Theor. Appl. Genet. 55, 169-176 (1979)

Mode of Inheritance of Dwarf Stature and Allelic Relationships Among Various Spontaneous and Induced Dwarfs of Cultivated Rice *Oryza sativa* L.

V.P. Singh, E.A. Siddiq and M.S. Swaminathan
Indian Agricultural Research Institute, New Delhi (India)

Summary. Genetic study of spontaneous and induced dwarfs included the mode of inheritance of dwarf stature and the allelic relationships among various dwarfs. Qualitative genetic analysis involving crosses of fourteen dwarfs with a common tall variety 'IARI 11124' showed that the degree of dominance in the F_1 hybrids varied with the cross. With the exception of the crosses of IARI 6579 and IARI 10560 with the tall variety, all crosses exhibited incomplete dominance. The segregation pattern in F_2 populations of height classes showed dwarfness to be a monogenic recessive trait functioning, however, in association with modifier complexes of varied strength. From F_2 behaviour of all possible crosses involving the fourteen different dwarfs, the allelic relationships were deduced. Three major groups of dwarfs could be recognised. Group I, comprised of FF 36, IARI 5842, IARI 5906-2B, IARI 5923, IARI 10061, IARI 10560 and IARI 11445, was allelic to I-geo-tse and Dee-Gee-Woo-Gen with modifiers of predominantly negative effects, while group-2, comprised of dwarfs IARI 5901-2, IARI 5924, IARI 6579 and IARI 7312B, was also allelic to Dee-Gee-Woo-Gen and I-geo-tse but with large and equal number of modifiers of positive and negative effects. The induced mutant, Central Africa Mutant (CAM) which constituted the third group seemed to possess a dwarfing gene that was non-allelic to those of the above mentioned two groups of dwarfs, with equal strength of modifiers of plus and minus effects. Unlike the dwarfs of spontaneous origin, which are invariably allelic to 'Dee-Gee-Woo-Gen', the induced dwarf was non-allelic. Thus, induced mutagenesis appears to give rise to dwarfing genes different from those found in the naturally occurring dwarfs.

Key words: *Oryza sativa* L. – Spontaneous dwarfs – Induced dwarfs – Inheritance – Allelic relationship

Introduction

Although with the discovery and exploitation of the plant type concept the tropical rice world witnessed a major break-through in the yield potential of indica rice varieties, the use of these varieties has been limited in many Asian countries, including India. Of the various factors, a high degree of susceptibility to diseases and insect pests and a narrow choice of quality grades have been found important. The association of these two major drawbacks with most of the high yielding varieties has been attributed to the dwarfing gene Dee-Gee-Woo-Gen.

While research efforts to identify and study new sources of dwarfing genes are underway at the International Rice Research Institute, the Philippines, an initiative was made at the Indian Agricultural Research Institute, New Delhi, to collect and study dwarfs of spontaneous and induced origin. This led to the identification of a number of spontaneous dwarfs from a vast North-East Indian rice collection and a few induced mutants from different centres. The genetics and breeding value of the dwarf collection have been extensively studied in relation to the widely used dwarfing gene sources like Dee-Gee-Woo-Gen and I-geo-tse. The present paper, second in the series, deals with the mode of inheritance of various dwarfs and their allelic relationships.

Material and Methods

Allelic Relationships Among Various Dwarfs

Fourteen representative dwarfs, viz. FF 36, IARI 5842, IARI 5901-2, IARI 5906-2B, IARI 5923, IARI 5924, IARI 6579, IARI 7312B, IARI 10061, IARI 10560, IARI 11445, I-geo-tse, Dee-Gee-Woo-Gen and Central Africa Mutant (CAM) (Fig. 1), chosen on the basis of the findings of the Mahalanobis D^2 analysis (Singh et

