

THE UNIVERSITY OF MANITOBA

MONOSOMIC AND CONVENTIONAL GENETIC ANALYSES OF  
SEMI-DWARFISM AND GRASS CLUMP DWARFISM  
IN COMMON WHEAT

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## ABSTRACT

Monosomic analyses of two homozygous, temperature sensitive dwarf lines were made by crossing each to the complete monosomic series of the varieties Rescue and Chinese Spring.

The two dwarfs Marquillo-Timstein and Marquillo-Kenya Farmer were found to carry major dwarfing genes in chromosomes 2A and 2D in the case of the former and on chromosomes 2A and 4B in Marquillo-Kenya Farmer. Each was found to be influenced by several modifying genes, some of which appears to affect the temperature sensitivity of the hybrid. The major difference between the two dwarfs appear to be due to chromosome 4B.

Study of height variation within each of the deficient  $F_2$  populations revealed that height inheritance is more complex than "grass clump" dwarfism and that the majority of chromosomes that influence dwarf frequency also influence the height variance in the normal portion of the  $F_2$  population. In addition, however, there are several chromosomes which influence plant height but are not involved in the inheritance of dwarfism. This would indicate that either some genes have a pleiotropic effect or else the inheritance of height and "grass clump" dwarfism are separate characteristics.

Intercrosses between the above dwarfs and the semi-dwarf varieties Sonora 64, Norin 10 and Tom Thumb showed that these new lines are very different from the others in mode of inheritance and that they may be of value as sources of germ plasm in the production of new dwarf varieties.

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## INTRODUCTION

The occurrence of dwarf plants in intervarietal wheat hybrids was first reported in 1898 by Farrer (10). In the subsequent period many such reports have been recorded especially during the course of disease resistance studies.

In the course of the genetic investigations on dwarfism, plant breeders and geneticists recognized the ability of dwarfs to withstand lodging even under conditions of very high fertility and irrigation. This attribute has become particularly important in recent years with the advent of more intensive production.

Commercial interest in dwarf varieties developed in the early 1950's in Washington State in the United States (45,46). Since then they have become the basis of extensive Rockefeller Foundation wheat programs in North and Latin America.

The genes for dwarfism in almost all present semidwarf varieties were derived from the "Norin 10" variety or its derivatives. The fact that this source of dwarfism is recessive and complexly inherited has stimulated attempts to locate other sources of dwarfism that would be equally productive and easier to utilize in wheat breeding programs.

Two dwarf lines have been produced at the University of Manitoba which are dominant and temperature sensitive. The present project was undertaken with the object of studying the mode of inheritance of dwarfism in these lines and to study their genotypic relationship with those of Norin 10, Sonora 64 and Tom Thumb.



## REVIEW OF LITERATURE

Many plant breeders and geneticists have recorded the occurrence of different types of dwarfs in wheat, including "grass clumps". The first such report was by Farrer in 1898 (10). He speaks of "grass clumps" which tillered profusely but rarely produced heads.

Neethling (19) first attempted to account for the occurrence of dwarfism on the basis of a one factor hypothesis. In a cross of Rieti x Gluyas Early, he obtained only normal  $F_1$  plants and 8 dwarfs in a total of 31  $F_2$  plants. He considered dwarfing to be controlled by a single recessive factor. He later re-examined his material and suggested a "multiple factor hypothesis" including an inhibitor factor to account for the genetic behaviour (20).

Sax (26) in the reciprocal crosses of Bluestem x Amby obtained grassy dwarf  $F_1$  plants. The failure of these plants to develop beyond the rosette stage was ascribed to a lethal or inhibitor factor.

A large number of investigators have explained dwarfism on the basis of two interacting genetic factors.

In a cross of Kota x Marquis, Hayes and Aamodt (13) obtained an  $F_2$  ratio of 666 normals to 121 dwarfs or a 13:3 ratio which indicated that two factors were involved. They assumed that one of the parents contained two factors, a gene D dominant for dwarf habit, and I which inhibits the expression of the dwarf factor whereas the other parent possessed the recessive alleles.

Goulden (12) studied the  $F_3$  of this material and confirmed the results. In the same cross Clark and Quisenberry (7) obtained the same results and assumed a factor, DD, for dwarfism and a factor, NN, for normal plants which inhibits the action of D. Kota was assigned the genotype DDNN and Marquis ddnn.

Stephens (38) studying the cross Federation x Master, Stewart and Tingey (40) with the cross Marquis x Federation and Clark and Hooker (6) with the cross Marquis x Hard Federation all arrived at similar two factor explanations.

Others with similar results include Stewart and Bischoff (39), Waterhouse (48), Churchward (5), Nieves (21), Tingey (43) and Tanaka (41).

Thompson (42) reported results from the cross Pusa 12 x Chul. The  $F_1$ 's were dwarfs, but they produced some seed and the cross was carried through to the  $F_4$ . By combining with the dwarfs 150 seeds which failed to germinate in the  $F_2$  he obtained the ratio of 181 dwarfs to 115 talls which fits the theoretical ratio of 39:25. He explained this on the basis of three factors D, I and E. D being necessary for the development of dwarfs, I inhibits D, and E inhibits I. Hence plants of the constitution of E-I-D, E-iiD- and eeiD- were dwarf and all others were normal. The above hypothesis is supported by the work of Goulden (12) who demonstrated that Chul carries a dwarf factor and an inhibiting factor. The other parent must carry the factor E which inhibits the inhibitor I of Chul.

