INHERITANCE OF SEMIDWARFISM IN RICE, *ORYZA SATIVA* L.

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ABSTRACT

The inheritance of plant height was investigated in a ten-parent diallel cross of diverse rice cultivars. Parents included two tall japonica lines and eight semidwarf lines. Data from parent, F_1, F_2, and F_3 generations indicated that the majority of height variation among the ten parents could be accounted for by three major genes with additive loci effects. D51, 72/2234–11, and G33 (derived from the known major-gene indica semidwarf Dee-geo-woo-gen) all were found to possess an allelic, partially recessive semidwarfing gene (sd_1). Additional semidwarfing genes were detected in D66 (sd_2, fully recessive) and in CI 9858 (sd_3, partially to fully recessive). Relative magnitudes of additive effects were $sd_1 > sd_2 \geq sd_3$. Hokuriki 76, Tedoriwase, and IV 29–4 were found to be dwarfed by a multiple-gene system. Hayman-Jinks diallel cross analysis on parent and F_1 information (1974 and 1975) and on parent and F_2 information demonstrated the presence of significant additive and dominance variation, but epistasis was not detected. A preponderance of dominant alleles with partial dominance for increased plant height was observed. Since diallel statistics reflect properties of genes with larger effects, the genetic model proposed from segregation analysis was in substantial agreement with predictions of the Hayman-Jinks analysis.

AN important aspect of experimental genetics is the analysis of measurement characters. We are particularly interested in the recognition of major genes segregating in the presence of genes with small effects. Casual observation of continuous phenotypic distributions often obtained in such instances can lead to erroneous conclusions of exclusively polygenic control of the character under study. Neither classical Mendelian nor quantitative genetic techniques alone can adequately describe such genetic systems. The possibility that combining the two approaches could provide more information than either alone was the basis for conducting the present experiments. We chose an important measurement

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character, mature plant height in rice, as the experimental system. A group of cultivars and experimental lines believed to possess genes with a range of additive effects for mature plant height was used to initiate the study.

Extensive studies have been carried out at the International Rice Research Institute (IRRI) to determine genetic control of height in the semidwarfs Taichung (Native)1 (T(N)1), I-geo-tze (IGT), and Dee-geo-woo-gen (DGWG), the semidwarf parent of IR8 (IRRI 1966). A single gene partially recessive for shortness was responsible for most of the height reduction in all three semidwarfs (IRRI 1964; CHANG *et al.* 1965; AQUINO and JENNINGS 1966; HEU, CHANG and BEACHELL 1968).

That the morphologically similar T(N)1, IGT, and DGWG all carry the same semidwarfing gene has also been demonstrated (IRRI 1966; IRRI 1967). At least 14 additional semidwarf varieties or lines of possibly distinct origin are allelic to DGWG (IRRI 1974; LI, HU and WOO 1966), while several dwarfs nonallelic to DGWG are also known (IRRI 1974; REDDY and PADMA 1976). However, the majority of presently known semidwarfs possess the same, or an allelic, dwarfing gene.

The objectives of the present study were:

(1) to identify reduced-height lines carrying major semidwarfing genes in crosses with a typical California genotype, and

(2) to determine the allelic status of any such gene(s) detected.

MATERIALS AND METHODS

Ten rice genotypes (Table 1) selected on the basis of diversity in height and genetic background were crossed in all combinations, excluding reciprocals. G30 and Huang-to-do represent tall japonica lines, with G30 (a sister selection of the California variety S6) being typical of tall California varieties. Three lines, CI 9858, G33, and IV29-4 were derived from indica × japonica crosses. G33 and IV29-4 were included because they presumably derived their short stature from

TABLE 1

Origin and parentage of parental lines used in height diversity studies

Genotype designation	Plant height†, cm	Origin	Parentage
Huang-to-do	139	Korea	
G30	111	California	CS-M3 × Colusa
CI 9858	102	Louisiana	RRU-RR250 × Bluebelle
D66	97	California	Calrose mutant
Hokuriki 76	92	Japan	
D51	89	California	Calrose mutant
Tedoriwase	86	Japan	
G33	82	California	T(N)1 × Earlirose/2
IV29-4	80	IRRI-California	Jinheung/2 × IR262-43-8-11*
72/2234-11	70	California	Calady male sterile × Norin 20

* IR262-43-8-11 = (Peta/3 × T(N)1).
† Mean of 1974 and 1975 direct-seeded plants.

the semidwarfing gene in DGWG. The remaining five short-stature selections are all japonicas. D66 and D51 are induced short-stature mutants from the variety Calrose (RUTGER *et al.* 1976). D51 probably arose from the same mutagenic event giving rise to the short-stature mutant D7 (RUTGER *et al.* 1976), which was subsequently released as the variety Calrose 76. Hokuriki 76 and Tedoriwase, both from Japan, are short-statured varieties when grown in California. 72/2234–11 was an extremely short plant found in an otherwise tall F_3 population from the cross between the two tall varieties, Calady male sterile and Norin 20.

Three experiments were carried out at Davis, California, in 1974 and 1975. Plant height in all experiments was measured at maturity as the distance from the soil surface to the tip of the tallest culm, excluding awns. The first experiment consisted of parent and F_1 generations grown both years. In 1974 parents and F_1 plants were transplanted to the field in rows 2.4 m long and 30 cm apart. Plant spacing within rows was 30 cm, giving 7 competitive plants/plot. Alternate rows had been previously seeded to a tall check variety, CS-M3, to afford uniform competition. Similar procedures were followed in 1975, except that plot lengths were 1.5 m, giving 5 competitive plants/plot at 25 cm spacings. The experimental design was a four-replicate randomized block. Despite slightly different plot configurations in the two years, error variances (based on plot means) were homogeneous. Measurements on transplanted materials were well correlated with equivalent measurements on direct seeded plants, except for G30, which was relatively shorter under transplant conditions. Therefore F_1 data from crosses involving G30 should be viewed with caution.

