because of the small number of parental varieties in this set of diallel crosses, the individual parents and crosses are the main objects of interest and the limited information on combining ability, either general or specific, derived from such a diallel set may not apply to broad inferences about the feasibility of using hybrid vigor in rice. But since intervarietal  $F_1$  hybrid sterility frequently occurs in varieties coming from the same geographical area (Engle, Chang and Ramirez, 1969), a large number of crosses must be studied to assess the extent of heterobeltiosis and to identify highly fertile cross combinations.

**Table 3.** *Percent epistatic effect in the array means of the 1967 experiment*

Array	Heading date	Plant height	Panicle length	Panicle number
Sigadis	-0.42n. s.	2.19n. s.	-0.09n. s.	0.72n. s.
Dawn	1.31*	2.65n. s.	2.36*	9.65**
H-4	0.54n. s.	3.19*	-0.21n. s.	10.98**
S-20	-0.85n. s.	4.15*	-1.12n. s.	2.12**
Over-all mean	0.15	3.04	0.23	5.87

\*, \*\* Significant at 5% and 1% levels.

n. s. Non-significant.

#### *Transgressive Segregates in F<sub>2</sub>, F<sub>3</sub>, and F<sub>4</sub> Populations*

Table 4 shows the breeding behavior of transgressive F<sub>2</sub> segregates with respect to tiller number, panicle length, and number of days to heading. While F<sub>2</sub>, F<sub>3</sub>, and F<sub>4</sub> progenies surpassing the high parent in tiller number or in panicle length were obtained, the breeding behavior showed a dissipating trend through three successive generations. Only a small proportion of the progenies was significantly superior to the extreme parent in tiller number or panicle

**Table 4.** *Breeding behavior of transgressive segregates on panicle length, tiller number, and earliness*

Character and cross	Generation	Number of lines giving lower or higher value than the extreme parent	
		A	B
Tiller number (Dawn × H-4)	F <sub>2</sub>	179	13
	F <sub>3</sub>	158	131
	F <sub>4</sub>	30	11
Tiller number (H-4 × Sukhwel 20)	F <sub>2</sub>	56	4
	F <sub>3</sub>	35	2
	F <sub>4</sub>	1	1
Panicle length (Dawn × H-4)	F <sub>2</sub>	169	42
	F <sub>3</sub>	165	161
	F <sub>4</sub>	36	36
Number of days to heading (Dawn × H-4)	F <sub>2</sub>	70	0
	F <sub>3</sub>	54	0
	F <sub>4</sub>	17	0
Number of days to heading (H-4 × Sukhwel 20)	F <sub>2</sub>	8	0
	F <sub>3</sub>	7	0
	F <sub>4</sub>	0	0

A numerically higher (or lower) than the extreme parent.

B significantly higher (or lower) than the extreme parent by the LSD test at 5% level (for F<sub>2</sub>, the error term used is from the variation in the parents).



length. However, those  $F_2$  and  $F_3$  progenies which appeared to be earlier than the early heading parents did not differ significantly from the extreme parent. The proportion of Dawn $\times$ H-4 plants that exceeded the high parent in tiller number or panicle length was higher in the  $F_3$  progenies grown in the dry season than in the  $F_2$  and  $F_4$  progenies grown in the wet seasons.

The means of  $F_2$  plants and  $F_3$  lines from Dawn $\times$ H-4 showed a positive correlation for tiller number and for panicle length; the  $F_3$  and  $F_4$  line means, a positive association for tiller number. Heritability estimates based on phenotypic variance, genotypic variance, and environmental components were 0.16 for tiller number in the  $F_3$  lines, and 0.20 and 0.15 for panicle length in the  $F_3$  and  $F_4$  lines, respectively.

The failure to obtain truly transgressive segregates for early maturity in the  $F_2$  and subsequent generations could be explained by the basic vegetative phase (BVP) genes largely responsible for the growth duration in photoperiod-insensitive genotypes. Since a very short BVP is controlled by the cumulative effect of several dominant *Ef* allelic pairs (Chang, Li and Vergara, 1969), the parents in this study might not have differed much in the BVP loci. Since the number of BVP loci involved was rather small, the *Ef* loci could have become largely fixed in the  $F_2$  generation.

Transgressive segregation for tiller number in Dawn $\times$ H-4 and H-4 $\times$ Sukhwel 20 and for panicle length in Dawn $\times$ H-4 dissipated from the  $F_3$  through  $F_4$ . The breeding behavior indicates that epistatic effects are rather small in the  $F_2$  (Table 3) and that they decrease rapidly with reduction in heterozygosity. It also suggests that the genetic variance due to dominance effect and the fixation of additive genetic effect decreased markedly from  $F_2$  through  $F_4$ . It is plausible that the superiority of transgressive segregates in the  $F_2$  and  $F_3$  generations resulted from additive $\times$ dominance effects and dominance $\times$ dominance effects in heterozygous combinations. Such types of gene interactions are not readily fixed in the later generations of a self-pollinated crop, especially when the size of a progeny-line is rather small (Mather and Jinks, 1971). It now appears that additive and dominance effects are more important than was indicated by the  $F_1$  data (Li and Chang, 1970).

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## 水稻完全互交後裔間的性狀相關，雜交優勢， 自交低落和越親分離的研究

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在包括四親本完全互交第二代後裔間株高與抽穗期有正相關，株高與穗長亦有正相關，株高與穗數、抽穗期與穗數、抽穗期與穗長之關係則隨不同組合而異，無一致或顯著之相關。

第一代雜種之株高、穗數、穗長與每株產量較二親本之平均值為高，但無真正之雜交優勢 (heterobeltiosis)；第一代雜種之產量構成因子性狀均不及較高之親本。第二代羣體之平均值與第一代平均值比較下並無因自交後有低落之趨勢 (inbreeding depression)。

雜交後代間缺乏雜交優勢或自交低落現象甚可能因各產量構成因子性狀大半由因子相加性效應 (additive effects) 所控制之故；不同因子間相互交感作用 (non-allelic interaction) 僅在株高及穗數上表現，但程度不高；某些雜交組合間之不孕性使第一代雜種產量減低。

超越親本之後代在第三、四代間逐漸失却在早熟、多分蘖與長穗方面之優勢，猜測為越親之因子交感作用組合經繼續自交後開始分散失效。