0040-5752/79/0055/0169/$ 1.60

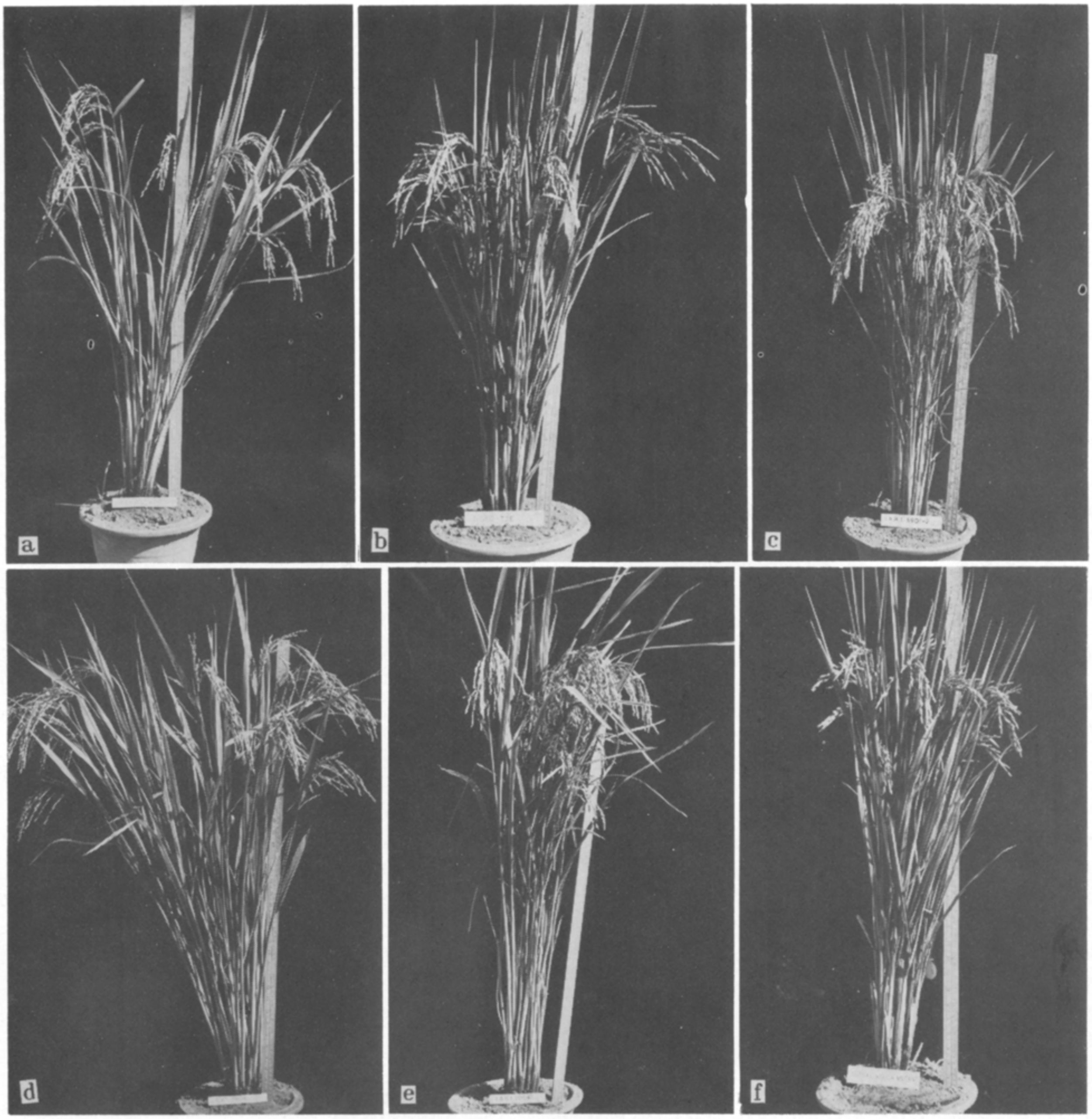

Fig. 1a-f. Photographs showing some of the representative dwarfs used in the study. **a** Dee-Geo-Wu-Gen, **b** I-geo-tse, **c** IARI 5901-2, **d** IARI 5924, **e** IARI 10061, **f** Central Africa Mutant (CAM)

al. 1978), were crossed in all possible combinations, excluding reciprocals. In all, 91 F_1 and F_2 populations were raised along with the parents in a randomised block design with two replications. Each plot consisted of eleven rows, each four meters long. Twenty-five day-old seedlings were transplated into a space of 20 × 15 cm with one seedling per hill. To ensure uniform spacing F_1's were transplanted along with their respective parents. Height observations were recorded at the time of maturity. The number of plants studied, parental, F_1 and F_2 populations, were 50, 10-15 and 200 respectively.

Data on height observations were subjected to the appropriate statistical analysis to estimate the mean, variance and standard error (Panse and Sukhatme 1954). Segregation for height in different crosses has been represented as frequency distribution along with the respective parents and F_1's.

Mode of Inheritance of Dwarfing Gene in Different Dwarfs

The same set of dwarfs were crossed with a common tall variety 'IARI 11124' in order to study the mode of inheritance of dwarf stature. Parental, F_1 and F_2 populations were raised in the same

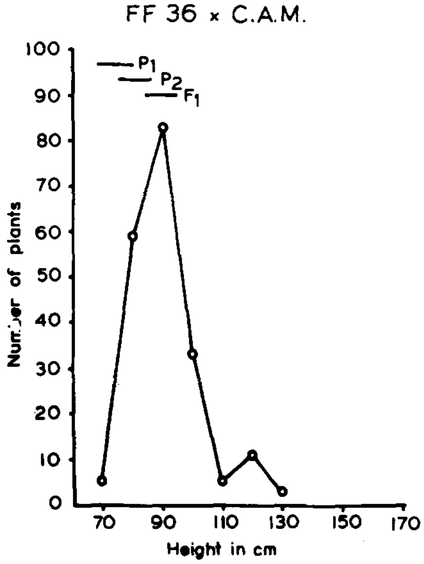

Fig. 2.