In the second experiment, parent and F_2 generations were grown for diallel cross analysis (1975) and for segregation analysis (1974 and 1975). Single F_2 seeds were space-planted 20 cm apart in 30 cm rows. Rows were 3.2 m long, allowing for 15 competitive hills and 2 end-of-row guard hills. The experimental design was a two-replicate randomized block. F_2 plots consisted of 10 rows, or 150 plants/replication. Parents were represented by 2 four-row plots (60 plants/plot) per replication. Both plots were used in segregation analysis, but one plot was chosen at random for use in diallel analysis.

The third experiment consisted of F_3 progeny tests grown from single F_2 plants. Fifteen to eighteen plants in a single, unreplicated 1.5 m row usually resulted. Plant height was measured on a row mean basis, taking into account frequency of segregates.

Diallel cross analysis as developed by HAYMAN and JINKS (HAYMAN 1954; JINKS 1954) for F_1 data and its extension to accommodate F_2 data (JINKS 1956; HAYMAN 1958) was utilized in conjunction with, and as an interpretive aid to segregation analysis. The method allows rapid evaluation of a set of genotypes differing at many loci. But, diallel cross parameter estimates containing squared effects terms are weighted by genes with larger effects (CRUMPACKER and ALLARD 1962). Therefore, in the presence of major, but subqualitative genes, diallel analysis may reflect more closely the properties of these genes of larger effect which are of greater interest in breeding applications.

Diallel cross variance component estimates are unbiased only if several assumptions are met (HAYMAN 1954). Those assumptions believed fulfilled include parental homozygosity, diploid segregation, and lack of maternal effects. Remaining assumptions are: no epistasis, no multiple allelism, and uncorrelated gene distribution. Analysis of variance of $(W_r - V_r)$ was used to test the assumptions (HAYMAN 1954), where significant heterogeneity of $(W_r - V_r)$ suggests failure of one or more assumptions. If the assumptions are violated, subdiallels which conform may be constructed by removing those arrays which cause heterogeneity of $(W_r - V_r)$.

A factorial analysis of variance of W_r and V_r statistics from diallel cross experiments repeated in space or time provides a specific test for certain types of epistasis. The Arrays $\times$ Dominance interaction is a measure of types of gene interaction present in classical epistatic models (ALLARD 1956).

Genotypic variances in the F_2 generation were estimated as the difference between total F_2 variance and an estimate of environmental variation. The geometrical mean variance of the two parents involved in each cross was used to estimate environmental variation (WEBER and MOORTHY 1952).

RESULTS AND DISCUSSION

Analysis of variance of $(W_r - V_r)$ values detected significant heterogeneity ($0.01 < P < 0.05$) in 1974 F_1 and 1975 F_2 diallels, and highly significant ($P < 0.01$) heterogeneity in the 1975 F_1 experiment. Thus epistasis, multiple allelism, and/or correlated gene distribution seems to be a general feature of the system. It was necessary to delete two arrays in each of the F_1 diallels and one array in the F_2 diallel to restore homogeneity to $(W_r - V_r)$ statistics (Table 2).

Estimates of diallel cross variance components are provided in Table 2. Estimates should not be directly compared across experiments as different arrays were deleted. However, the large magnitudes (relative to standard errors) of D, and H_1 and H_2 indicate that additive and dominance variation, respectively, are significant. $(H_1/D)^{1/2}$ is an estimate of overall level of dominance. Averaged over the three experiments, $(H_1/D)^{1/2}$ was 0.8, in the range of partial to full dominance. The ratio $[(4DH_1)^{1/2} + F]/[(4DH_2)^{1/2} - F]$ predicts a greater proportion of dominant alleles, being 1.2 as a mean of three experiments. Any proposed genetic model should be consistent with these observations from diallel analysis.

A factorial analysis of variance (ALLARD 1956) was performed on transformed W_r and V_r statistics in 1974 and 1975 10-parent F_1 diallels. The Arrays × Dominance term was nonsignificant, suggesting that epistasis is not an important contributor to variation in this system. Since epistasis apparently is lacking, the source of $(W_r - V_r)$ heterogeneity must be sought through multiple allelism or correlated gene distribution. Failure of either assumption leads to complex results (HAYMAN 1954; HAYMAN 1957). Thus, proposed genetic models need not include epistasis but may include multiple allelism and/or correlated gene distribution.

Means $(\bar{x})$ and genotypic variance estimates (s_g^2) of the F_2 generation are given for 17 crosses in 1974 and 19 crosses in 1975 (Table 3). An adequate description of the genetic system involved in all 45 crosses can be made by considering these selected crosses. The crosses are arranged in four groups representing

TABLE 2

Estimates of variance components and standard errors for plant height in two 8-parent F_1 subdiallels and a 9-parent F_2 subdiallel

	F_1		F_2
Component	1974*	1975†	1975‡
D	136.6 ± 10.3	274.8 ± 7.8	464.8 ± 5.2
H_1	211.7 ± 23.6	110.8 ± 17.9	190.2 ± 11.6
H_2	142.0 ± 20.6	87.4 ± 15.5	132.4 ± 10.0
F	−13.6 ± 24.3	38.8 ± 18.4	123.9 ± 12.3

* Huang-to-do and G30 arrays omitted.
† G30 and Tedoriwase arrays omitted.
‡ CI 9858 array omitted.

tall × major-gene semidwarfs, tall × polygenic semidwarfs, crosses between allelic major-gene semidwarfs, and crosses between nonallelic major-gene semidwarfs.

