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HALF-DIALLEL AND F_2 ANALYSES OF CULM LENGTH IN DWARF, SEMIDWARF AND TALL STRAINS OF RICE (*ORYZA SATIVA* L.)

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Abstract

Half-diallel cross involving two dwarfs, seven semidwarfs, and two tall rice cultivars was analyzed to elucidate the gene systems governing culm length. Semidwarf, Fanny, and dwarf, Daikoku (d_1), showed an excess of dominant alleles in an eleven-parent half-diallel cross, but their position from the line of unit slope in the Vr, Wr graph showed non-allelic gene interaction. After taking out the two arrays, tall Peta showed an excess of dominant alleles, while Ai-yeh-lu Dwarf showed an excess of recessive alleles in the nine-parent half-diallel cross.

The relative order of dominance of the nine-parent half-diallel cross is as follows: Peta, IR8, BPI-76, Acc. 6993, Acc. 100027 (Intermediate-Dwarf), Taichung Native 1, FF 36, IR273 selsction, Ai-yeh-lu Dwarf.

Analysis of F_2 data indicated that Fanny Dwarf and Acc. 6993 are controlled by the same set of polymeric genes for short stature. Two or more major recessive genes control the short stature of Acc. 100027 (Intermediate-Dwarf). The extremely short stature of Ai-yeh-lu Dwarf and Daikoku (d_1) dwarf is each controlled by two major recessive genes. The four semidwarfs, IR8, Taichung Native 1, FF 36 and IR273 selection are controlled by the same major recessive gene. BPI-76 may have a set of polygenes for tallness which is different from that of Peta.

Thus, the genetic control of plant stature is relatively simple and the heritability is generally high, although many other genes with small and cumulative effect are present in every parent but in different combinations. Genotype-environment interaction complicates the manifestation of different gene systems when the crosses are planted in the dry and wet seasons. This kind of interaction may account for the difficulty in dealing with the phenotypic variability of plant height.

Introduction

One of the important components of a physiologically efficient rice plant is short and sturdy culms. The tall, vigorous-growing tropical varieties frequently lodge long before maturity during the wet season and much of the yield losses are attributable to an increase in sterile florets and incomplete grain filling. The development of short-statured, stiff-strawed, nitogen-responsive semidwarf varieties has led to substantial yield increases in many rice-growing areas. The semidwarf varieties also produce many tillers, most of which develop into grain-bearing panicles.

At present there is only one source of semidwarfing gene, originating from Dee-geo-woo-gen type, which has been intensively used in the breeding programs of many institutions, including the International Rice Research Institute (IRRI). Elucidation on the genetic control of plant height and identification of different dwarfing genes would accelerate the progress of a rice breeding program and provide genetic diversity to the commercial cultivars.

Previous studies on the inheritance of plant heigh in rice have been based on a single-cross at a time. The first study was reported by Parnell *et al.* (1922), wherein a simple Mendelian ratio of three normal to one dwarf was obtained in the F_2 of a cross between a dwarf plant (71 cm) and a normal plant (126 cm). Since then, several workers have reported simple Mendelian inheritance in the control of short stature. In crosses each involving the tall Peta and one of Taiwan's semidwarfs such as I-geo-tze or Taichung Native 1, a typical 3:1 Mendelian ratio was observed (Chang *et al.*, 1965; Aquino and Jennings, 1966; Heu *et al.*, 1968). However, in a cross between Basmati-370 and Taichung Native 1, a F_2 segregation of plant height differing from the above pattern was observed (IRRI, 1976b). In one case, a Japanese dwarf was inherited as a single dominant (Sugimoto, 1923).

A large array of dwarf, semidwarf, intermediate, intermediate-tall and tall genotypes has been acquired since the IRRI germ plasm bank project began in 1963. For the benefit of breeding programs, it is equally important to identify the inheritance of individual categories of plant stature and to know the allelic relationship between different categories. Grant (1964) has pointed out that the segregation of a quantitative character observed in the progenies of a cross does not necessarily reveal all of the multiple genes involved in the development of that character. The segregation reveals only those genes that are represented by different alleles in the two parents.

An 11-parent half-diallel crose was analyzed in this study to gain information on the systems of genes that control plant height in different categories of plant stature. Because plant height is the sum of culm length and panicle length, culm length alone was studied to minimize the complicating effects of other genes controlling panicle length.

Materials and Methods

Eleven varieties and selections representing dwarf, semidwarf and tall types in the germ plasm bank of IRRI were used in this study (Table 1).

Table 1. *Parents representing different groups of plant height*

Name & group	Parentage	Culm length (cm) in wet season
	DWARFS	
Daikoku Dwarf (d_1)	Spontaneous mutant	33.0
Ai-yeh-lu Dwarf	Spontaneous mutant	40.9
	SEMIDWARFS	
Fanny Dwarf	—	54.4
IR273 selection	CP231/SLO-17//Taichung Native 1	55.7
FF36	Chianung 242/Taichung Native 1//Tainan 3	59.2
Taichung Native 1	Dee-geo-woo-gen/Tsai-yuan-chon	70.5
IR8	Peta/Dee-geo-woo-gen	77.6
Acc. 6993	CP231/SLO-17	72.4
Acc. 100027	Intermediate-Dwarf	81.8
	INTERMEDIATE-TALL	
BPI-76	Fortuna/Seraup Besar	116.9
	TALL	
Peta	Tjina/Latisail	148.6

A half-diallel set of 55 crosses was made from the 11 parents. Ten F_1 plants per cross and 10 plants for each parent were grown in a randomized complete-block design, replicated twice. Plant spacing was 30×25 cm. For planting in the dry season the F_2 population size per cross was 200 plants, spaced at 30×25 cm. For each parent, twenty plants were grown. A basal application of 30 kg nitrogen/ha was used both in the F_1 and F_2 plantings. A duplicate set of F_2 and the eleven parents were planted in the following wet season to assess the effect of the environment.

Whole plants were harvested. Measurements of culm length were made from the base of the culm to the panicle base of the main culm or the tallest tiller.

Hayman's diallel analysis (1954) was used to compute variance (Vr) and covariance (Wr) in the analysis of the F_1 data in Table 2. The Vr and Wr graphs were constructed to determine the order of dominance in this study. The relationship between the order of dominance (Vr+Wr) and culm length was determined by the standardized deviation graph of parental measurement ($\bar{Y}r$) and the order of dominance of the parents (Vr, Wr) (Johnson, 1953; Johnson and Aksel, 1959).