Florell (11) studied the inheritance of dwarfs in the  $F_2$  and backcrosses of Jenkin x Quality and Jenkin x Marquis. He explained the results on the basis of a three factor hypothesis, two dominant factors  $D_1$  and  $D_2$  being complementary for dwarfing and  $N$ , a factor for normal growth which was dominant to  $D_1D_2$ . Quality and Marquis were assigned the genotype  $nnd_1d_1d_2d_2$  and Jenkin  $NND_1D_1D_2D_2$ .

In a genetic study of plant height by Everson et al (9) dwarf plants appeared in the  $F_2$  progeny of the semi-dwarf selection (Norin 10 x Brevor 14) x Burt and in the backcross of the  $F_1$  to (Norin 10 x Brevor 14). The data indicated that the parents differed by two genes, a factor  $I$  for normal height which inhibits a dwarfing factor  $D$ . At the same time Norin 10 x Brevor - 1978 which is a sister selection of Norin 10 x Brevor 14, produced all dwarf  $F_1$  plants when crossed with Burt. To account for the appearance of dwarfs in the latter cross Burt was assigned the genotype (DDIIee), Norin 10 x Brevor 1978 (ddiEE) and Norin 10 x Brevor 14 (ddiiee).

The most comprehensive conventional genetic study on dwarfism was conducted by McMillan (18). Ninety-seven varieties were used in the investigation and 945 crosses studied. He obtained the following types of result:  $F_1$  dwarf and 7 normal to 9 dwarf in  $F_2$ ,  $F_1$  dwarf and 34 normal to 30 dwarf in  $F_2$ ,  $F_1$  normal and 13 normal to 3 dwarf in  $F_2$ . Because of the varying ratios found in the  $F_2$  and  $F_3$ , it was impossible to arrive at an explanation which would satisfy all situations. Therefore he proposed a hypothesis based, first of all, on the presence

or absence of grass clumps in the  $F_1$  and  $F_2$  without regard to the ratios.

The hypothesis involves four genes: G, a gene for the grass clump habit, I which inhibits the expression of G and A and B which act in complementary way to inhibit the inhibitor I. In addition, it was proposed that Bi and bI were closely linked in repulsion. According to this proposal only genotypes ABig, AbIG, abIG, aBig, AbIg and abIg could exist in nature as normals. The different types of grass clumps produced are determined by modifying genes, some of which modify the grass clumps to such an extent that under adverse conditions their viability is very low. The same genes do not affect the viability of normal plants.

McMillan extended his hypothesis to the data of Waterhouse (48), Richardson (24,25), Waldron (47), Goulden (12), Florell (11), and Thompson (42) and when certain assumptions were made concerning the semi-lethality of dwarfs, their data fit his hypothesis.

Three complementary factors,  $D_1D_2D_3$  and three duplicate factors  $D'_1D'_2D'_3$  and an inhibitor, I, have been used by Pao et al (23) to account for dwarfness in several crosses of wheat.

Hsu et al (15) made crosses between five spring wheat varieties. The  $F_1$  plants of Kenya 338 crossed to (Na 101-Timstein x Mayo), Frontana and Marquis and of Timstein crossed to Frontana and Marquis, were less than 1 foot in height. All segregated in the ratio of 9 dwarf: 7 normal

in  $F_2$ . They postulated that dwarf habit was determined by the interaction of two of four factors, A, B, C and D. Interaction between A and C, A and D and B and D resulted in dwarf habit whereas the remainder were normal. The varieties were assigned the following genotypes: Kenya 338-AAbbccdd, Timstein-aaBBccdd, Na 101-Timstein x Mayo-aabbCCdd, Frontana and Marquis-aabbccDD.

It was suggested that the four factors may have originated from the three different genomes with two of them which produce dwarfism belonging to the same genome.

Aneuploid studies have been undertaken to supplement information obtained from conventional studies.

Hurd and McGinnis (16) studied crosses between the Redman monosomic series and Kenya Farmer and found that all 42-chromosome  $F_1$  hybrids and all 41-chromosome  $F_1$  plants, except those in which Redman 2A (XIII) or 4B (VIII) were lacking, were grass clump dwarfs.

It was concluded that at least three complementary dominant genes are responsible for dwarfing in this cross and that the absence of any one of these genes allows normal plant growth. Two of these genes were located on chromosomes 2A and 4B of Redman, the third being in Kenya Farmer.

Hermesen (14) has assumed there are three genes for dwarfing:  $D_1$ ,  $D_2$  and  $D_3$  which produce the same "dwarfing substance" but vary as to the quantity of substance produced. He has localized genes  $D_1$

and  $D_3$  in the variety, Timstein, on chromosomes 2D and 4B and on the basis of the results of Hurd and McGinnis (16) assumed  $D_2$  to be on chromosome 2A. He stated however, that the inheritance of dwarfing in wheat is presumably more complicated in view of McMillan's and others data.