The tall California parent, G30, and short parents D51, G33, and D66 all have Calrose as an ultimate common ancestor (Table 1). G30 was produced by a cross with a Calrose derivative (CS-M3), G33 from crossing and backcrossing an early maturing Calrose mutant (Earlirose) with T(N)1, followed by selection for short sature. T(N)1 is known to possess a major semidwarfing gene (AQUINO and

TABLE 3

Means and variances of parents and F_2 generations for 19 crosses in 1974 and 1975

	Population	1974 n	1974 $\bar{x}$ cm	1974 s^2	1975 n	1975 $\bar{x}$ cm	1975 s^2	$\overline{s^2}$
	Parent			s_p^2			s_p^2	
1	Huang-to-do	62	138	108.1	214	141	72.9	90.5
2	G30	47	108	16.1	202	113	24.0	20.0
3	CI 9858	54	104	15.4	205	100	26.4	20.9
4	D66	59	96	11.4	188	99	11.8	11.6
5	Hokuriki 76	55	89	14.9	208	96	14.6	14.8
6	D51	60	90	14.1	181	88	10.9	12.5
7	Tedoriwase	51	88	12.6	209	84	20.7	16.2
8	G33	63	88	18.1	148	76	8.5	13.2
9	IV29–4	27	78	12.2	166	81	14.5	13.4
10	72/2234–11	59	71	18.1	201	70	11.5	14.8
	F_2			s_g^2			s_g^2	
Tall × major-gene semidwarfs								
	$P_2 \times P_4$	156	107	86.8	241	111	79.6	83.2
	$P_2 \times P_6$	151	105	72.4	177	102	67.5	70.0
	$P_2 \times P_8$	133	104	67.1	271	98	88.0	77.6
	$P_3 \times P_2$	102	114	31.6	236	108	35.4	33.5
Tall × multiple-gene semidwarfs								
	$P_5 \times P_1$	213	118	14.2	277	121	23.1	18.6
	$P_7 \times P_1$	214	109	5.2	274	117	23.9	14.6
	$P_9 \times P_1$	192	111	17.3	255	108	33.0	25.6
	$P_2 \times P_5$	—	—	—	249	102	35.8	35.8
	$P_7 \times P_2$	—	—	—	248	100	30.5	30.5
	$P_2 \times P_9$	207	91	18.7	258	95	66.4	42.6
Allelic semidwarfs								
	$P_8 \times P_6$	66	86	7.6	247	92	49.2	28.4
	$P_{10} \times P_6$	203	83	−1.8	211	78	30.0	14.1
	$P_{10} \times P_8$	98	74	0.4	219	70	64.5	32.4
Non-allelic semidwarfs								
	$P_8 \times P_4$	102	99	171.8	265	98	183.2	177.5
	$P_6 \times P_4$	189	99	85.2	246	100	86.6	85.9
	$P_3 \times P_6$	189	105	63.6	260	102	109.4	86.5
	$P_3 \times P_4$	29	110	85.5	253	109	109.1	97.4
	$P_3 \times P_8$	162	106	123.7	278	106	157.9	140.8
	$P_4 \times P_{10}$	24	91	92.2	263	91	156.5	124.4

JENNINGS 1966). Both D51 and D66 are short-stature Calrose mutants (RUTGER *et al.* 1976). Thus, these four parents constitute a relatively simple genetic system. This assumption is supported by estimates of the number of effective factors, N (WRIGHT 1968), controlling height in G30 crosses to each of the short-stature parents. Assuming no dominance, N averaged 1.2 for the three crosses over two years. The assumption of no dominance reduces N by a maximum of 33%, compared to complete dominance (WRIGHT 1968). Therefore, as an initial hypothesis, D66, D51 and G33 are dwarfed by single genes.

F_2 distributions for G30 × D66, G30 × D51 and G30 × G33 were all bimodal except for the cross G30 × D51 in 1974, which yielded a trimodal distribution (Figure 2 A, B, C). Phenotypic classification was precluded by the continuous nature of the distributions, but both parental types were recovered in large numbers. Relatively simple genetic control was indicated by the oligomodal distributions. Skewness toward short plants, and intermediate to tall F_2's (Figure 1 A, B, C) indicated dominance for increased height.

While the three F_2 distributions are suggestive of single-gene segregations, F_3 information is required for a definitive test. In progeny tests of random F_2 plants it was possible to classify visually each F_3 row unambiguously into one of three classes; semidwarf, segregating, or tall. χ^2 tests (Table 4) support the hypotheses of single-gene differences in all three crosses ($0.10 < P < 0.75$).

The ability to distinguish heterozygous from homozygous tall F_2 plants on the basis of a progeny test allows an estimate of the dominance level of the semidwarfing gene. The following formula

$$h = (\hat{F}_1 - MP)/(HP - MP)$$

yields an estimate, h, of the degree of dominance where $\hat{F}_1$ is an estimate of the height of the F_1 obtained from heterozygous F_2 plants, and HP and MP are high parent and midparent, respectively. This formula is applicable only where a single gene accounts for a majority of the variation (MATHER and JINKS 1971). t-tests showed significant ($P < 0.05$) height difference between homozygous tall and heterozygous plants in G30 × D51 (110.9 *versus* 107.5 cm) and in G30 × G33 (110.4 *versus* 105.1 cm), while homozygous tall and heterozygous F_2 plants in G30 × D66 did not differ significantly (112.0 *versus* 111.9 cm). Midparent

TABLE 4

Distribution of F_3 lines in phenotypic height classes in three crosses

F_3 class	Cross G30 × D51	G30 × D66	G30 × G33
Tall	43	33	41
Segregating	72	80	61
Semidwarf	36	40	29
	151	153	131
$P\ \chi^2$ 1:2:1	0.50–0.75	0.50–0.75	0.10–0.25

Entries are numbers of F_3 lines. Tests are of single-gene hypotheses.