The magnitude of dominance in the F_1 plants was estimated by the potence ratio of Griffing (1950).

Table 2. *Culm length (cm) of the eleven parents and F_1 means in a half-diallel cross*

	Daikoku	Ai-yeh-lu	Fanny	Intermediate Dwarf	IR273 selection	Acc. 6993	FF36	TN1	IR8	BPI-76	Peta
Daikoku	33.0	37.1	56.6	95.7	84.9	63.8	68.7	64.6	77.4	59.1	75.8
Ai-yeh-lu	37.1	40.9	65.5	106.4	74.8	92.3	81.2	94.5	88.9	111.5	125.2
Fanny	56.6	65.5	54.4	79.3	59.8	65.8	53.2	72.0	67.4	80.1	88.1
Intermediate-Dwarf (Acc. 100027)	95.7	106.4	79.3	81.8	104.3	104.8	116.2	132.3	122.8	147.1	152.9
IR273 Selection	84.9	74.8	59.8	104.3	55.7	68.0	70.5	76.2	75.1	96.6	130.0
CP231/SLO17 (Acc. 6993)	63.8	92.3	65.8	104.8	68.0	72.4	91.0	91.2	105.8	94.9	124.9
FF36	68.7	81.2	53.2	116.2	70.5	91.0	59.2	76.2	74.1	106.1	125.2
Taichung Native 1	64.6	94.5	72.0	132.3	76.2	91.2	76.2	70.5	78.6	109.0	129.8
IR8	77.4	88.9	67.4	122.8	75.1	105.8	74.1	78.6	77.6	109.5	109.7
BPI-76	59.1	111.5	80.1	147.1	96.6	94.9	106.1	109.0	109.5	116.9	143.1
Peta	75.8	125.2	88.1	152.9	130.0	124.9	125.2	129.8	109.7	143.1	148.6

Results

Analysis of F_1 data

The variance (Vr) and covariance (Wr) graph of culm length, F_1 arrays, in an eleven-parent half-diallel cross is shown in Fig. 1. Points near the origin indicates increasing dominance while points ascending the unit line of slope indicates increasing recessiveness. Arrays with lower values of variance (Vr) and convariance (Wr) correspond to dominant parents, while arrays with higher values to recessive parents. Array 2 (Ai-yeh-lu Dwarf) gave the highest Vr Wr values indicating recessiveness, while arrays 1 (Daikoku Dwarf) and 3 (Fanny Dwarf) gave the lowest Vr Wr values, indicating an excess of dominant alleles. Arrays 1 and 3 are, however, distantly located from the line of unit slope indicating non-allelic gene interaction. The regression coefficient of 0.7882 is significantly different from 1.

Array	Selection	Vr	Wr
1	Daikoku ($\underline{d_1}$) Dwarf	353.2	282.2
2	Ai-yeh-lu Dwarf	764.8	831.6
3	Fanny Dwarf	130.4	327.8
4	Intermediate-dwarf (Acc. 100027)	582.8	587.8
5	IR273 selection	466.5	560.3
6	Acc. 6993	376.4	485.6
7	FF36	545.4	619.0
8	Taichung Native 1	561.2	584.3
9	IR8	352.2	403.5
10	BPI-76 N.S.	631.2	599.7
11	Peta	568.5	531.6

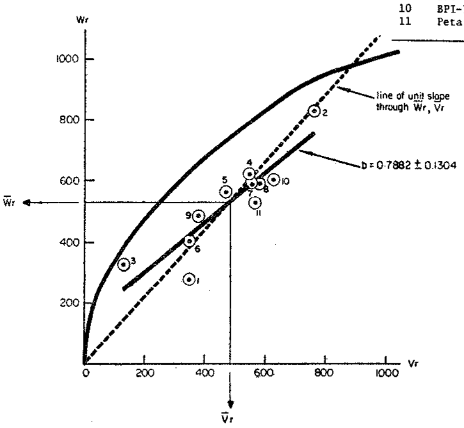
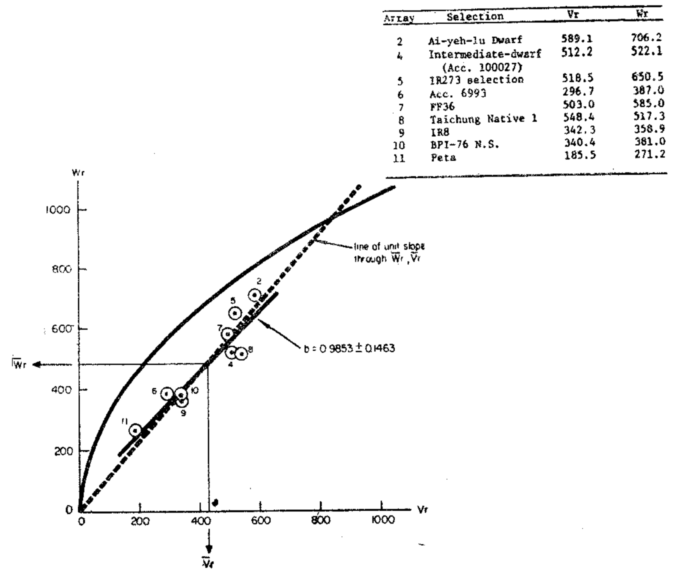


Fig. 1. Variance (Vr) and covariance (Wr) graph of culm length, F_1 arrays, in an eleven-parent half-diallel analysis. Points near the origin indicate an excess of dominance and points ascending the line indicate increasing recessiveness.

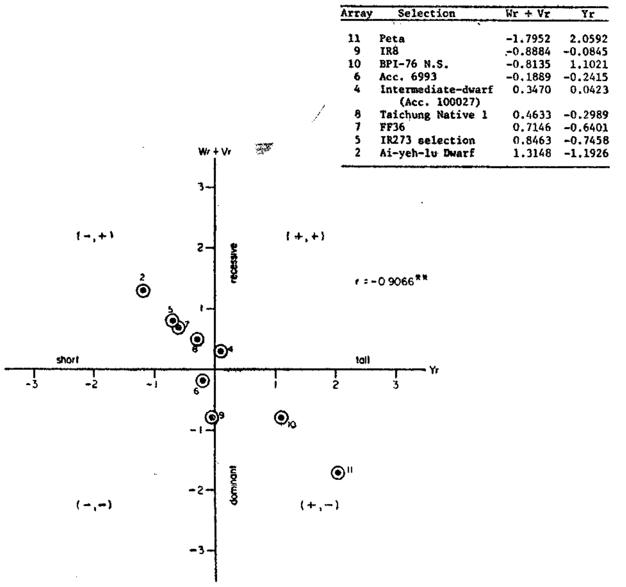
After removing arrays 1 and 3, the nine-parent half-diallel cross shows a Vr Wr graph with a regression coefficient (b=0.9853) almost equal to 1 or unity (Fig. 2). The condition of Hayman in a diallel analysis is thus satisfied. The relative order of dominance of the parents can now be determined.