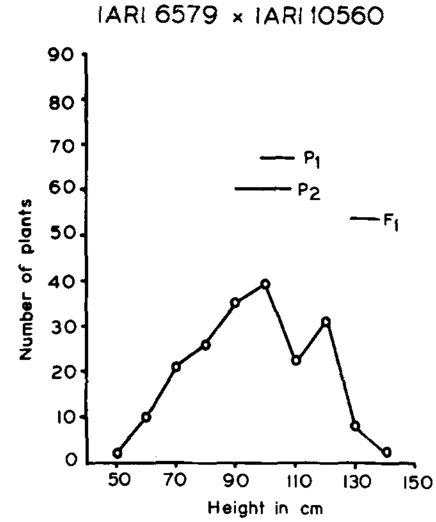

Fig. 4.

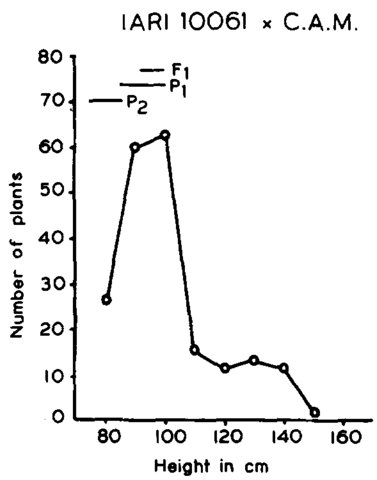

Fig. 3.

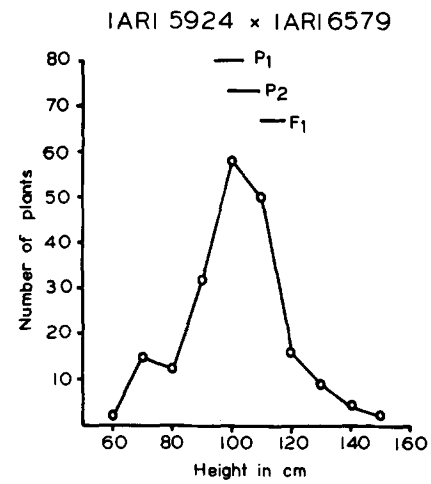

Fig. 5.

Figs. 2-5. Frequency distribution of height classes in F_1, F_2 and parents of four representative crosses involving spontaneous and induced dwarfs. 2 FF-36 X Central Africa Mutant (CAM), 3 IARI 10061 X CAM, 4 IARI 6579 X 10560, 5 IARI 5924 X ARI 6579

way as described in the previous experiment. A x^2 test of goodness of fit was performed crosswise to see whether the observed proportion of talls to dwarfs in the F_2's followed assumed Mendelian ratios.

Results

Allelic Relationships Among Various Dwarfs

Mean height of the fourteen dwarf parents under study varied from 63.51 cm in FF 36 to 104.46 cm in IARI 6579 (Table 1). Of all the possible 91 F_1 cross combinations, twenty-four exceeded the height of the respective better parent while height in thirty F_1s exceeded their respective midparental values. In the remainder the attained height was lower than their mid-parental values.

Frequency distribution of height classes and variance estimates in the F_2 populations varied with the cross. The F_2 behaviour of all the cross combinations is detailed below by group.

F_2 populations of FF 36 with all other dwarfs showed a continuous and normal distribution except for a slight skewness in the cross involving C A M (Fig. 2). The percentage of transgressive segregants also varied with the combination. FF 36 in combination with I-geo-tse, IARI 11445 and C A M was producing segregants with increased height while combinations with IARI 5842, IARI 5901-2, IARI 6579 etc. produced transgressive segregants of shorter height than either of the parents. In crosses of IARI 5842 with all the other dwarfs, the segregation pattern was continuous. Whereas its' combinations with IARI 6579 and C A M manifested transgression on both sides,

Table 1. Range, mean, variance and S.E. of parents and F_2 populations among crosses of spontaneous and induced dwarfs in respect of height (in cm)