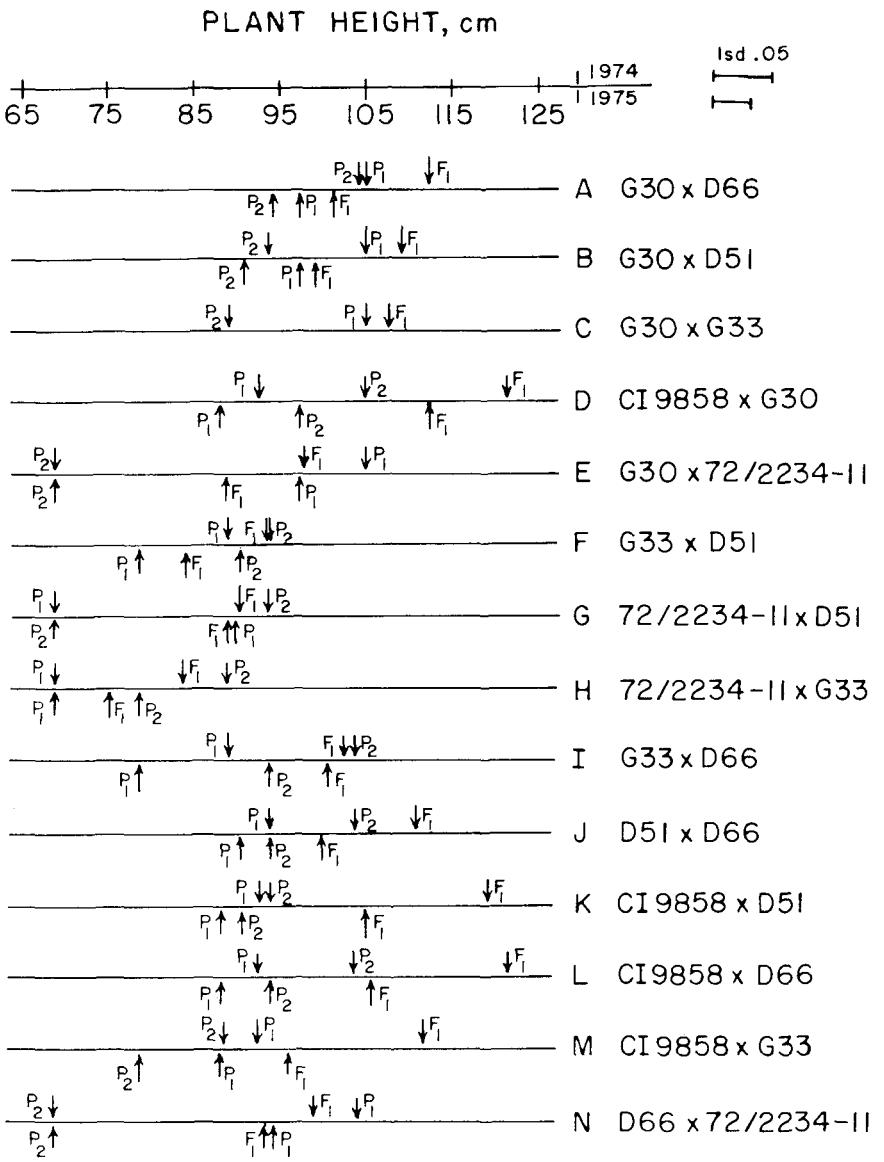

FIGURE 1.—Parent and F_1 plant heights for 14 selected crosses in 1974 and 1975. Heights are indicated by ↓ (1974) and ↑ (1975). P_1, P_2, and F_1 are the female and male parents, and the F_1 between them, respectively.

heights for the three crosses were 103.7, 102.0, and 101.7, respectively. Complete dominance ($h = 1$) is indicated in G30 × D66, while in the former two crosses partial dominance is indicated. Applying the above formula, h was 0.53 for G30 × D51 and 0.37 for G30 × G33. This level of dominance could explain the greater number of intermediate F_2 plants in crosses G30 × D51 and G30 × G33 in comparison to G30 × D66.