Figure 3 shows the relationship of the quadrants to recessiveness and dominance and of short to tall culm length in a nine-parent half-diallel cross. As the Wr+Vr (order of dominance) increase, there is an increasing frequency



Array	Selection	Vr	Wr
2	Ai-yeh-lu Dwarf	589.1	706.2
4	Intermediate-dwarf (Acc. 100027)	512.2	522.1
5	IR273 selection	518.5	650.5
6	Acc. 6993	296.7	387.0
7	FF36	503.0	585.0
8	Taichung Native 1	548.4	517.3
9	IR8	342.3	358.9
10	BPI-76 N.S.	340.4	381.0
11	Peta	185.5	271.2

Fig. 2. Variance (Vr) and covariance (Wr) graph of culm length, F_1 arrays, in a nine-parent half-diallel cross after removing arrays 1 and 3.



Array	Selection	Wr + Vr	Yr
11	Peta	-1.7952	2.0592
9	IR8	-0.8884	-0.0845
10	BPI-76 N.S.	-0.8135	1.1021
6	Acc. 6993	-0.1889	-0.2415
4	Intermediate-dwarf (Acc. 100027)	0.3470	0.0423
8	Taichung Native 1	0.4633	-0.2989
7	FF36	0.7146	-0.6401
5	IR273 selection	0.8463	-0.7458
2	Ai-yeh-lu Dwarf	1.3148	-1.1926

Fig. 3. Standardized deviation graph between Yr, (parental measurement) and Wr+Vr, (order of dominance) of culm length in a nine-parent half-diallel cross. Highly significant correlation coefficient between Yr and Wr+Vr indicates that negative dominant alleles are in excess.

of recessive alleles, while decreasing values indicate increasing frequency of dominant alleles.

Peta shows the lowest Wr+Vr value indicating a greater degree of dominance than the other varieties. BPI–79, an intermediate tall variety, and two semi-dwarfs, IR8 and Acc. 6993, also shows the presence of dominant alleles. The order of dominance of the nine parents are as follows: Peta, IR8, BPI–76, Acc. 6993, Acc. 100027 (Intermediate Dwarf), Taichung Native 1, FF 36, IR273 selection, and Ai-yeh-lu Dwarf.

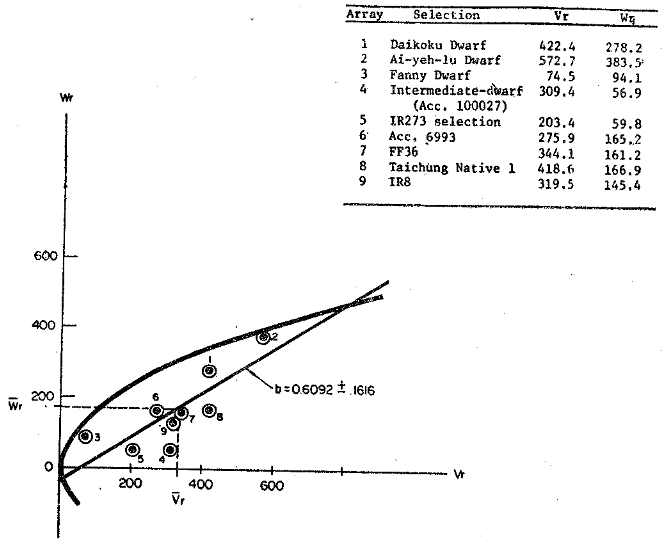
The correlation coefficient ($r=-0.9066$) between parental means (Yr) and the order of dominance (Wr+Vr) was highly significant. High minus or plus correlation between parental measurements (Yr) and parental order of dominance (Wr+Vr) indicates that positive or negative dominant alleles are in excess, while decreasing values of either sign indicate that both positive and negative alleles are in equal proportions in constituting dominance. In this case the correlation coefficient ($r=-0.9066$) suggest that there is an excess of negative dominant alleles, and that taller varieties have more dominant alleles than the dwarfs, semidwarfs or intermediate tall varieties.

Likewise, the variance (Vr) and covariance (Wr) of the dwarfs and semidwarfs were also analyzed (Fig. 4). Again, Fanny Dwarf was distantly located from the regression line indicating non-allelic gene interaction. It has also the lowest Vr Wr value indicating dominance as well. Another parent Acc. 100027 was also located further from the regression line. Taking out these two parents, the 7×7 parent-diallel was analyzed (Fig. 5) to determine the allelic relationship of the two dwarfs and the five semidwarfs. The regression value is now almost approaching unity ($b=0.7970$). The line of unit slope tend to move downwards indicating the presence of overdominance. IR273 selection showed an excess of dominant alleles after the interaction of the tall parent and the non-allelic gene interaction of Fanny Dwarf and Acc. 100027 were removed. In crosses of dwarfs×semidwarfs, F_1 analysis showed overdominance e.g. ($hp=1.7189$) in Daikoku Dwarf×IR273 sel. and no dominance ($hp=0.0450$) in Daikoku Dwarf×IR8 cross.

The two Vr Wr graphs (Fig. 4 and 5) show that the two dwarfs have an excess of recessive alleles, but Daikoku Dwarf has less recessive alleles than Ai-yeh-lu Dwarf. The semidwarfs seem to have an equal proportion of negative and positive alleles. In the 7×7 parent-diallel analysis (Fig. 5), the correlation value between Vr+Wr and parental means (Yr) was not significant ($r=-0.6824$) suggesting that there is an equal proportion of positive and negative alleles in constituting dominance.