In recent years great emphasis has been placed on the development of semi-dwarf wheat varieties (3,45,46). Widespread use has been made of the semi-dwarf trait found in the Japanese variety Norin 10. Allan et al (2) recently reviewed the information available on the inheritance of semi-dwarfism from this source. According to their review, there are 1 or 2 major genes, partially recessive in expression and several modifying factors which in combination with the semi-dwarfing factors produce a wide range in culm length. Monosomic analysis, by Allan and Vogel (1) indicated that eleven chromosomes influenced culm length in crosses of the Chinese Spring monosomic series x the semi-dwarf variety Norin 10-Brevor 14. In the monosomic condition, absence of all members of homoeologous group 5 produced greater culm length, whereas the absence of 2 members of group 3 (3A and 3D) and all members of groups 2 and 4 resulted in shorter  $F_2$  culm length. Of the 5  $F_2$  monosomic populations which produced the shortest mean culm length, three were members of the D genome. The suspected 2 major semi-dwarfing factors in Norin 10-Brevor 14 have not been definitely located, although it is suggested that these factors may be located on chromosomes 2A, 2B, 3D, or 4B

of this variety.

It can be concluded from the present literature review that many varieties which produce dwarfs upon crossing can be traced to a common ancestor, and that many crosses which produced dwarfs were originally made in attempts to transfer rust resistance.

The majority of investigators explained their results on a two gene basis, although 1, 3 and 4 gene hypothesis have been advanced involving complementary gene systems interacting with inhibitors.

The most comprehensive concept was proposed by McMillan (18) which involves 4 interacting genes, however it too requires certain unusual assumptions to account for all situations.

Aneuploid studies confined to grass clumps have indicated 3 genes on chromosomes 2A, 4B and 2D influence this character. On the basis of conventional genetic analysis it appears that the inheritance of dwarfism involves more than 3 genes.

## MATERIALS AND METHODS

The aneuploids in common wheat developed by Sears (27,28,29,30,34,35) have made it possible to identify chromosomes having genes responsible for the control of specific characters. Sears (32) outlined four methods of associating specific genes with individual chromosomes. The most commonly used technique involves the analyses of chromosome deficient hybrid lines. In this method the 21 nullisomic or monosomic lines of one variety are each crossed to another variety carrying the opposite allele(s) for the character being studied. Deficient lines that produce modified  $F_2$  and  $F_3$  segregations are regarded as critical with respect to the genetic control of the character in question. This technique has been used in studying dwarfism in this project.

### MATERIALS

Monosomic series in the varieties Chinese Spring and Rescue were used. These series were produced by E. R. Sears (31) and R. I. Larson (17) respectively. The Rescue series was produced from Chinese Spring by means of backcrossing. Chinese Spring is a soft red spring wheat and Rescue a hard red spring wheat. Both are tall growing varieties. The dwarf lines used as parents were advanced hybrids produced at the University of Manitoba namely: a Marquillo-Timstein derived line which is short growing (20-25 inches) under normal conditions but which is temperature sensitive and will not head if grown continuously under low temperatures ( $60^{\circ}\text{F}$ ) and a



Marquillo-Kenya Farmer derivative which is a grass clump dwarf that will not head under normal growing conditions but will elongate and head if grown under continuous light at 80°F (4,8).

Ten seeds of each of the 21 monosomic lines of Rescue and Chinese Spring were germinated on filter paper in germination boxes at room temperature. Root tips were collected and cytological examination made as described by Tsunewaki and Jenkins (44). Only the 41 chromosome plants were retained and transplanted into pots in growth chambers. These were used as female parents in crosses to the two dwarf lines. In addition each dwarf line was crossed reciprocally to disomic Rescue and Chinese Spring. Chromosomes were designated by the system outlined by Sears (33) and further clarified by Okamoto (22).

The following disomic crosses were also made and studied in order to compare their genotypes relative to dwarfism:

1. Marquillo-Timstein x Sonora 64
2. Marquillo-Timstein x Norin 10
3. Redman x Federation
4. Redman-Federation x Sonora 64
5. Redman-Federation x Norin 10
6. Sonora 64 x Norin 10
7. Tom Thumb x Redman-Federation
8. Marquillo-Timstein x Tom Thumb

9. Tom Thumb x Sonora 64

10. Tom Thumb x Norin 10

Sonora 64 is a semi-dwarf, Mexican variety which has dwarfing genes from Norin 10. Norin 10 is a semi-dwarf-winter variety, introduced from Japan. Redman-Federation is an advanced generation dwarf derived from the cross Redman x Federation which segregated for tall and dwarf plants in the  $F_2$  generation. Tom Thumb is a dwarf, late winter wheat.

#### GROWING THE $F_1$

##### I. Monosomic series x Marquillo-Timstein

Up to twenty  $F_1$  plants of each monosomic hybrid line were checked for chromosome number and the 41 chromosome plants grown to maturity. In cases where counts were not determined in the  $F_1$ , six  $F_2$  progeny were examined cytologically, if all were disomic the  $F_1$  parent was regarded as disomic. All monosomic and some disomic  $F_1$  plants of each chromosome line of Chinese Spring and Rescue monosomics x Marquillo-Timstein were transplanted into the greenhouse beds in spring of 1964. In addition, the disomic parents and the  $F_1$  of their reciprocal crosses were planted for comparison. When the heading of the  $F_1$  hybrids began, young spikes were collected and fixed in Carnoy's solution. The pollen mother cells were examined at metaphase by means of the acetocarmine smear technique (36).