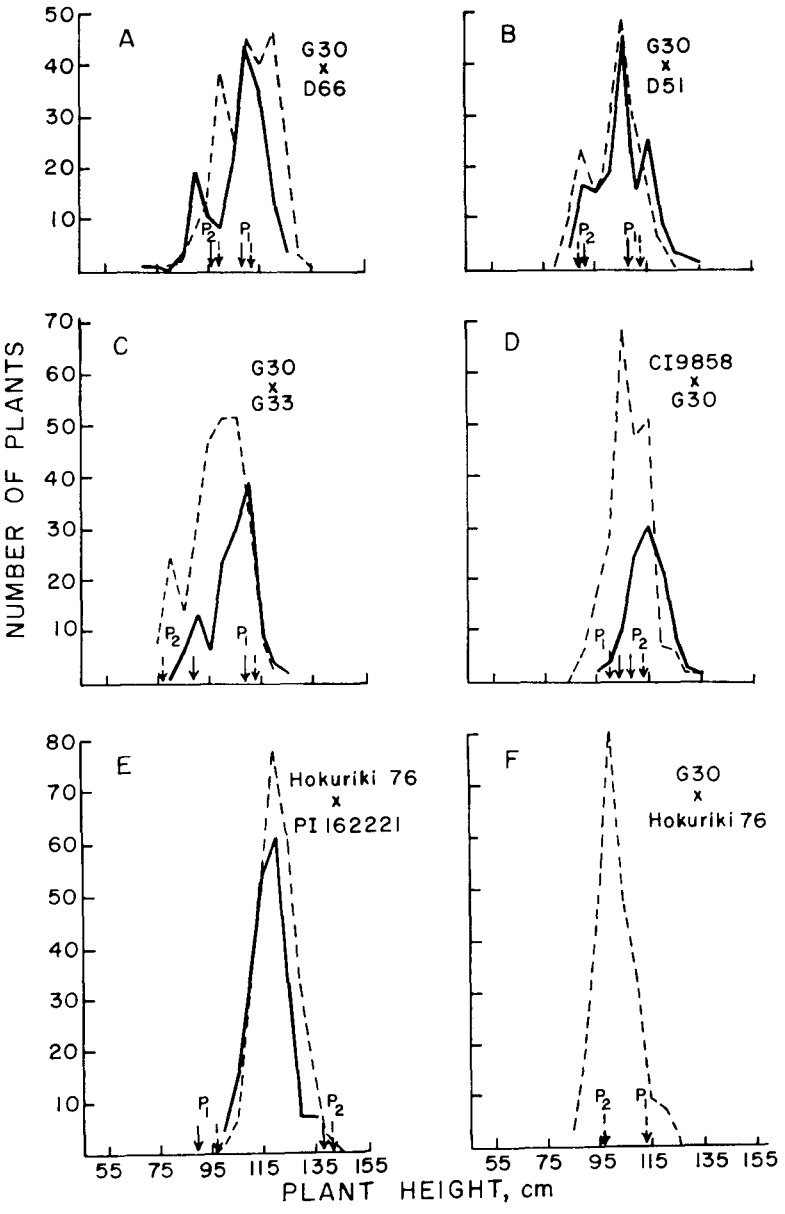

FIGURE 2.—Two-year F_2 plant height distributions for six crosses. A, B, C, and D are tall × major-gene semidwarf crosses; E and F represent tall × multigenic semidwarf crosses. —— 1974 - - - 1975. P_1 and P_2 represent female and male parents in each cross.

Crosses among the three semidwarf parents, G33, D51, and D66, determined their allelic relationships. If, as shown above, each line differs from a tester line, *e.g.*, G30, by a single gene, the lines must either be allelic or differ at two loci, only. These two possibilities should be easily distinguished in the F_2 generation.

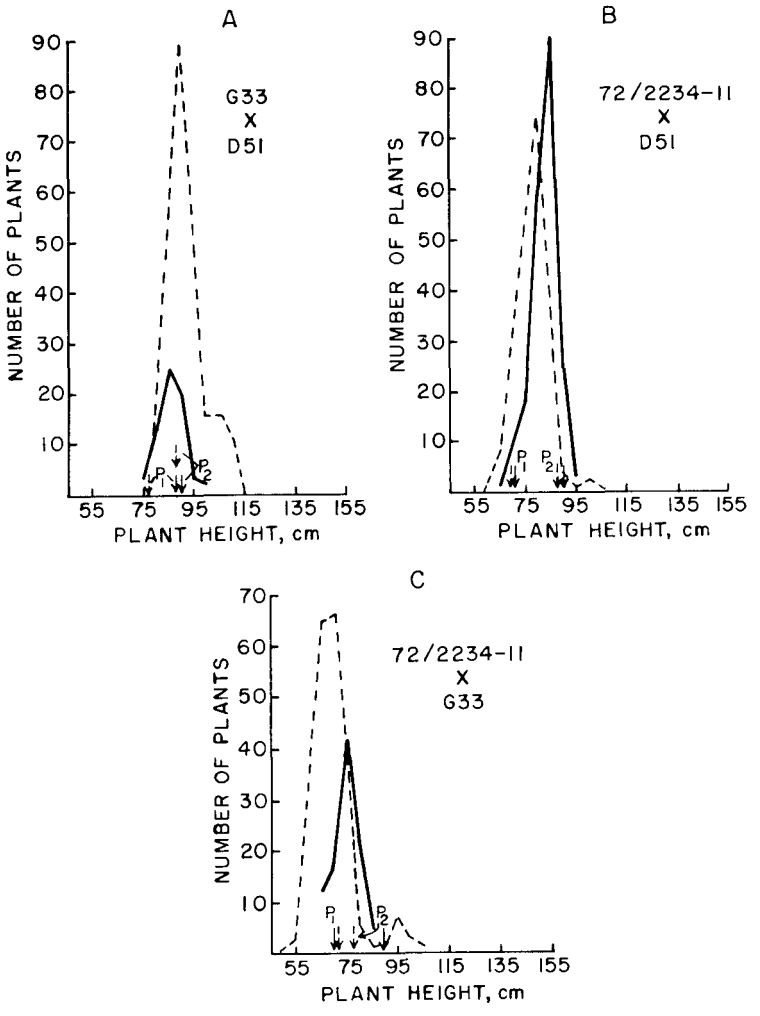

FIGURE 3.—Two-year F_2 plant height distributions for crosses among three allelic major-gene semidwarfs. —— 1974 - - - 1975. P_1 and P_2 represent female and male parents in each cross.

In marked contrast to the above is the cross G33 × D66, in which the genotypic F_2 variances were much larger than for G33 × D51 (Table 3). The F_1 was significantly taller than D66 in 1975, but not in 1974 (Figure 1I). A wide range of

The F_1 generation of G33 × D51 was of semidwarf height in both years (Figure 1F), and few F_2 plants exceeded parental extremes. The relatively narrow range of segregates in each year (Figure 3A), suggests identity of semidwarfing loci in G33 and D51. The small 1974 F_2 was progeny-tested in its entirety in 1975. Minimal segregation, either within or between lines, was observed in the population of 66 F_3 families, and the mean height of only one line lay outside the range of the parents (Table 5). This supplies substantial support for the identity hypothesis.

TABLE 5

Height distributions of parents and random F_3 lines from crosses among three allelic semidwarf parents

Cross or parent	n	Class center, cm 60	65	70	75	80	85	90	95	100	105
G33	13	..	..	..	2	7	3	1	..	..	..
G33 × D51 F_3	66					8	18	23	11	5	1
D51	12					1	4	3	3	1	
2234-11	3	2	1								
2234-11 × G33 F_3	94	1	5	17	31	29	9	1	1		
G33	5				1	2	1	1			
2234-11	7	2	3	2							
2234-11 × D51 F_3	202			4	10	34	70	52	28	4	
D51	9						1	2	5	1	

segregates transgressing parental extremes in both directions was observed in the F_2 in both years (Figure 4A). These results strongly implicate nonallelic major dwarfing genes. The appearance of transgressive segregates further suggests that the gene effects are additive.