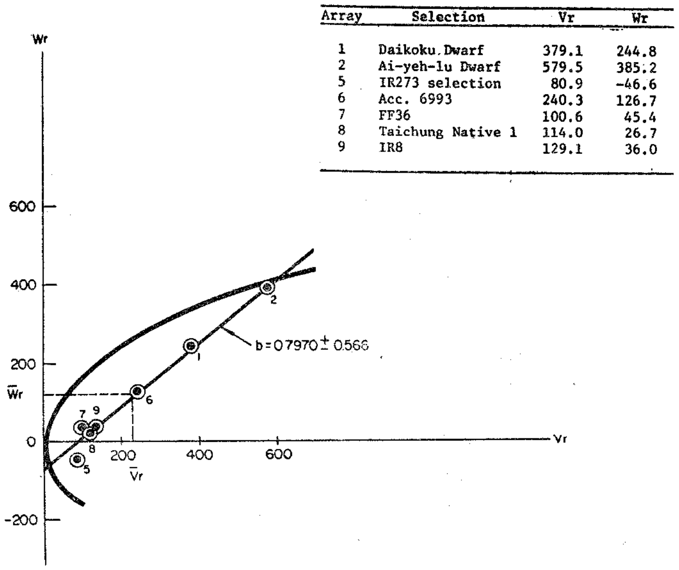
Analysis of F_2 data

Table 3 shows the different F_2 segregation pattern of the 11×11 parent



Array	Selection	Vr	Wr
1	Daikoku Dwarf	422.4	278.2
2	Ai-yeh-lu Dwarf	572.7	383.5
3	Fanny Dwarf	74.5	94.1
4	Intermediate-dwarf (Acc. 100027)	309.4	56.9
5	IR273 selection	203.4	59.8
6	Acc. 6993	275.9	165.2
7	FF36	344.1	161.2
8	Taichung Native 1	418.6	166.9
9	IR8	319.5	145.4

Fig. 4. Variance (Vr) and covariance (Wr) graph culm length, F_1 arrays, of two dwarfs and seven semidwarfs.



Array	Selection	Vr	Wr
1	Daikoku. Dwarf	379.1	244.8
2	Ai-yeh-lu Dwarf	579.5	385.2
5	IR273 selection	80.9	-46.6
6	Acc. 6993	240.3	126.7
7	FF36	100.6	45.4
8	Taichung Native 1	114.0	26.7
9	IR8	129.1	36.0

Fig. 5. Variance (Vr) and covariance (Wr) graph of culm length, F_1 arrays, of two dwarfs and five semidwarfs.

Table 3. *F_2 segregation of an eleven parent half-diallel cross in descending order of culm length*

	Peta	BPI-76	Interme-diate-Dwarf	IR8	Acc. 6993	Taichung Native 1	FF36	IR273 selection	Fanny	Ai-yeh-lu	Daikoku
Peta	148.6	C_T	${}_TC_T$	1:3	C	1:3	1:3	1:3	C	1:3:3:9	1:3:3:9
BPI-76	C_T	116.9	${}_TC_T$	C	C	C	C	C	C_T	1:3:3:9	1:3:3:9
Intermediate-Dwarf (Acc. 100027)	${}_TC_T$	${}_TC_T$	81.8	${}_TC_T$	${}_TC_T$	C_T	C_T	${}_TC_T$	${}_TC_T$	1:3:12	1:15
IR8	1:3	C	${}_TC_T$	77.6	${}_TC_T$	C	C	C	${}_TC_T$	C_T	C_T
CP231/SLO-17 (Acc. 6993)	C	C	${}_TC_T$	${}_TC_T$	72.4	${}_TC_T$	C_T	C_T	C_T	1:3	1:3
Taichung Native 1	1:3	C	C_T	C	${}_TC_T$	70.5	C	C	${}_TC_T$	C_T	C_T
FF36	1:3	C	C_T	C	C_T	C	59.2	C_T	${}_TC_T$	1:3	1:3
IR273 selection	1:3	C	${}_TC_T$	C	C_T	C	C_T	55.7	${}_TC_T$	1:3	1:3
Fanny	C	C_T	${}_TC_T$	${}_TC_T$	C_T	${}_TC_T$	${}_TC_T$	${}_TC_T$	54.4	1:3	1:3
Ai-yeh-lu	1:3:3:9	1:3:3:9	1:3:12	C_T	1:3	C_T	1:3	1:3	1:3	40.9	C
Daikoku	1:3:3:9	1:3:3:9	1:15	C_T	1:3	C_T	1:3	1:3	1:3	C	33.0

1:3—Mendelian ratio of single major recessive gene; 1:3:12, 1:3:3:9, 1:15—two major recessive genes.

C—continuous distribution; C_T—continuous distribution with transgressive segregation to the right; ${}_TC_T$—continuous distribution with transgressive segregation to left and right.

diallel. The parents are arranged in a descending order of culm length.

1. Toll×intermediate-tall combinations The F_2 population of an intermediated-tall×tall cross (BPI-76×Peta) showed a continuous distribution with a slight negative kurtosis (Fig. 6F). No F_2 plants were found to exceed parental limits in the dry season. However, about 16% of the F_2 plants exceeded both parental limits in the wet season. The F_2 mean was 101.8 cm and 128.7cm in the dry and wet season, respectively. The results indicate that these two tall *indica* varieties differ in many genes of rather small effects.

2. Tall×semidwarf combinations Another type of segregation was observed in the cross of intermediate-statured Acc. 100027 with tall Peta. The F_2 population showed a continuous F_2 distribution with few plants transgressing beyond both parental limits. A slight negative kurtosis and a deficiency of the semidwarf phenotypes was also observed. The culm length of the F_2 population ranges from 50–150 cm. F_2 mean was 104.1 cm.

The crosses of tall Peta with either IR8, FF36, Taichung Native 1 and IR273 selection showed the expected F_2 segregation of 3 tall: 1 semidwarf.

While the cross of Acc. 6993×Peta showed a continuous unimodal F_2 distribution, no F_2 plants were found to exceed either parental limit. The data show that many genes of small effect are operating in the cross and that Acc. 6993 does not have the semidwarfing gene of the other semidwarf.

The cross of Fanny Dwarf with the tall Peta produced a continuous F_2 distribution with slight positive kurtosis in the dry season and an essentially normal distribution in the wet season (Fig. 7B). The F_2 distribution was within the range of the two parents. A deficiency of Fanny Dwarf phenotypes were observed in the wet season planting, and no F_2 plants of the Peta height were recovered in the dry season. The F_1 hybrids measured shorter than the mid-parent value and gave a potence ratio of –0.40 indicating partial domiance of genes for shorter culm length over the genes for tallness in Peta. The data confirms the F_1 diallel analysis that an excess of dominant alleles was present in Fanny Dwarf (Fig. 1 and 4).