S No.	Parents Crosses		Range	Mean	Variance	S.E.
	Parents					
1.	FF 36		55.80-67.50	63.51	21.00	± 0.458
2.	IARI 5842		80.40-89.50	85.47	23.04	± 0.678
3.	IARI 5901-2		86.00-100.00	91.64	21.35	± 0.635
4.	IARI 5906-2B		75.60-98.70	89.73	9.66	± 0.439
5.	IARI 5923		70.50-77.60	72.56	26.44	± 0.727
6.	IARI 5924		91.00-109.00	102.12	12.00	± 0.490
7.	IARI 6579		98.00-109.00	104.46	5.64	± 0.336
8.	IARI 7312B		85.40-97.00	92.10	10.58	± 0.459
9.	IARI 10061		85.50-105.00	94.22	24.96	± 0.705
10.	IARI 10560		90.00-109.50	101.52	22.56	± 0.671
11.	IARI 11445		84.00-94.50	87.59	13.44	± 0.517
12.	I-geo-tse		80.50-93.00	83.21	24.66	± 0.701
13.	DGWG		84.60-93.50	88.32	24.36	± 0.694
14.	C A M		75.50-86.00	81:36	5.64	± 0.336
	F_2 of crosses					
15.	FF 36	X IARI 5842	40.00-77.10	59.65	84.37	± 0.649
16.	"	X IARI 5901-2	41.00-89.20	62.75	113.93	± 0.754
17.	"	X IARI 5906-2B	54.50-117.50	80.95	210.01	± 1.020
18.	"	X IARI 5923	67.70-114.40	92.55	103.99	± 0.720
19.	"	X IARI 5924	55.00-129.00	83.05	278.19	± 1.178
20.	"	X IARI 6579	51.00-100.50	70.85	127.77	± 0.799
21.	"	X IARI 7312B	58.00-100.00	70.25	98.43	± 0.702
22.	"	X IARI 10061	48.00-84.70	70.50	91.94	± 0.677
23.	"	X IARI 10560	76.00-132.00	99.70	70.50	± 0.622
24.	"	X IARI 11445	75.00-133.00	99.20	66.95	± 0.578
25.	"	X IGT	71.00-106.00	86.95	70.18	± 0.591
26.	"	X DGWG	54.50-85.40	67.70	64.71	± 0.568
27.	"	X C A M	75.00-126.00	90.87	139.11	± 0.833
28.	IARI 5842	X IARI 5901-2	52.60-83.90	62.50	74.75	± 0.611
29.	"	X IARI 5906-2B	54.00-100.60	75.45	135.91	± 0.823
30.	"	X IARI 5923	37.10-76.00	52.00	98.00	± 0.699
31.	"	X IARI 5924	51.00-110.00	70.50	158.70	± 0.890
32.	"	X IARI 6579	44.00-127.50	69.10	269.19	± 1.159
33.	"	X IARI 7312B	50.40-88.60	64.30	77.51	± 0.622
34.	"	X IARI 10061	44.00-86.60	58.95	98.90	± 0.702
35.	"	X IARI 10560	50.50-92.80	67.55	139.49	± 0.835
36.	"	X IARI 11445	40.00-88.00	52.45	70.83	± 0.594
37.	"	X IGT	47.70-89.00	68.90	109.79	± 0.740
38.	"	X DGWG	86.00-127.00	89.45	41.19	± 0.453
39.	"	X C A M	67.00-138.00	91.00	230.00	± 1.072
40.	IARI 5901-2	X IARI 5906-2B	55.00-146.50	93.20	218.04	± 1.040
41.	"	X IARI 5923	51.50-88.10	68.75	81.93	± 0.640
42.	"	X IARI 5924	77.00-145.50	99.44	127.46	± 0.841
43.	"	X IARI 6579	45.00-119.80	80.95	291.59	± 1.207
44.	"	X IARI 7312B	77.00-99.50	82.50	60.50	± 0.549
45.	"	X IARI 10061	53.70-97.00	67.50	112.75	± 0.750
46.	"	X IARI 10560	71.00-153.00	104.90	142.99	± 0.819
47.	"	X IARI 11445	48.00-100.50	62.65	129.47	± 0.804
48.	"	X IGT	65.00-134.00	93.30	96.71	± 0.695
49.	"	X DGWG	56.40-90.00	74.10	90.19	± 0.671
50.	"	X C A M	52.00-89.50	66.15	94.67	± 0.688
51.	IARI 5906-2B	X IARI 5923	47.00-98.60	67.25	75.93	± 0.615
52.	"	X IARI 5924	56.70-99.00	74.60	100.84	± 0.710
53.	"	X IARI 6579	59.00-113.50	80.55	118.08	± 0.768
54.	"	X IARI 7312B	40.00-110.00	76.70	161.11	± 0.897
55.	"	X IARI 10061	54.70-97.00	67.55	82.49	± 0.642

Table 1. (Continuation)