Since the semidwarfing genes in D33 and D51 were shown to be allelic, and G33 and D66 appear to be differentiated by two genes, the cross D51 × D66 would be predicted to show a two-gene segregation. Observations on F_1 (Figure 1J) and F_2 (Figure 4B) generations were consistent with this prediction.

Progeny testing of random F_2 plants was again instrumental in evaluating the above hypotheses. Among the 102 F_3 lines of G33 × D66 it was possible to distinguish visually seven phenotypic classes (Table 6). Thus, the test of goodness of fit in F_3 was equivalent to testing a 9:3:3:1 ratio in F_2. The observed fit was excellent, $(0.25 < P < 0.50)$, confirming nonallelism for semidwarfing genes in G33 and D66.

TABLE 6

Distribution of random F_3 lines in phenotypic height classes from the cross G33 × D66

F_3 class	Observed	Expected Number	Expected Ratio
Tall, uniform	10	6.4	1
Tall, segregating	49	51.0	8
Semidwarf (D66), uniform	5	6.4	1
Semidwarf (D66), segregating	19	12.8	2
Semidwarf (G33), uniform	5	6.4	1
Semidwarf (G33), segregating	10	12.8	2
Double dwarf	4	6.4	1
	102	102	
P χ^2 6 df	0.25–0.50		

Test of two-gene hypothesis with expectations based on a 9:3:3:1 F_2 segregation.

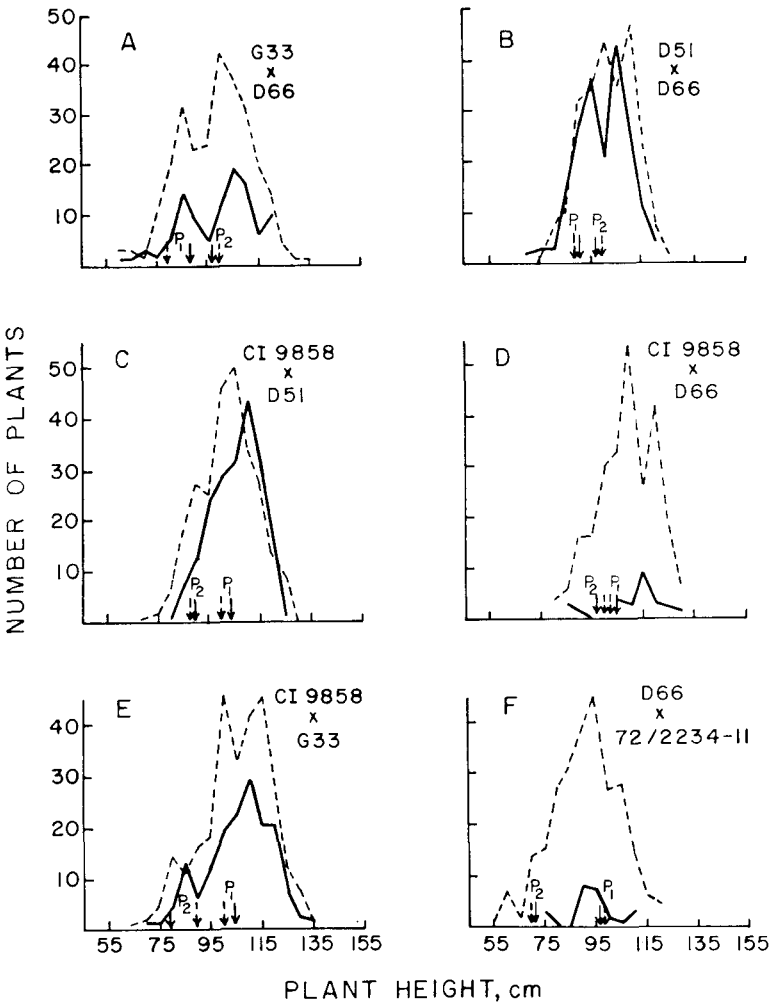

FIGURE 4.—Two-year F_2 plant height distributions for six crosses between nonallelic major-gene semidwarfs. —— 1974 - - - 1975. P_1 and P_2 represent female and male parents in each cross.

Greater difficulty was encountered in classifying the F_3 of D51 × D66 than the F_3 of G33 × D66. Parental phenotypes were not sufficiently different to distinguish visually, so both semidwarf types were pooled. In addition, detection of segregation was more difficult because of the similar heights of D51 and D66 (88.5 cm *versus* 98.9 cm) and the observed partial dominance of the D51 gene. Therefore, the poor fit ($P < 0.005$) to the expected 1:8:2:4:1 is not surprising (Table 7). Examination of table entries shows the major contribution to the large χ^2 lies in an excess of nonsegregating types in both tall and semidwarf classes. When segregating and uniform types were pooled within semidwarf and tall classes, the test became one of a 9:6:1 ratio, but was a weaker *a posteriori* test. Prior note of the classification difficulties somewhat lessens the weakness.

TABLE 7

Distribution of random F_3 lines in phenotypic height classes in the cross D51 × D66

F_3 class	Observed	Expected No.	Expected Ratio	Observed	Expected* No.	Expected* Ratio
Tall, uniform	29	11.8	1	108	105.8	9
Tall, segregating	79	94.1	8			
Semidwarf, uniform	33	23.5	2	70	70.5	6
Semidwarf, segregating	37	47.0	4			
Double dwarf	10	11.8	1	10	11.8	1
	188	188		188	188	
$P\ \chi^2$	4 df < 0.005			2 df	0.75–0.90	

Test of two-gene hypotheses with expectations based on a 9:6:1 F_2 segregation.