3. Tall×dwarf combinations The cross of Ai-yeh-lu Dwarf×Peta showed a wide F_2 segregation, ranging from 15–120 cm in the dry season and from 40–155 cm in the wet season. A deficiency of the dwarf phenotypes was observed in the wet season (Fig. 7D). Several F_2 plants exceeded the height of Peta. The F_2 distribution approximated a 9 tall (121–155 cm): 3 intermediate-tall (100–120 cm):3 semidwarf (55–95 cm):1 dwarf (40–54 cm) ratio ($P=.50-.25$). The dwarf stature of Ai-yeh-lu Dwarf could be controlled by two pairs of recessive alleles. A similar segregation was obtained in the cross of Ai-yeh-lu Dwarf×BPI-76.

The cross of Daikoku Dwarf with Peta also showed a discontinuous F_2

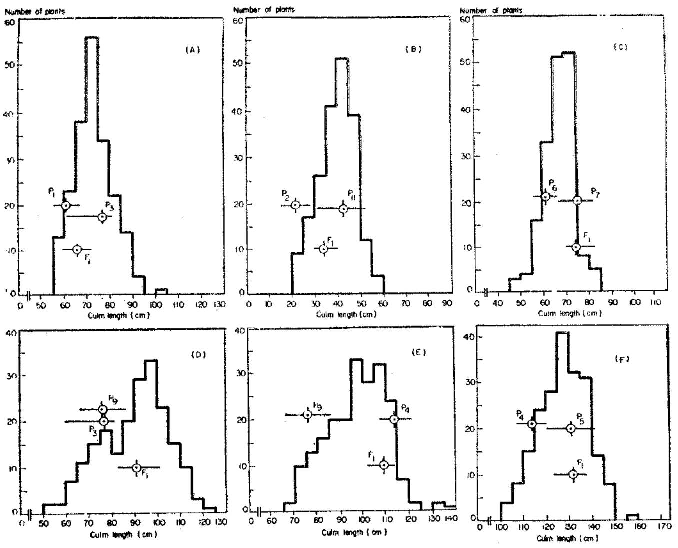


Fig. 6. Continuous distribution of F_2 plants by culm length in six crosses: (A) Fanny Dwarf (P_1) × Acc. 6993 (P_3), (B) Daikoku Dwarf (P_2) × Ai-Yeh-Lu Dwarf (P_{11}), (C) FF36 (P_6) × IR8 (P_7), (D) Acc. 6993 (P_3) × Taichung Native 1 (P_9), (E) Taichung Native 1 (P_9), × BPI-76 (P_4), (F) BPI-76 (P_4) × Peta (P_5). Solid horizontal lines indicate the range of parents and F_1 hybrids about the means (dotted circles).

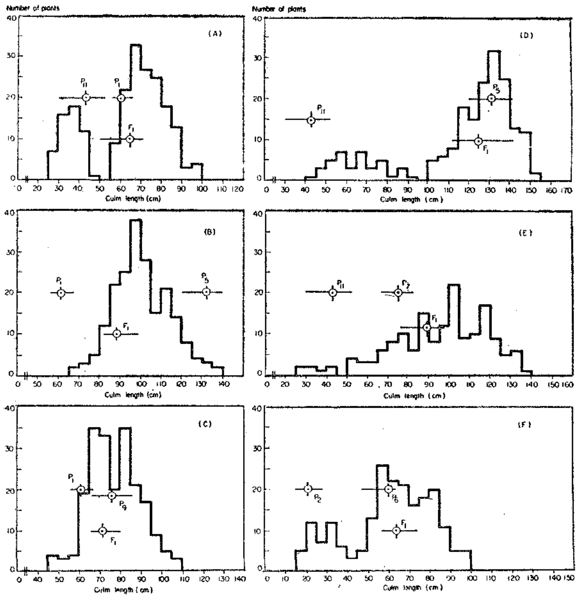


Fig. 7. Discontinuous and continuous distribution of F_2 plants by culm length in six cross: (A) Ai-Yeh-Lu Dwarf (P_{11}) × Fanny Dwarf (P_1), (B) Fanny Dwarf (P_1) × Peta (P_5), (C) Fanny Dwarf (P_1) × Taichung Native 1 (P_9), (D) Ai-Yeh-Lu Dwarf (P_{11}) × Peta (P_5), (E) Ai-Yeh-Lu Dwarf (P_{11}) × IR8 (P_7), (F) Daikoku Dwarf (P_2) × FF36 (P_6). Solid horizontal lines indicate the range of parents and F_1 hybrids about the means (dotted circles).

segregation approximating a 9 tall:3 intermediate-tall:3 semidwarf: 1 dwarf ratio (P=.50—.25)—similar to that found in the cross of Ai-yeh-lu Dwarf× Peta. However, no F_2 plants were observed to be taller than Peta. Deficiency of dwarf phenotypes were also observed in the wet season planting. This could be due to the dwarf's poor competitive ability for growth and development in the field. The results suggest that Daikoku Dwarf and Ai-yeh-lu Dwarf have similar sets of recessive alleles for dwarf height, but Daikoku Dwarf has more dominant alleles than Ai-yeh-lu Dwarf (Fig. 4 and 5).

The cross of either Daikoku Dwarf or Ai-yeh-lu Dwarf with BPI-76 was similar to that found in Peta (Table 3).

4. Intermediate-tall×semidwarf combinations The cross of Acc. 100027× BPI-76 showed a continuous F_2 segregation with transgression beyond both parental limits. The two parents differ by 35.1 cm in the wet season. Most of the F_2 plants were taller than BPI-76, but did not approach the height of Peta. The F_2 mean was 90.2 cm.

The crosses of either IR273 selection, IR8, Taichung Native 1, FF36 or Acc. 6993 with BPI-76 produced continuous unimodal distributions within parental limits (Table 3). This type of segregation is clearly demonstrated in the cross of Taichung Native 1×BPI-76 (Fig. 6E). The lack of clear-cut expression of the major recessive gene in the F_2 may be attributed to the rather small number of dominant alleles for tall height found in BPI-76 (Fig. 2 and 3).

The cross of Fanny Dwarf×BPI-76 showed a continuous F_2 segregation approaching a normal curve (range: 50–140 cm) with few plants exceeding the height of BPI-76 in the wet season. In the dry season, the F_2 plants were within parental limits with a narrow range of 40–90 cm. This also indicates that the genes controlling the height of this cross is easily affected by the environment.