##### 2. Monosomic series x Marquillo-Kenya Farmer

Since the grass clump phenotype proved to be dominant the  $F_1$

generation was grown in a growth chamber at 80°F with continuous light. Simultaneously, one monosomic plant of each of the 42 hybrid lines plus  $F_1$  disomic hybrids and parents, were grown under normal greenhouse conditions.

### 3. Disomic $F_1$ Hybrids

All other intervarietal  $F_1$  hybrids were grown in the greenhouse.

## GROWING THE $F_2$

### 1. Monosomic series x Marquillo-Timstein

The  $F_2$  populations were all grown in greenhouse beds, during the period of September 1964 to January 1966. The  $F_2$  populations of each line were derived from at least three monosomic  $F_1$  plants. The population size of the Rescue x Marquillo-Timstein  $F_2$  monosomic lines varied from 98 to 205 plants, and a population of 606 disomic  $F_2$  plants were grown simultaneously. The  $F_2$  populations of the Chinese Spring monosomic series x Marquillo-Timstein varied from 100 to 245 plants, and the disomic population contained 733 plants.

### 2. Monosomic series x Marquillo-Kenya Farmer

The population size of  $F_2$  lines of Chinese Spring and Rescue x Marquillo-Kenya Farmer ranged from 58 to 214 plants. The disomic  $F_2$  populations were 568 and 870 plants respectively.

### 3. Disomic $F_2$ Hybrids

All  $F_2$  populations derived from the disomic crosses (except Redman Federation x Norin 10 and reciprocal and Sonora 64 x Norin 10) and  $F_3$  families of the Rescue monosomics x Marquillo-Timstein were grown in

the field in 1965. The  $F_2$  seeds from the crosses involving the winter varieties, Tom Thumb and Norin 10 were vernalized at temperatures of  $32^{\circ}$ - $35^{\circ}$ F for 8 weeks prior to planting. Before harvest the height of all plants in segregating families was measured or the number of tall and dwarf plants counted.

Sixteen hours of light per day were provided for material grown under greenhouse conditions. The temperature of the greenhouses was set at  $60^{\circ}$ F for the Rescue x Marquillo-Timstein  $F_2$  series, and 65 to  $70^{\circ}$ F for all other material. Mildew was controlled by sulphur dusting and red spider and aphids were controlled by spraying with Meta-Systox 250.

#### ANALYSIS OF THE $F_1$ AND $F_2$

At maturity, height of all plants in the  $F_1$  and  $F_2$  populations was measured. In the  $F_1$  generation of the monosomic crosses all spikes of the main tillers were used for fertility determinations. The spikelets of the two lower internodes of the spike were disregarded and the fertility of the plant was recorded as the percentage of seed set in the next 20 spikelets. The  $F_2$  generations from the crosses with both monosomic series and Marquillo-Timstein were classified into three classes; non-heading dwarf plants, late heading dwarf plants and normal plants. The  $F_2$  population of the monosomic series crossed to the grass clump parent, Marquillo-Kenya Farmer, were classified into two classes: grass clump and normal plants.

Two discrete categories, dwarfs and tall, were used in the chi-square test of goodness of fit to genetic ratios. Individual plants progenies that seemed to deviate from one another with regard to segregation were tested for homogeneity (37) before they were pooled. Height measurements of the  $F_1$  and  $F_2$  normal plants were recorded to the nearest centimeter. Measurements were made from the crown to the tip of the spike of the longest tiller of each plant. Average height per line was determined for the  $F_1$  and  $F_2$  populations. Height classes were established at intervals of 3 cm. The number of plants in each interval was recorded in percentage. Height distribution pattern was also determined for the  $F_2$  of all other disomic crosses except Redman x Federation, Senora 64 x Tom Thumb and Redman-Federation x Tom Thumb.

The mean and standard error were computed for the height of all headed plants of each  $F_2$  monosomic line of Rescue and Chinese Spring x Marquillo-Timstein, Chinese Spring monosomics x Marquillo-Kenya Farmer, their respective  $F_2$  disomic populations and the parents. The height differences, between each  $F_2$  monosomic line and the comparable  $F_2$  disomic population were tested for significance by means of the "t" test. Most calculations were made by computer in the Engineering Department, the University of Manitoba.

## RESULTS AND DISCUSSION

### $F_1$ MONOSOMIC ANALYSES

#### 1. $F_1$ MONOSOMIC HYBRIDS WITH MARQUILLO-TIMSTEIN

In the hybrids of the Rescue monosomic series x Marquillo-Timstein a ring of four or a chain of three was regularly present indicating that they differed by a reciprocal translocation. The  $F_1$  hybrids of the Chinese Spring monosomics x Marquillo-Timstein gave regular chromosome pairing, except for a few cases where two univalents were present at the metaphase plate.

The average height of the disomic  $F_1$  hybrids (Table 1) was 83.1 cm as compared to 102.7 cm for Rescue and 53.2 cm for Marquillo-Timstein, indicating a partial dominance of the tall genotype. The average height of the  $F_1$  monosomic lines ranged from 75.4 cm to 95.1 cm, the shortest being 3B, followed by 1B, 2B and 7B with all other lines being similar to or taller than the  $F_1$  disomic.

The fertility of all monosomic lines except 1A, 2D and 7D was below that of the disomic  $F_1$  populations. The greatest sterility occurred in 2A, 2B, 3B, 4B, 6B and 4D.