S No.	Parents Crosses		Range	Mean	Variance	S.E.
56.	"	X IARI 10560	59.20-114.00	90.55	148.19	± 0.860
57.	"	X IARI 11445	25.50-89.00	70.95	84.36	± 0.649
58.	"	X IGT	65.80-106.50	82.35	108.97	± 0.737
59.	"	X DGWG	52.20-92.20	71.60	69.44	± 0.589
60.	"	X C A M	58.40-123.20	68.95	165.39	± 0.909
61.	IARI 5923	X IARI 5924	52.10-111.60	73.30	125.11	± 0.790
62.	"	X IARI 6579	37.00-91.60	64.05	183.08	± 0.958
63.	"	X IARI 7312B	59.30-105.50	80.40	112.84	± 0.751
64.	"	X IARI 10061	32.00-95.50	60.94	140.75	± 0.834
65.	"	X IARI 10560	55.00-95.50	75.45	122.79	± 0.783
66.	"	X IARI 11445	33.30-85.50	51.40	78.60	± 0.626
67.	"	X IGT	45.00-80.00	59.50	95.14	± 0.689
68.	"	X DGWG	48.00-90.00	62.38	101.45	± 0.071
69.	"	X C A M	71.00-140.20	90.00	184.50	± 0.960
70.	IARI 5924	X IARI 6579	65.00-155.00	101.15	281.80	± 1.186
71.	"	X IARI 7312B	63.60-109.80	82.55	134.39	± 0.821
72.	"	X IARI 10061	54.00-116.50	75.15	199.97	± 0.999
73.	"	X IARI 10560	55.00-118.60	86.10	170.78	± 0.923
74.	"	X IARI 11445	55.00-98.00	67.55	95.49	± 0.690
75.	"	X IGT	40.60-100.20	75.85	172.36	± 0.927
76.	"	X DGWG	66.00-125.00	100.60	124.98	± 0.788
77.	"	X C A M	53.00-128.00	84.10	125.18	± 0.790
78.	IARI 6579	X IARI 7312B	63.00-136.00	93.22	246.46	± 1.108
79.	"	X IARI 10061	41.30-118.20	76.45	215.11	± 1.036
80.	"	X IARI 10560	53.00-136.00	96.00	404.00	± 1.420
81.	"	X IARI 11445	40.00-116.00	64.45	195.69	± 0.988
82.	"	X IGT	52.40-112.50	83.90	196.78	± 0.991
83.	"	X DGWG	54.50-129.40	87.90	260.58	± 1.141
84.	"	X C A M	50.00-96.90	68.39	104.95	± 0.726
85.	IARI 7312B	X IARI 10061	74.00-121.00	95.65	88.57	± 0.665
86.	"	X IARI 10560	53.50-107.60	80.10	118.98	± 0.770
87.	"	X IARI 11445	49.00-106.50	76.90	146.19	± 0.855
88.	"	X IGT	40.60-97.00	75.65	103.51	± 0.719
89.	"	X DGWG	45.50-91.00	72.10	139.58	± 0.835
90.	"	X C A M	68.00-122.50	90.00	42.00	± 0.458
91.	IARI 10061	X IARI 10560	47.20-103.00	73.05	167.72	± 0.915
92.	"	X IARI 11445	40.60-101.00	63.45	180.61	± 0.949
93.	"	X IGT	54.30-103.30	74.70	103.82	± 0.719
94.	"	X DGWG	51.00-106.00	73.75	71.49	± 0.597
95.	"	X C A M	78.70-145.00	100.65	270.07	± 1.161
96.	IARI 10560	X IARI 11445	53.00-133.00	71.40	173.90	± 0.932
97.	"	X IGT	60.60-103.20	83.30	79.02	± 0.628
98.	"	X DGWG	51.50-99.80	75.75	99.51	± 0.705
99.	"	X C A M	46.30-98.30	75.35	131.87	± 0.811
100.	IARI 11445	X IGT	46.00-93.00	56.88	94.81	± 0.690
101.	"	X DGWG	57.80-94.00	68.90	109.79	± 0.740
102.	"	X C A M	46.50-85.50	66.75	98.43	± 0.701
103.	IGT	X DGWG	54.20-89.80	73.20	85.75	± 0.654
104.	"	X C A M	55.00-105.60	69.65	96.37	± 0.693
105.	DGWG	X C A M	45.50-104.00	64.00	90.00	± 0.674

in crosses with the rest of the parents the transgressive segregation was towards the negative direction. Crosses of IARI 5901-2 with FF 36, IARI 5842, IARI 6579 and I-geo-tse produced a good number of plants shorter than the shortest parent in a given cross. Interestingly, in the cross with FF 36 about 8% of plants were taller than the tallest parent. In cross combinations of IARI 5923 with all other parents except C A M the pattern of frequency distribution was normal. The height range of F_2 segregants in crosses of IARI 5923 with such dwarfs as FF 36, IARI 5842 etc. fell almost within the range of the parents. However, in F_2 populations of its crosses with other dwarfs such as IARI 5901-2, IARI 5924, I-geo-tse and DGWG it produced a large number of shorter plants than the shortest parent in a particular cross. In crosses with C A M, however, there was hardly any plant having a height of less than that of the shortest of the parents and instead about 21.5% of the plants were taller than the tallest parent.

In crosses of different dwarfs with IARI 10061, the nature of the F_2 segregation spread was found to vary with the cross. Except for crosses with IARI 7312 B, followed by IARI 5924 and IARI 6579, most of the combinations had segregants with their heights transgressing the respective tall parents. However, in almost all the crosses the segregants were found to invariably transgress the minimum range of the respective short parent. In certain crosses (IARI 5842 × IARI 10061) the F_2 population mean was 58.75 cm against the parental mean of 89.84 cm. Among the various crosses maximum F_2 variation was found in the cross IARI 10061 × C A M (Fig. 3). The F_2 behaviour of IARI 10560 in crosses with most of the parents was the same as in the case of IARI 10061. The occurrence of segregants markedly exceeding the parental limits on both sides was, however, characteristic of its crosses with I-geo-tse, DGWG and CAM. Of the crosses that showed transgressive segregation on both sides, IARI 6579 × IARI 10560 showed the highest variation of 404.00 (Fig. 4). The nature and spread of height classes in cross combinations of IARI 11445 with other parents varied with the cross. For instance , in crosses with FF 36 and IARI 10560 there were segregants with their heights exceeding the parental range in both directions, while in crosses with the rest of the dwarfs the extreme segregants were restricted to negative side only.