5. Semidwarf×semidwarf combinations A unimodal F_2 distribution within parental limits was observed among crosses of four semidwarfs with a common genetic background: IR273 selection, Taichung Native 1, IR8 and FF36 (Fig. 6C). Few F_2 plants transgressed the parental limits. In the cross of IR273 selection×FF36, a majority of the F_2 plants was slightly taller than FF36 (70–90 cm) but they still belonged to the semidwarf category. From Table 1, these dwarfs have a common background, i.e. they have the Dee-geo-woo-gen gene for short stature. Results indicated that the semidwarfing genes of these semidwarfs are allelic to each other. In addition other genes of small effect might also be involved.

Crosses of Acc. 100027 with either IR8, Taichung Native 1, FF36 and IR273 selection, showed a unimodal F_2 distribution with transgression beyond parental limits (Table 3). About 105 out of 210 F_2 plants were taller than Acc. 100027 but they did not approach the height of Peta. The F_2 plants ranges from 30–120 cm.

Crosses of Acc. 6993 with either IR8, Taichung Native 1, FF36 or IR273 selection showed continuous F_2 segregations with transgression beyond both parental limits (Fig. 6 D). The F_2 distribution showed slight negative kurtosis. The results indicate that Acc. 6993 has a different set of genes for short stature and that it differs from the four semidwarfs by many genes of small effects.

The crosses of Fanny Dwarf with either IR8, Taichung Native 1, FF36 and IR273 selection also showed a continuous F_2 distribution with transgressive segregation beyond parental limits on both ends (Table 3). However, no F_2 plants approached the height of Peta. This also shows that Fanny Dwarf has different set of semidwarfing genes.

The crosses of Fanny Dwarf with Acc. 100027 also showed a continuous F_2 distribution with transgressive segregation beyond parental limits on both ends (Fig. 7C). However, no F_2 plants approached the height of Peta. Similarly, the cross of Acc. 6993 × Acc. 100027 also showed a continuous transgressive F_2 segregation with a slight negative kurtosis.

The cross of Fanny Dwarf × Acc. 6993 showed a continuous F_2 distribution, ranging from 55–95 cm in the wet season and from 40–75 cm in the dry season (Fig. 6A). About 19 percent of the F_2 population transgressed the upper limit of the taller parent in the wet season, but only four such plants were found in the dry season. Moreover, crosses of Acc. 6993 and Fanny Dwarf with either of the four semidwarfs with a common genetic background, and the two dwarfs showed similar F_2 distribution in most cross combinations (Table 3).

6. Dwarf × semidwarf combinations The cross of Ai-yeh-lu Dwarf × Acc. 100027 showed an F_2 segregation approximating a ratio of 12 intermediate: 3 dwarf: 1 double dwarf ($P = .50–.25$). It was shown from the F_1 analysis that Acc. 100027 has nearly an equal proportion of dominant and recessive alleles and that Ai-yeh-lu Dwarf has an excess of recessive alleles. Plants of the double-dwarf type (10–30 cm) could result from the combined effect of recessive alleles from both parents.

On the other hand, the cross of Daikoku Dwarf with Acc. 100027 showed a bimodal distribution but it was not clearly discontinuous. A number of the F_2 plants were taller than the intermediate or semidwarf parent but they did not reach the height of the tall parents. No F_2 plants were observed to be shorter than the height of Daikoku Dwarf. The segregation approximated a 15 Intermediate: 1 Daikoku ratio ($P = .50–.25$). The recovery of the Daikoku height in the F_2 segregation could result from the combined action of two pairs of recessive alleles, and the intermediate types were produced by the complementary action of the two pairs of dominant alleles.

The above data further indicated that Acc. 100027 may have more than one gene for its semidwarf stature and that these genes are nonallelic to either those of the dwarfs--Daikoku Dwarf and Ai-yeh-lu Dwarf—or to those of the recessive gene of the other semidwarfs—Taichung Native 1, IR8, FF36, and IR273 selection, and the multigenes of Fanny Dwarf and Acc. 6993.

A continuous F_2 segregation pattern was observed in the cross of Ai-yeh-lu Dwarf×IR8 (Fig. 7E). The F_2 distribution ranged from 15 to 110 cm and from 25 to 140 cm in the dry and wet seasons, respectively. The distribution curved showed a slight negative skewedness. Such a distribution was also observed in the cross of Ai-yeh-lu Dwarf×Taichung Native 1. The data suggest that the recessive dwarfing genes of Ai-yeh-lu Dwarf are nonallelic to the recessive semidwarfing genes of IR8 and Taichung Native 1. The slight negative kurtosis and the recovery of taller phenotypes (100 to 140 cm) could be attributed to the interaction of several dominant alleles with unequal additive effects. Overdominance was indicated by the potence ratio, $hp = 1.61$.

The F_2 sample of Ai-yeh-lu Dwarf×Acc. 6993 gave a ratio of 3 semidwarf: 1 dwarf ($P = >0.90$). Most of the F_2 plants in the intermediate group were slightly taller than the taller parent, Acc. 6993. But the maximum F_2 culm length was only 100 cm in the dry season and 130 cm in the wet season. A similar F_2 distribution was observed in the cross of Ai-yeh-lu Dwarf with either the IR273 selection or FF36.

Similarly, in the cross of Ai-yeh-lu Dwarf and Fanny Dwarf the F_2 distribution showed a clear-cut segregation of 3 semidwarf: 1 dwarf ($P = >0.95$) (Fig. 7A). The majority of the F_2 plants were taller than Fanny Dwarf or the F_1 plants, however. Transgressive segregation beyond the taller parents could be due to overdominance, which was indicated by the potence ratio of 2.66 estimated from the F_1 and parental data.

The cross of Daikoku Dwarf with either FF36 (Fig. 7F), Acc. 6993, or IR273 selection also showed a Mendelian distribution of 3 semidwarf: 1 dwarf ($P = >0.90$). About 75% of the F_2 plants were taller than the semidwarf parent but they did not approach the height of Peta. Very few Daikoku Dwarf types were recovered during the wet season.

On the other hand, the cross of Daikoku Dwarf×Taichung Native 1 showed a distinctly continuous F_2 distribution in the wet season. The culm length of the F_2 plants ranges from 20 to 125 cm. About 38 percent of the F_2 plants transgressed the upper limit of Taichung Native 1 and only 2 percent of the

Daikoku height were recovered. Although the F_2 distribution in the dry season was continuous, two peaks were distinct. This was similar to the F_2 distribution found in Ai-yeh-lu Dwarf×Taichung Native 1, and Ai-yeh-lu Dwarf×IR8.