Partial dominance of tall habit was also recorded in the  $F_1$  from the cross of the Chinese Spring monosomic series by Marquillo-Timstein (Table 1). The average height of the  $F_1$  disomic hybrid was 104.3 cm and Chinese Spring and Marquillo-Timstein 118.7 cm and 72.1 cm respectively.

TABLE 1. Average height and fertility of F<sub>1</sub> monosomic and disomic lines from crosses between the two monosomic series and Marquillo-Timstein.

Line	Rescue x Marquillo-Timstein			Chinese Spring x Marquillo-Timstein		
	Height cm	No. of Plants	Fertility %	Height cm	No. of Plants	Fertility %
1A	95.1 $\pm$ 2.9	8	92.3	85.9 $\pm$ 2.1	10	91.6
2A	82.2 $\pm$ 2.8	4	35.5	92.9 $\pm$ 1.8	7	56.4
3A	94.7 $\pm$ 4.0	5	80.0	96.7 $\pm$ 1.6	14	78.9
4A	87.1 $\pm$ 3.1	10	77.3	98.1 $\pm$ 1.4	4	66.1
5A	89.0 $\pm$ 0.7	13	69.6	97.9 $\pm$ 2.6	7	84.6
6A	85.2 $\pm$ 1.2	15	80.6	88.5 $\pm$ 1.7	10	93.5
7A	84.0 $\pm$ 0.9	16	82.4	96.2 $\pm$ 2.1	7	93.3
1B	79.4 $\pm$ 3.0	18	75.2	97.4 $\pm$ 4.2	4	53.3
2B	79.5 $\pm$ 1.1	4	65.0	87.1 $\pm$ 1.8	10	48.5
3B	75.4 $\pm$ 2.1	15	23.9	89.3 $\pm$ 2.2	6	55.5
4B	84.9 $\pm$ 3.6	11	64.1	91.0 $\pm$ 5.3	4	29.6
5B	90.3 $\pm$ 2.7	9	75.0	90.5 $\pm$ 3.4	4	59.3
6B	83.5 $\pm$ 2.6	12	40.0	93.7 $\pm$ 1.3	13	39.5
7B	79.9 $\pm$ 1.4	17	68.1	96.3 $\pm$ 1.8	7	68.7
1D	85.1 $\pm$ 3.2	10	85.3	102.9 $\pm$ 1.9	8	74.3
2D	89.8 $\pm$ 1.4	7	96.9	89.3 $\pm$ 4.0	3	57.2
3D	83.4 $\pm$ 3.0	6	75.0	92.1 $\pm$ 1.8	15	72.5
4D	92.6 $\pm$ 1.2	10	56.9	96.7 $\pm$ 1.8	15	54.9
5D	81.0 $\pm$ 2.3	17	86.5	93.3 $\pm$ 2.7	6	83.7
6D	84.8 $\pm$ 2.0	16	85.2	91.4 $\pm$ 2.6	5	96.8
7D	82.0 $\pm$ 2.0	5	89.6	88.6 $\pm$ 3.3	5	87.6
Disomic						
F <sub>1</sub>	83.1 $\pm$ 2.9	12	89.1	104.3 $\pm$ 2.1	20	96.7
Tall Parent	102.7 $\pm$ 1.9	20	93.0	118.7 $\pm$ 3.8	10	99.2
Dwarf Parent	53.2 $\pm$ 2.1	20	86.8	72.1 $\pm$ 1.2	14	85.5

In this series lines 1A, 5A and 2B are not comparable with the others since they were not grown simultaneously. The mean height of the other 18  $F_1$  monosomic lines varied from 88.5 cm to 102.9 cm. The shortest lines were: 6A, 2B, 3B, 2D and 7D. Only line 1D attained the height of the normal  $F_1$  population. The fertility of the  $F_1$  monosomic lines was generally lower than the disomic  $F_1$  population. The lowest fertility occurred in lines 2A, 1B, 2B, 4B, 6B and 4D agreeing with the results from the Rescue x Marquillo-Timstein series (Table 1). The decreased fertility in homoeologous group 2, agrees with Sears (31) results with monosomics of Chinese Spring.

## 2. $F_1$ MONOSOMIC HYBRIDS WITH MARQUILLO-KENYA FARMER

Marquillo-Kenya Farmer used as a male was grown in a growth cabinet at 80°F with continuous light. It was found that under these conditions the flowering period was extremely short and the anthers usually dehisced within the glumes making crossing very difficult. To overcome this problem the following precautions were taken: (i) planting of Marquillo-Kenya Farmer were made every 10 days until all crosses were completed, (ii) each plant was transferred, one day before flowering, to a greenhouse or growth cabinet at 70°F with a 16 hour day. Although subsequent growth of young tillers was arrested under these conditions, the flowering period was extended and more abundant pollen was obtained.