Crosses of different dwarfs with IARI 5901-2 also showed a normal frequency distribution in the F_2s as in earlier sets of crosses. Its crosses, involving IARI 10560, IARI 5906-2B and IARI 5924, were characterized by producing taller plants than the respective tallest parents. Variance estimates of the different F_2 populations varied from as high as 291.59 in crosses such as IARI 5902-2 × IARI 6579 to as low as 60.5 in IARI 5901-2 × IARI 7312B. The height range in the F_2 populations of the crosses of IARI 5924 with FF 36, IARI 7312B, IARI 10061, DGWG and CAM transgressed the parental limits on both sides (Figure 5). In combination with dwarfs such as IARI 5842, IARI 5923, IARI 10560 etc., however, it failed to produce taller plants than the respective tall parent. Among all the thirteen populations studied, the cross IARI 5924 × IARI 6579 exhibited the maximum variation. IARI 6579 in crosses with FF 36, IARI 5842, IARI 10061, I-geo-tse and CAM resulted in a number of shorter plants than the respective dwarf parents in the F_2 while the transgression was towards the positive side in crosses with IARI 10560. In crosses such as IARI 5901-2 × IARI 6579, IARI 6579 × IARI 7312B and IARI 6579 × DGWG the segregants transgressed the parental limits on both sides. The study of the F_2 populations of IARI 7312B with most of the parents showed the height range to fall within the range of the respective tallest parent and whatever transgression observed was beyond the lower limit of the respective shortest parent. In the cross IARI 6579 × IARI 7312B the transgression was bidirectional and the crosses IARI 6579 × IARI 7312B and IARI 6579 × IARI 10061 showed very high variances.

In the set of crosses involving I-geo-tse as a common parent, dwarfs such as IARI 5901-2, IARI 5906-2B and IARI 10560 threw segregants that transgressed the parental limits on both sides while the remainder showed predominantly segregants which exceeded the lower height range of the shortest of the parents. The segregation pattern of crosses of different dwarfs with DGWG was more or less similar to that of I-geo-tse except in the crosses IARI 5842 × DGWG where the F_2 height range fell within the parental limits and in the crosses IARI 5924 × DGWG and IARI 6579 × DGWG where both positive and negative segregants could be realized. DGWG with the rest of the parents invariably showed transgressive segregation towards the negative direction. Like the spontaneous dwarfs, C A M, the dwarf of induced origin, also showed normal F_2 distribution in all the combinations. The crosses FF 36 × CAM, IARI 5842 × CAM and IARI 5924 × CAM, which showed quite high variance estimates, were found to produce many transgressive segregants in the positive direction. With the height variation transgressing the limits of both parents, crosses such as IARI 5906-2B × CAM also showed high population variances. Transgressive segregants predominantly in the negative direction brought the population mean of this cross down lower than that of the parental mean. Crosses with IARI 7312B, though, produced largely plants having their heights within the parental limits, only rarely were transgressive segregants observed in the positive side.

Mode of Inheritance of Dwarf Stature

To study the nature of inheritance of dwarf stature all the fourteen dwarfs were crossed with a common tall variety 'IARI 11124'. Data on the parental mean and range, range, mean and variance of F_1 and F_2 populations are summarised in Table 2. It is evident from the table that F_1's of crosses of IARI 5901-2, IARI 5842, IARI 6579 and IARI 10560 with IARI 11124 could attain the height of the tall parent, whereas in the rest of the cases, the F_1 height remaind below that of the tall parent. F_2 popula-

Table 2. Parental mean, range, F_1 mean, variance and F_2 range, mean and variance among crosses of spontaneous and induced dwarfs when crossed with a common tall IARI 11124 in respect of height in cm

S No.	Crosses		P_1 range	P_1 mean	P_2 range	P_2 mean	F_1 mean	F_1 variance	F_2 range	F_2 mean	F_2 variance
1.	FF36	X IARI 11124	55.80- 67.50	63.51	140.00-156.00	148.10	125.90	0.16	53.00-137.00	105.94	450.39
2.	IARI 5842	X IARI 11124	80.40- 89.50	85.47	140.00-156.00	148.10	147.10	0.17	60.00-180.00	121.41	543.94
3.	IARI 5901-2	X IARI 11124	86.00-100.00	91.64	140.00-156.00	148.10	145.60	0.08	61.50-184.00	119.67	572.80
4.	IARI 5906-2B	X IARI 11124	75.60- 98.70	89.73	140.00-156.00	148.10	138.90	0.34	74.00-181.00	121.81	471.32
5.	IARI 5923	X IARI 11124	70.50- 77.60	72.56	140.00-156.00	148.10	134.80	0.03	66.00-159.50	118.69	390.85
6.	IARI 5924	X IARI 11124	91.00-109.00	102.12	140.00-156.00	148.10	140.90	0.28	77.50-160.00	121.50	694.00
7.	IARI 6579	X IARI 11124	98.00-109.00	104.46	140.00-156.00	148.10	149.70	0.32	55.00-168.00	130.75	255.34
8.	IARI 7312B	X IARI 11124	85.40- 97.00	92.10	140.00-156.00	148.10	131.40	0.12	51.00-170.00	106.56	598.95
9.	IARI 10061	X IARI 11124	85.50-105.00	94.22	140.00-156.00	148.10	137.10	0.16	59.50-158.00	116.36	350.57
10.	IARI 10560	X IARI 11124	90.00-109.50	101.52	140.00-156.00	148.10	148.60	3.65	54.00-173.00	124.75	856.17
11.	IARI 11445	X IARI 11124	84.00- 94.50	87.59	140.00-156.00	148.10	124.80	0.05	56.00-176.00	121.90	877.65
12.	IGT	X IARI 11124	80.50- 93.00	83.21	140.00-156.00	148.10	129.70	0.23	53.00-174.50	114.02	533.10
13.	DGWG	X IARI 11124	84.60- 93.50	88.32	140.00-156.00	148.10	129.20	0.21	52.20-146.00	119.14	686.87
14.	C A M	X IARI 11124	75.50- 86.00	81.36	140.00-156.00	148.10	121.00	0.20	70.00-181.00	126.75	285.44