* Values based on pooled uniform and segregating types within semidwarf and tall classes.

The agreement of observed with expected results became $0.75 < P < 0.90$ and the two-gene hypothesis was accepted.

Ten double-dwarf F_3 families were identified in D51 × D66. Eight were selected for further evaluation in a winter nursery in Hawaii. Eighty-four F_4 lines averaged 70.9 ± 0.4 cm compared to 79.0 ± 0.7 cm for D51 and 89.2 ± 0.8 cm for D66 with double-dwarf lines ranging from 64 to 79 cm. These results indicate the significantly shorter nature of the putative double dwarfs when compared to the shorter parent, and are indirect evidence supporting the two-gene model.

When CI 9858 is crossed to G30, D66, D51, and G33, the F_1 plants are considerably taller than G30 (Figure 1D, K, L, M). Because G30, D66 and D51 have similar genetic backgrounds, heterotic effects should be approximately equal when each is crossed to CI 9858. The near equality of height in the three crosses therefore suggests an additional contribution from nonallelism of recessive genes for shortness. The F_2 distributions of CI 9858 × G30 (Figure 2D) are inconclusive, but a considerable number of segregates taller than G30 were observed. In F_3, a slightly wider range of types was observed. Ninety-seven random F_3 lines ranged from 82 to 118 cm while CI 9858 ranged from 86 to 100 and G30 from 92 to 115 cm. In all, 11 of 97 F_3 lines transcended the parents, indicating segregation of factor(s) large relative to the 12.7 cm differential between the parents.

The F_2 distributions of CI 9858 × D51, CI 9858 × D66, and CI 9858 × G33 (Figure 4C, D, E) differed sharply from that of CI 9858 × G30 (Figure 2D). These populations were characterized by a very wide range in plant heights. Transgressive segregates, especially for tallness, were observed in every case. Supporting these visual contrasts were estimates of genotypic variances, having a mean of 108.2 for the three CI 9858 × semidwarf crosses compared to 33.5 for CI 9858 × G30 (Table 3).

F_1 and F_2 data from crosses of CI 9858 with three semidwarf parents (*i.e.*, D51, D66, C33) possessing two nonallelic genes indicate that a third dwarfing gene is

present in CI 9858. A definitive test of this hypothesis may be afforded by F_3 progeny tests. Unfortunately, due to apparent segregation for minor height genes contributed by CI 9858, it was impossible to classify lines phenotypically. However, uniformly short putative double-dwarf lines were observed in each cross, and their expected frequency (1/16) is useful as an approximate test (Table 8).

One of 27 F_3 lines in CI 9858 × D66 was classified as a double dwarf. This provides a χ^2 of 0.30 with $0.50 < P < 0.75$. In CI 9858 × D51, 12 of 176 lines were identified as double dwarfs. This yields a χ^2 of 0.10 with $0.75 < P < 0.90$. Finally, a χ^2 of 1.06 for 7 of 163 observed double-dwarf lines in CI 9858 × G33 gives a probability range of 0.25 — 0.50. Combining this information with that from the F_2 progenies described above, and the fact that substantial numbers of F_3 lines exceeded the taller parent in mean height, provides good evidence for three segregating, mutually nonallelic genes in these crosses.

Lack of information from G30 × 72/2234–11 prevented clarification of the genetic control of reduced height in 72/2234-11. Consequently, crosses of 72/2234–11 with other short parents must be relied on. Contrasting the results obtained in crosses 72/2234–11 × D51 and 72/2234–11 × G33 with the cross D66 × 72/2234–11 is illuminating. All 3 F_1 lines were intermediate to the parents in both years (Figure 1G, H, N), but differences were observed in F_2 and F_3 generations.

The crosses 72/2234–11 × D51 and 72/2234–11 × G33 were consistent in displaying little variation. A narrow range of segregates were observed in F_2 (Figure 3B, C), with mean genotypic variance being only 23.3 (Table 3). With a single exception, F_3 line means fell within the parental range (Table 5), and segregation within lines was minimal. Thus, results indicate that 72/2234–11 carries a semidwarfing gene at the same locus as D51 and G33, with the height differentials between 72/2234–11, and D51 and G33 attributable to a number of genetic factors with small effects. Conversely, the situation in D66 × 72/2234–11 is quite different. Transgressive F_2 segregates were observed despite a small ($n = 24$) population in 1974 (Figure 4F), and mean genotypic variance (124.4) was much larger than in the previous two crosses (Table 3). No double-dwarf F_3 progenies

TABLE 8

Height comparisons between putative double dwarf F_3 lines and their parents

Cross	Double dwarf lines			P_1			P_2		
	Frequency	Mean	Range	*n*	Mean	Range	*n*	Mean	Range
CI 9858 × D51	12/176	81.4	75–88	6	92.2	82–105	7	89.7	85–95
D51 × D66	10/188	81.1	77–87	9	92.6	86–95	9	99.9	93–105
CI 9858 × G33	7/168	73.3	70–80	9	95.8	79–105	7	81.7	74–90
G33 × D66	4/102	67.8	65–70	5	78.8	75–85	7	86.6	75–100
CI 9858 × 2234–11	11/192	66.8	60–73	8	97.8	85–110	8	62.9	55–70
D66 × 2234–11	0/24	—	———	–	—	———	–	—	———
CI 9858 × D66	1/27	90.0		4	108.8	100–120	6	100.8	100–105

Heights in cm.

were identified, but the number of progenies grown was small (Table 8). Since 72/2234–11 was shown to possess a major semidwarfing gene allelic to that in D51, segregation in the cross CI 9858 × 72/2234–11 should bear some similarity to that of D66 × 72/2234–11, since both CI 9858 and D66 are nonallelic to D51. In fact, results of the cross CI 9858 × 72/2234–11 were very similar to D66 × 72/2234–11 (data not shown), except that the F_1 exceeded CI 9858 in height in the former cross in both years. No F_2 plants shorter than 72/2234–11 were identified, nor were any F_3 lines shorter than 72/2234–11. Nonetheless, a group of uniform F_3 lines considerably shorter than the remaining progenies was observed. Since 72/2234–11 probably possesses multiple factors for reduced height in addition to its major gene, plants shorter than 72/2234–11 would be rare in the modest F_2 populations grown ($n = 446$ over two years). Therefore, the observed short progenies probably represent doubly recessive genotypes, in terms of major genes.