It was observed, both with the Marquillo-Kenya Farmer parent and with the  $F_1$  of the monosomic series x Marquillo-Kenya Farmer that the best growth, and seed production was obtained when single plants were



grown in 4 inch pots, this prevented excessive tillering and caused more rapid development of the main tillers resulting in greater height and longer spikes. The  $F_1$  hybrids from the monosomic series x Marquillo-Kenya Farmer showed a complete dominance of the grass clump character. This was proven by growing one monosomic  $F_1$  plant, from each of the 42 crosses in the greenhouse at  $70^{\circ}\text{F}$ , with disomic  $F_1$  and parental plants. The monosomic  $F_1$  hybrids under these conditions were grass clumps which tillered profusely, failed to head and often died before the parental non-dwarf plants flowered. This genetically controlled specific temperature requirement for normal growth seems to differ with the stage of growth. The loss of a portion of the  $F_1$  hybrid population of the Chinese Spring monosomic series x Marquillo-Kenya Farmer as a result of a temperature fluctuation from  $70-80^{\circ}\text{F}$  for 4 days in a growth cabinet caused by failure of the temperature controlling system supports this conclusion. Plants at the heading or near heading stage at that time ceased growth and never resumed growth after the temperature was returned to  $80^{\circ}\text{F}$ . The plants in which the spikes had already emerged from the sheaths ceased their growth but flowered and produced some seed. In other plants the spikes were formed but failed to emerge from the sheaths. After growth ceased the plants gradually became necrotic and soon died.

The high temperature requirement does not seem to be as critical in the seedling stage of growth in that the  $F_1$  plants of one series were transplanted from the germination boxes to pots and kept in the greenhouse for 10 days before being transferred to the hot growth cabinet. These

plants grew and headed normally.

The height of Rescue monosomics x Marquillo-Kenya Farmer  $F_1$ 's ranged from 45.5 cm to 63.3 cm as compared to 57.4 cm for the disomic  $F_1$  plants (Table 2). The shortest lines were 2A, 2B and 7D which were slightly shorter than the Marquillo-Kenya Farmer parent. The fertility of all  $F_1$  monosomics was less than the  $F_1$  disomics, the lowest being 2A, 2B, 4B and 4D.

The height of Chinese Spring monosomics x Marquillo-Kenya Farmer  $F_1$  ranged from 49.5 cm to 64.4 cm as compared to 58.9 cm for the disomic  $F_1$  sibs. The  $F_1$  means of 3B, 6B, 2D and 3D were the shortest and similar to the Marquillo-Kenya Farmer parent. The fertility of most lines was higher than in the corresponding lines of the other series, the least fertile lines being 2B, 4B, 6B and 2D.

On the basis of  $F_1$  results chromosomes of homoeologous group 2, lines 3B, 3D and 7D appear to be involved in the inheritance of height.  $F_1$  lines deficient for chromosomes 3B are short in all four crosses whereas lines deficient for chromosomes of homoeologous group 2 are short in six cases.

With respect to fertility all four crosses are similar in that lines deficient for chromosomes 2A, 2B, 4B, 4D and 6B were among the least fertile.

TABLE 2. Average height and fertility of  $F_1$  monosomic and disomic lines from crosses between the two monosomic series and Marquillo-Kenya Farmer.

Line	Rescue x Marquillo-Kenya Farmer			Chinese Spring x Marquillo-Kenya		
	Height cm	No. of Plants	Fertility %	Height cm	No. of Plants	Fertility %
1A	56.9 $\pm$ 4.5	6	77.6	56.1 $\pm$ 2.8	4	78.4
2A	45.5 $\pm$ 4.5	6	19.8	60.3 $\pm$ 6.5	3	74.5
3A	55.1 $\pm$ 2.6	7	58.0	59.9 $\pm$ 2.5	12	83.4
4A	62.9 $\pm$ 1.5	8	60.7	61.8 $\pm$ 2.3	6	92.1
5A	59.2 $\pm$ 2.1	8	64.7	64.4 $\pm$ 1.9	11	73.7
6A	57.8 $\pm$ 3.8	8	81.7	55.6 $\pm$ 1.5	11	87.6
7A	53.0 $\pm$ 1.8	9	64.9	55.2 $\pm$ 2.3	12	84.2
1B	57.3 $\pm$ 3.5	7	59.4	58.9 $\pm$ 2.3	10	90.6
2B	51.1 $\pm$ 4.1	5	31.9	57.2 $\pm$ 1.6	4	69.9
3B	54.1 $\pm$ 2.7	8	66.7	53.0 $\pm$ 4.8	4	88.7
4B	55.9 $\pm$ .9	7	29.7	55.7 $\pm$ 4.7	8	62.1
5B	54.7 $\pm$ .9	8	51.8	56.8 $\pm$ 3.0	9	78.7
6B	59.4 $\pm$ 1.5	9	79.7	49.7 $\pm$ 9.2	6	28.1
7B	58.9 $\pm$ 1.4	8	76.1	57.9 $\pm$ 2.7	8	84.2
1D	60.8 $\pm$ 1.7	9	61.4	58.7 $\pm$ 2.2	14	89.2
2D	58.6 $\pm$ 2.3	8	74.4	51.5 $\pm$ .5	3	63.9
3D	57.7 $\pm$ 1.4	8	63.4	49.5 $\pm$ 3.1	4	86.2
4D	54.7 $\pm$ .2	3	50.0	57.6 $\pm$ 2.5	11	75.0
5D	63.3 $\pm$ 2.6	8	82.2	63.8 $\pm$ 2.3	11	82.2
6D	58.7 $\pm$ 1.9	7	83.3	55.9 $\pm$ 2.0	13	87.5
7D	51.1 $\pm$ 3.5	4	82.8	60.7 $\pm$ 2.0	12	90.9
Disomic $F_1$	57.4 $\pm$ 1.1	12	89.6	58.9 $\pm$ 1.3	15	81.7
Marquillo- Kenya Farmer	52.0			52.0		

$F_2$  MONOSOMIC ANALYSIS(a) DWARFISM VERSUS NORMAL GROWTH HABIT1. Rescue Monosomics x Marquillo-Timstein  $F_2$ 

The dwarf and normal segregates were distinguishable very early due to the shorter coleoptiles and later emergence of the dwarfs. The dwarf seedlings were also characterized by earlier and more profuse tillering, darker color and shorter, narrower leaves.