The cross of Daikoku Dwarf×IR8 showed a continuous F_2 distribution ranging from 15–90 cm and 20–115 cm in the dry and wet seasons, respectively. About 67 out of 210 F_2 plants were taller than IR8 but did not approach the height of BPI-76 or Peta. A deficiency of the Daikoku Dwarf height was also observed. Jodon (1955) attributed such low population of dwarf class to differential survival after the initial inundation of the field.

The cross of Daikoku Dwarf×Fanny Dwarf showed a bimodal segregation although not entirely discontinuous. The F_2 segregation approximates a ratio of 3 semidwarf: 1 dwarf ($P=.50$–$.25$), similar to that found in Ai-yeh-lu Dwarf×Fanny Dwarf.

7. Dwarf×dwarf combinations The cross of the two dwarfs, Daikoku Dwaf×Ai-yeh-lu Dwarf, showed a continuous F_2 segregation within parental limits (Fig. 6B). From the analysis of the F_1 data, the Vr, Wr graph shows that Daikoku Dwarf and Ai-yeh-lu Dwarf have an excess of recessive alleles with Ai-yeh-lu Dwarf as having more recessive alleles (Fig. 4 and 5).

Table 3 also shows that most of the cross combinations involving Ai-yeh-lu Dwarf and Daikoku Dwarf have similar F_2 segregation patterns.

With the above results it is likely that Ai-yeh-lu Dwarf and Daikoku Dwarf have similar genes for dwarf height.

Discussion

Previous studies on the inheritance of plant stature in rice largely dealt with either one of the three categories of crosses: dwarf×tall (Akemine, 1925; Jodon and Beachell, 1943; Butany *et al.*, 1959; Hsieh and Yen, 1966; Shastri and Misro, 1963), semidwarf×tall (Chang *et al.*, 1965; Aquino and Jennings, 1966; Heu *et al.*, 1968; Heu and Suh, 1974), and intermediate-tall×tall or tall×tall (Mohamed and Hanna, 1964; Li and Chang, 1970).

Most of the investigations led to interpretations based on Mendelian inheritance. This study is one of the few investigations that involved both diallel analysis of F_1 hybrids and parents as well as a study of the F_2 populations. Moreover, it was indicated by earlier studies that while the dwarfs respond to gibberellic acid treatments (Harada and Vergara, 1972; Suge, 1975), semidwarfs carrying the Dee-geo-woo-gen recessive gene as well as the tall Peta fail to respond to low dosages of the chemical (G. C. Loresto, unpublished). Therefore, the dwarf×semidwarf crosses would elucidate the genetic relationship between the dwarfs and semidwarfs.

The 9×9 parent diallel analysis including the tall parent of the F_1 data indicated that Ai-yeh-lu Dwarf has an excess of recessive alleles (Fig. 2). This was confirmed in the 9×9 parent diallel analysis of the F_1 data involving dwarfs and semidwarfs alone (Fig. 4). Daikoku Dwarf was also shown to have a higher variance, covariance value indicating the presence of recessive alleles (Fig. 4 and 5). The Daikoku Dwarf is known to have a major recessive gene (Nagao and Takahashi, 1963) for its extremely short stature (33.0 cm). On the other hand, the slightly taller Fanny Dwarf (54.4 cm) carries an excess of dominant alleles (Fig. 1 and 4) and based on our F_2 data, we reclassified it as a semidwarf.

It was also observed that Fanny Dwarf exhibited nonallelic gene interaction in the 11×11 and 9×9 parent diallel analysis (Fig. 1 and 4).

The high correlation coefficient ($r=-0.9066$) of the 9 parent diallel cross. excluding Fanny Dwarf and Daikoku Dwarf, suggests that taller varieties have more dominant alleles than the dwarfs, semidwarfs or intermediate tall varieties. However, in Fig. 1 and 4, it is likely that the short culm length of Fanny Dwarf is not necessarily controlled by recessive alleles.

Sugimoto (1923) found that a pair of dominant alleles controls the short stature of a dwarf mutant obtained from a pure line of a cross between Sekitori and Aikoku. The dominance of tallness is frequently found when the genic system involves largely additive effects, however. Such findings were reported by Wu (1968) and Li and Chang (1970) in their diallel analysis of parents that do not differ markedly in plant height.

Culm length was used to evaluate the differences in the segregation patterns of the F_2 populations (Table 3).

The F_2 segregation patterns can be classified into two general groups: (1) bimodal distribution—obtained in crosses where a distinctly discontinuous segregation pattern was observed, indicative of simple Mendelian inheritance, and (2) unimodal distribution—obtained from crosses where no discrete classes could be differentiated and the continuous F_2 distribution is typical of quantitative inheritance.

The unimodal distribution can be further subdivided into three categories: a) continuous distribution within parental limits, b) continuous distribution with transgressive segregation to the right, and c) continuous distribution with transgressive segregation to left and right.

From Table 3, the F_2 distribution of the 55 F_2 populations showed the following generalization: 1) a major gene controls the semidwarf expression of the four semidwarfs with a common genetic background, 2) two major recessive genes control the short stature of the dwarfs, 3) two or more major genes confer semidwarfism in another strain, Acc. 100027, and 4) a polymeric system controls the short stature of Fanny Dwarf and Acc. 6993.

In addition to these major genes, many genes with relatively smaller and cumulative effects are present in every parent to account for the large range in variation of plant height found in the parents and in their F_2 progenies.

The action of the major genes was more clearly identified in crosses between extreme parents, i. e., tall×dwarf, or tall×semidwarf and between semidwarfs and dwarfs. In such crosses the discontinuous segregation pattern could be explained by the postulate that the two parents differ in one or two major genes. This type of gene interaction is most pronounced in the crosses of Peta with either IR8, Taichung Native 1, FF36 or IR273 selection, which resulted in a typical 3 semidwarf: 1 dwarf ratio.

The role of modifiers or modifying genes is indicated by crosses among parents that did not differ much in culm length and (or) in dominance level. The F_2 populations of this type showed the highest frequency of unimodal segregations. The F_2 distributions generally suggest the parents do not differ in any of the major genes but the F_2 phenotypes are primarily controlled by many genes, each having only a small effect on plant stature. The resulting segregation approximates that of quantitative characters but the distribution may not be strictly normal. This is clearly shown in crosses of semidwarfs×BPI-76, BPI-76×Peta, and semidwarf×semidwarf.