A comparison of mean heights of all putative double-dwarf lines with those of the parents is given in Table 8. With respect to three major genes, 3 types of double dwarfs are possible. CI 9858 × D51, CI 9858 × G33, and CI 9858 × 72/2234–11 should all produce a double dwarfs of similar genotope. A second group involves D51 × D66 and G33 × D66. Finally, CI 9858 × D66 double dwarfs should be distinct. Differentiation may occur within the former two groups if multiple alleles are present.

When the five semidwarf parents previously discussed are crossed to Huang-to-do, relatively wide segregation occurs as evidenced by large estimates of $\overline{s_g^2}$ (84.8 in 1974 and 113.0 in 1975). In contrast, crosses of short-stature genotypes Hokuriki 76, Tedoriwase, and IV29–4 with tall parents Huang-to-do and G30 show relatively little segregation ($\overline{s_g^2} = 13.8$ in 1974 and 35.4 in 1975) (Table 3). F_2 distributions of Hokuriki 76 × Huang-to-do (Figure 2E) and G30 × Hokuriki 76 (Figure 2F) are presented as representative of this group of six similar crosses. In addition, a continuous range in variation was observed in F_3 progenies of each cross. Therefore, it was concluded that height reduction in Hokuriki 76, Tedoriwase and IV29–4 is due to multiple genetic factors with effects smaller than those individually detectable by these experiments. Since G30 × Huang-to-do shows no convincing evidence of major gene segregation, it is possible to explain the majority of the variation in the diallel set of crosses on the basis of three major genes.

The genotype of each of the 10 parents can be specified in terms of three genes Sd_1, Sd_2, and Sd_3 (Table 9). The magnitudes of effects rank as follows, $Sd_1 > Sd_2 \geqslant Sd_3$. As shown by comparisons of heterozygous and homozygous tall F_2 plants, Sd_1 is partially dominant to sd_1 ($h = 0.5$), and Sd_2 is fully dominant to sd_2, while Sd_3 appears to be at least partially dominant to sd_3. The latter statement is based primarily on F_1 information, though the issue is clouded somewhat by possible additional factors for increased heght in CI 9858 not present in G30.

Surprisingly, IV29–4 was found not to possess the DGWG gene, despite being a derivative of T(N)1, which does carry the DGWG gene (AQUINO and JENNINGS 1966; HEU, CHANG and BEACHELL 1968). Short stature in IV29–4 is ap-

TABLE 9

Proposed genotypes of the ten diallel parents with respect to three major genes

Parent	Genotype
Huang-to-do	$Sd_1Sd_2Sd_3$
G30	$Sd_1Sd_2Sd_3$
Hokuriki 76	$Sd_1Sd_2Sd_3$
Tedoriwase	$Sd_1Sd_2Sd_3$
IV29-4	$Sd_1Sd_2Sd_3$
D51	$sd_1Sd_2Sd_3$
G33	$sd_1Sd_2Sd_3$
72/2234-11	$sd_1Sd_2Sd_3$
D66	$Sd_1sd_2Sd_3$
CI 9858	$Sd_1Sd_2sd_3$

parently instead derived in multigenic fashion from its japonica parent, Jinheung. In California, Jinheung is similar in height to Hokuriki 76 and Tedoriwase.

The predictions of diallel analysis are realized, in that a model with additive loci effects (no epistasis), partial to complete dominance for increased height, and a preponderance of dominant alleles was found to satisfactorily explain the observed variation.

As discussed above, multiple allelism or correlated gene distributions may be responsible for the observed heterogeneity in $(W_r - V_r)$ statistics. The model (Table 9) provides no evidence for correlated gene distribution. Therefore, evidence for multiple allelism should be examined. The most likely group of lines involved is G30, D51, G33, and 72/2234–11 (Sd_1 locus).

Several bits of indirect evidence for the presence of multiple alleles at the Sd_1 locus are available: (1) detection of non-epistatic heterogeneity in $(W_r - V_r)$; (2) extreme recessive position of G33 array in two of three diallel graphs; weighting of W_r, V_r statistics by genes of large effects may imply that the dwarfing gene in G33 has a greater effect than those in D51 and 72/2234–11 (CRUMPACKER and ALLARD 1962); (3) F_3 progeny tests in crosses with D66 and CI 9858 were much easier to classify for G33 than D51. Greater distinction of height classes in the G33 crosses implies greater genetic effects; (4) estimates of the number of effective factors (N) controlling the mean 7.5 cm height difference between C33 and D51 were less than one both years. Estimates of N should be valid here because little transgressive segregation was observed; and (5) in 10 of 12 crosses (over two years) involving common parents, s_g^2 for crosses with G33 were larger than for those with D51 or 72/2234–11. D51 and 72/2234–11 crosses each had the largest s_g^2 once and were approximately equal in overall s_g^2. This consistently larger s_g^2 suggests that the G33 allele has larger effect. These conclusions are by no means definitive, and elucidation of the true allelic status at the Sd_1 locus would require more suitable experiments.

At least 16 independent sources of the DGWG dwarfing gene have been reported, all in indica backgrounds (LI, HU and WOO 1966; HU 1973; IRRI 1974).

The lines D51 and 72/2234–11 represent alternative, japonica, sources of the same (or an allelic) semidwarfing gene.

The present results are in agreement with previous studies reporting major-gene dwarfing in DGWG and its derivatives.

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