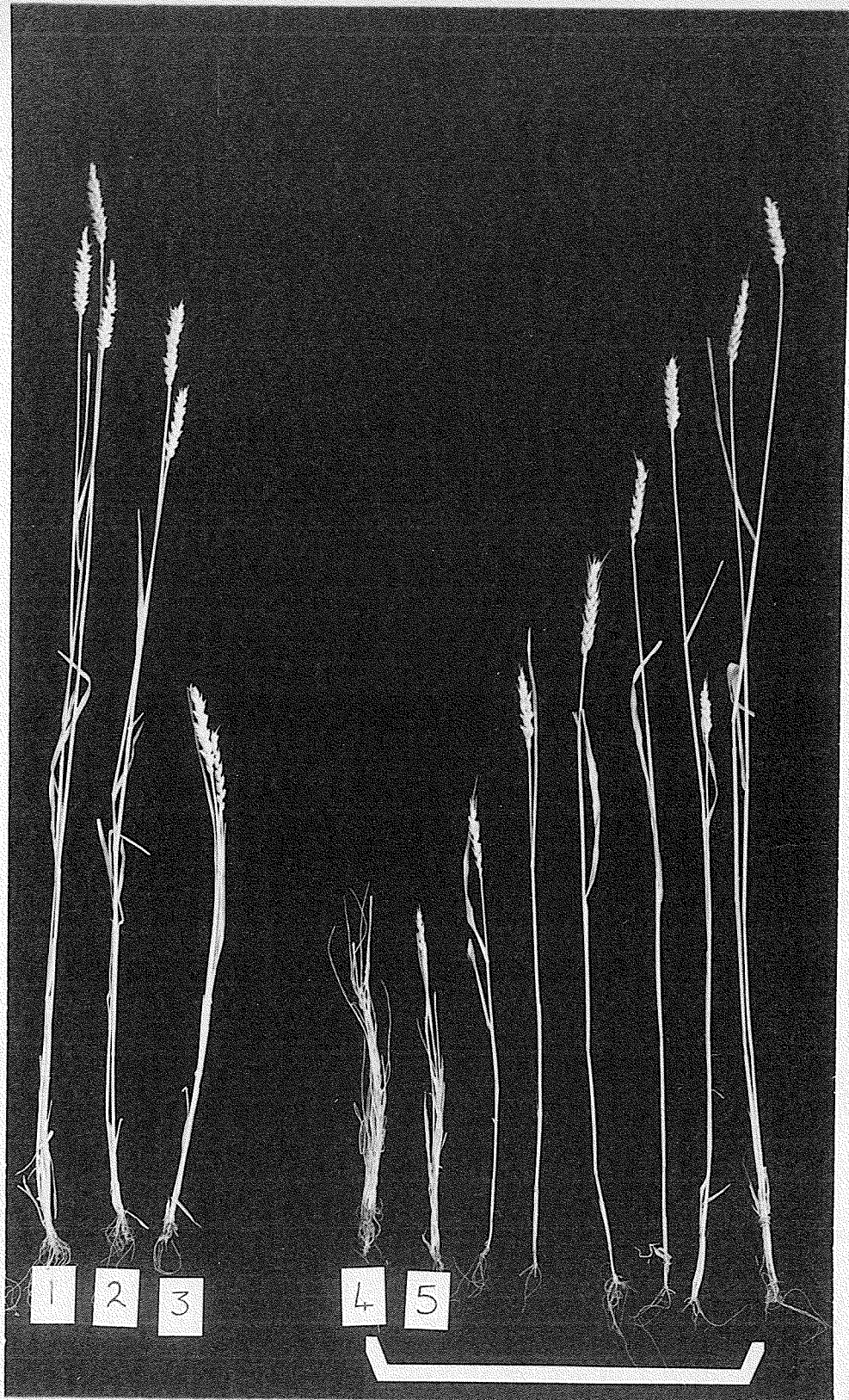
The Marquillo-Timstein parent checks failed to elongate and head under the cool (60°F) conditions whereas Rescue attained normal height (Plate 1). Under these conditions the  $F_2$  populations of both the normal disomics and the 21 deficient lines all segregated into three discrete classes: non-heading dwarfs, late heading dwarfs and normal headed plants (Plate 2). The latter class ranged in height from 50 to 105 cm in the disomic  $F_2$  population whereas the maximum height of plants in the first two classes was 46 cm with a clear break between classes as is shown in Figure I. The fact that such a height range occurs in the normal headed group indicated that the inheritance of temperature sensitivity and height are separate characteristics. The dwarf segregates in each population were combined and the ratio of normal to dwarf in each deficient line was compared to the segregation occurring in the disomic  $F_2$  population. These data are presented in Table 3. This comparison showed that eight deficient lines deviated significantly from the normal disomic ratio. The critical chromosomes were those of homoeologous groups 1 and 2 and chromosomes 7A and 7B of group 7. Lines deficient for chromosomes of groups 2 and



PLATE 2. Parents,  $F_1$  and typical  $F_2$  segregates from the Rescue x Marquillo-Timstein cross.