Table 3. Test of significance for segregation of F_2 populations of cross of various Assam dwarfs with a common tall variety IARI 11124

S No.	Crosses		Observed Tall	Observed Dwarf	Expected Tall	Expected Dwarf	Assured ratio Tall	Assured ratio Dwarf	$(0\text{-}E)^2$ E	P value
1.	FF 36	X IARI 11124	238.00	65.00	227.25	75.75	3	: 1	2.0201	0.10-0.20
2.	IARI 5842	X IARI 11124	229.00	80.00	231.75	77.25	3	: 1	0.1304	0.70-0.80
3.	IARI 5901-2	X IARI 11124	233.00	70.00	227.25	75.75	3	: 1	0.5818	0.30-0.50
4.	IARI 5906-2B	X IARI 11124	235.00	70.00	228.75	76.25	3	: 1	0.6829	0.30-0.50
5.	IARI 5923	X IARI 11124	236.00	77.00	234.75	78.25	3	: 1	0.0265	0.80-0.90
6.	IARI 5924	X IARI 11124	26.00	9.00	26.30	8.70	3	: 1	0.0137	0.90-0.95
7.	IARI 6579	X IARI 11124	266.00	80.00	259.50	86.50	3	: 1	0.6489	0.30-0.50
8.	IARI 7312B	X IARI 11124	229.00	71.00	225.00	75.00	3	: 1	0.2844	0.50-0.70
9.	IARI 10061	X IARI 11124	240.00	69.00	231.75	77.25	3	: 1	1.1742	0.20-0.30
10.	IARI 10560	X IARI 11124	194.00	64.00	193.50	64.50	3	: 1	0.0051	0.90-0.95
11.	IARI 11445	X IARI 11124	45.00	13.00	43.50	14.50	3	: 1	0.2068	0.50-0.70
12.	IGT	X IARI 11124	228.00	80.00	231.00	77.00	3	: 1	0.1557	0.50-0.70
13.	DGWG	X IARI 11124	230.00	78.00	231.00	77.00	3	: 1	0.0172	0.80-0.90
14.	C A M	X IARI 11124	85.00	25.00	82.50	27.50	3	: 1	0.3305	0.70-0.80

tions of the crosses of IARI 5842, IARI 5901-2, IARI 5906-2B, IARI 6579, IARI 10061, IARI 10560, IARI 11445, I-geo-tse and DGWG with the tall variety produced 3 to 15% tall segregants that were significantly taller than the tall parent. But almost all the populations produced shorter plants than the respective dwarf parents. The segregation pattern of the different F_2 populations summarised in Table 3 indicates that the talls and dwarfs are in the proportion of 3:1 in all cases with high probability values except with FF 36, IARI 6579 and CAM.

Discussion

For successful plant breeding a better understanding of the mode of inheritance of characters that are directly and indirectly associated with yield potential is a pre-requisite. Recent plant breeding history has shown that it is the new plant type, characterised by a dwarf stature and high harvest index, which has led to a major break-through in the yielding ability of tropical rice varieties. Much before the exploitation of the DGWG dwarfing gene, the genetics of dwarfness in dwarfs of spontaneous and induced origin was studied by many workers (Parnel et al. 1922; Akemine 1925; Kadam 1937; Yamaguti 1931; Nagai and Takahashi 1952; Butany et al. 1952; Hsieh 1962) and dwarfness has been reported to be inherited as a simple recessive. Also, allelic relationship studies have revealed the number of dwarfing genes to vary from 2 to 8 (Nagai and Takahashi 1952).

The present study on the mode of inheritance of all fourteen different types of dwarfs revealed that dwarfness, irrespective of type, is inherited as a monogenic recessive. This is in conformity with the findings of earlier workers which suggested that although plant height is a quantitative trait governed by more than three genes (Ramiah 1933; Kadam 1937), semidwarfness behaves like a monogenic recessive relative to tall stature. The degree of dominance of tallness was, however, found to vary with the dwarf type. For instance, in most of the crosses tallness manifested incomplete dominance while crosses that involved IARI 6579 and IARI 10560 as one of the parents showed complete dominance. This suggests that the dwarfing gene in IARI 6579 and IARI 10560 might be different from that of the others. This appears to be true to some extent from the allelic relationship studies. Combinations involving these dwarfs were found to throw directly tall plants though at very low frequencies.