The primary role of the recessive gene from Dee-geo-woo-gen or I-geo-tze (Chang *et al.*, 1965; Aquino and Jennings, 1966; Heu *et al.*, 1968) is reconfirmed in those crosses between the tall parents and any one of the four semidwarfs having Dee-geo-woo-gen in their ancestry—Taichung Native 1, IR8, IR273 selection, and FF36. The action of modifiers was also detected in the above crosses.

The crosses of dwarfs×semidwarfs showed that different major genes were involved. The F_2 plants segregated into either a 12:3:1, 15:1 or 3:1 ratio.

The crosses of Daikoku Dwarf×Acc. 100027 (Intermediate-Dwarf) and Ai-yeh-lu Dwarf×Acc. 100027 segregated into a 15:1 ratio and a 12:3:1 ratio, respectively. The two dwarfs and Acc. 100027 differ markedly in height as well as in their relative dominance level. We also found that crosses between Acc. 100027 and the four semidwarfs derived from Dee-geo-woo-gen showed a continuous F_2 segregation with transgression beyond the parental limits. Therefore, the one or more pairs of recessive alleles in Acc. 100027 differ from the major recessive gene in the four semidwarfs and the major recessive genes of the two dwarfs.

In all these crosses no F_2 plants approached the height of either BPI-76 (116 cm) or Peta (148 cm). This clearly indicates that the genes controlling short stature of dwarfs and semidwarfs are located at different loci. Most likely, these genes are in the same chromosome and probably close to each other so that recombinations may not occur. This could explain the nonrecovery of taller phenotypes. Another explanation is that the recessive alleles of the two dwarfs, Daikoku Dwarf and Ai-yeh-lu Dwarf, could inhibit the expression of tall height genes. Nakayama (1937) reported that the genes A and B for the dwarf habit in rice limited the growth of some vegetative organs such as the stem.

An exception to this observation is the unimodal F_2 segregation observed in the crosses of Ai-yeh-lu Dwarf×IR8 and Ai-yeh-lu Dwarf×Taichung Native 1, Daikoku Dwarf×IR8, Daikoku Dwarf×Taichung Native 1. Tall F_2 phenotypes (120 to 155 cm) were recovered. The modifying genes or the dominant alleles of Taichung Native 1 or IR8 could have enhanced the expression of tallness. Suge (1975) also found tall F_2 plants in the cross of a dwarf× semidwarf, Tan-ginbozu×Dee-geo-woo-gen. He concluded that plant height is modified by polygenes in addition to the major genes controlling tall and short forms. High gibberellic acid content was found from extracts of tall F_2 plants and virtually no gibberellic acid activity was found in dwarf F_2 plants.

The semidwarf stature of Acc. 6993 selection from CP231/SLO-17 has been reported to be govened by a complex of polygenic-additive genes in the cross with Taichung Native 1 (IRRI, 1967a; Heu *et al.*, 1968). Our findings confirm the postulate.

Likewise, the semidwart of Fanny Dwarf appers to be governed by a set of polymeric genes with an excess of dominant alleles, as shown in the cross of Fanny Dwarf×Peta. The F_2 distribution was continuous and very few plants of the height of Peta were recovered. The F_1 hybrids were shorter than the midparent values and gave a potence ratio of -0.40, indicating partial dominance of shorter culm length. This further confirms the finding for the F_1 diallel analysis (Fig. 1 and 4) about the presence of dominant alleles for shorter height.

In terms of allelic relationships, Daikoku Dwarf and Ai-yeh-lu Dwarf have the same major recessive dwarfing genes, but Daikoku Dwarf has more dominant alleles of minor effect than Ai-yeh-lu Dwarf. Similarly, the two semidwarfs, Fanny Dwarf and Acc. 6993, appeared to have the same set of genes for short culm length. The two check varieties, BPI-76 (intermediate-tall) Peta (tall), differ only in alleles of small effect. From the F_1 analysis, Peta appears to have more dominant alleles (Fig. 1 and 2). The potence alue of 0.65 indicates the partial dominance of long culms of Peta.

In this study the effect of the environment on the expression of plant height is obvious on the parents but it is difficult to assess the magnitude of its effect on different genotypes, because there is no way of identifying or relating F_2 plants were planted in different seasons. During the dry season, plants of the same parent generally mature earlier and the culms are shorter. The cooler temperatures during the early part of the dry season could also have reduced the culm length of the many F_2 plants. The recovery of tall F_2 phenotypes during the dry season planting was lower in frequency as compared to the frequent appearance of tall F_2 parental phenotypes when the plants matured much later during the wet season. Moreover, the genotype-environmental reactions may have led to the appearance of transgressive segregates in some crosses. Similarly, overdominance was indicated in some crosses as shown by those potence ratios larger than 1.25. Those factors could produce segregates that were outside the range of two parents.

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水稻矮性、半矮性及高稈品系間稈長之半互交法及第二代遺傳分析

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本試驗利用兩個矮性、七個半矮性和兩個高稈水稻品種或品系組成之半互交組合進行稈長之遺傳分析，藉以明瞭支配水稻稈長之遺傳因子體制。在所用親本材料中矮性品系 Daikoku、半矮性品系 Fanny Dwarf 及植株最高之 Peta 具有較多之顯性因子，而矮性品系 Ai-yeh-lu 有較多之隱性因子，其餘親本則有近乎相等之顯性與隱性因子。

分析第二代雜種之分離結果指出臺中在來一號、IR 8、FF 36 和 IR 273 品系四個半矮性水稻品種或品系之半矮性係由一對隱性因子所支配；Daikoku 和 Ai-yeh-lu 兩個矮性品種之矮性係由兩對隱性因子所支配；Acc. 100027 (Intermediate-Dwarf) 之半矮性則由兩個或更多之隱性因子所支配；另一組 Polymeric 因子支配 Fanny Dwarf 和 Acc. 6993（CP 231/SLD-17）兩個半矮性品種之矮性。此外，每一親本似有多個效用甚小而有累加作用之因子，但每親本內之因子組合互異。

兩個高稈親本 BPI-76 和 Peta 間亦顯示各有不同之次要因子；高稈之 Peta 對較短稈之 BPI-76 有完全顯性之現象。

本試驗曾在旱雨季重複試驗觀察親本和第二代雜種分離現象，但因遺傳質與環境的交感作用而使不同遺傳因子體制之表現不易辨別或分析。