Studies on allelic relationships between DGWG, I-geo-tse and T(N)1 revealed them to be allelic to each other but they appeared to differ in having modifier genes of varied strengths. Similar studies extended to short statured American dwarfs showed the inheritance to be of a quantitative and complex nature (IRRI Ann Rep. 1964, 1966, 1968). Further studies on the subsequently collected dwarfs by the international Rice Research Institute, the Philippines, (IRRI Ann. Rep. 1971, 1973, 1976) and on an induced mutant by Chang (1970) and Padma (1975) indicated the occurrence of a few non-allelic genes (K-8, CN 242 d3 and Chin-nan-ai). A few other dwarf sources though reported to be allelic to DGWG differed distinctly in their degree of dominance and the strength of their modifier systems.

From the F_2 behaviour of all the possible crosses among the fourteen different dwarfs, the following three groups could be recognised.

1) FF 36, IARI 5842, IARI 5906-2B, IARI 5923, IARI 10061, IARI 10560, IARI 11445, I-geo-tse and DGWG
2) IARI 5901-2, IARI 5924, IARI 6579 and IARI 7312B
3) Central Africa Mutant

In the first group, the short stature appears to be governed by a single recessive gene in association with a large number of modifiers which have a predominantly negative effect. In the second group also, height seems to be governed by a single recessive gene but one which functions in association with an equal number of modifies of positive and negative effects. The probability of their having either different alleles of the same gene or not easily recombinable non-allelic factors due to tight linkages cannot be ruled out. The last group, represented by the induced dwarf CAM, seems to possess a dwarfing gene that appears to be non-allelic to those of the previous two groups of dwarfs, with equal strength of positive and negative modifiers.

In material of this kind where the major gene is recessive and appears to be similar in most of the dwarfs, further studies are needed to understand the effects of modifiers and the genetic background of the phenotype. Since height decides largely the plant type, it is an important agronomic character. It is the association of height with other components of a morphological type, such as profuse tillering, upright leaves of appropriate size and sturdiness of the stem, that confers the ability to the plant to respond to good management. Therefore, an understanding of the nature of inheritance of the dwarf plant type and the type of transgressive segregation observed in different crosses could be of considerable plant breeding value.

Literature

Akemine, M.: On the inheritance of dwarf habit in rice. Rep. Jap. Ass. Adv. Sci. 1, 308-314 (In Jap.) (1925)

Butany, W.T.; Bhattachary, R.K.; Daiya, L.R.: Inheritance of dwarf characters in rice and its inter-relationship with the occurrence of anthocyanin pigment in various plant parts. Ind. J. Genet. 19, 64-72 (1959)

Chang, T.: Genetic studies on semidwarf rice. J. Taiwan Agric. Res. 19, 1-10 (1970)

Hsieh, S.C.: Genic analysis in rice. I. colouration gene and inheritance of other characters in rice. Bot. Bull. Acad. Sinica 1, 117-132 (1960)

International Rice Research Institute: Ann. Rep., 25-30 (1964)

International Rice Research Institute: Ann. Rep., 67-68 (1966)

International Rice Research Institute: Ann. Rep., 73-74 (1968)

International Rice Research Institute: Ann. Rep., 199-200 (1971)

International Rice Research Institute: Ann. Rep., 161 (1973)

International Rice Research Institute: Ann. Rep., (1976)

Kadam, B.S.: Genes for dwarfing in rice. Nature 139, 1070 (1937)

Nagai, S.; Takahashi, M.: Genetical studies on rice plant XIV. The order and distance of some genes belonging to Pl. linkage group in rice. Jap. J. Breed. 1, 237-240 (1952)

Padma, A.: Genetic and perioxidase isoenzyme studies on some induced and other dwarfs in rice. Ph. D. thesis, Osmania University, 1975

Panse, V.G.; Sukhatme, P.V.: Statistical methods for Agriculture Workers. New Delhi: Indian Council of Agricultural Research (1954)

Parnel, F.R.; Ramaswamy Aiyangar, G.N.; Ramiah, K.; Ayyangar, C.R.S.: Inheritance of characters in rice. II. Mem. Dept. Agric. Ind. Bot. Ser. 11, 185-208 (1922)

Ramiah, K.: Inheritance of plant height in rice. Ind. J. Agric. Sci. 3, 411-432 (1933)

Singh, V.P.; Swaminathan, M.S.; Mehra, R.B.; Siddiq, E.A.: Genetic divergence among dwarfs of cultivated rice *Oryza sativa*. Ind. J. Genet. (1978) (in press)

Yamaguti, Y.: Cross investigation of rice plants. III. Genetics of colour characters of various parts of plant, the growth habit and the time of heading. Ber Ohara Inst. 5, 1-56 (1931)

Received January 1, 1979
Communicated by B.R. Murty

Dr. V.P. Singh
Indian Agricultural Research Institute
Division of Genetics
New Delhi-110012 (India)