1. Rescue,
2.  $F_1$  hybrid,
3. Marquillo-Timstein,
4. Non-heading dwarf,
5. Late heading dwarf.

Remainder normal plants.



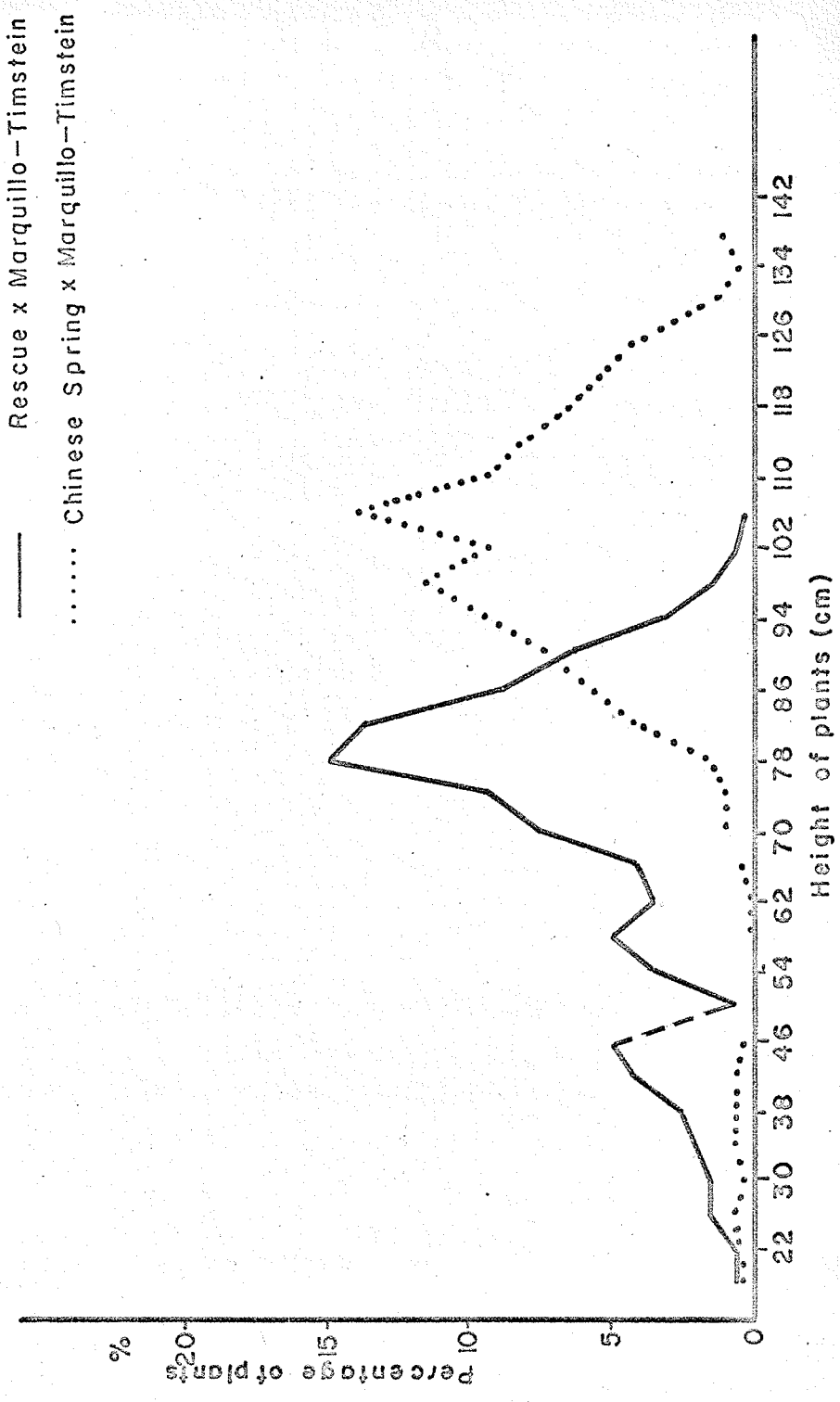


FIGURE 1. Height distribution within the headed portion of the disomic F<sub>2</sub> population of Rescue x Marquillo-Timstein and Chinese Spring x Marquillo-Timstein.



TABLE 3. The ratio of normal to dwarf plants in the  $F_2$  from crosses between the Rescue monosomic series and Marquillo-Timstein.

Line	Number of Plants		Total	$\chi^2$ Value 305:301
	Normal	Dwarf		
1A	83	51	134	7.18**
2A	35	63	98	8.41**
3A	105	97	202	.21
4A	84	97	181	1.13
5A	108	91	199	1.21
6A	95	106	201	.77
7A	84	111	195	4.14*
1B	121	70	191	12.89**
2B	63	90	153	5.16*
3B	62	81	143	2.81
4B	106	96	202	.36
5B	106	98	204	.21
6B	73	62	135	.74
7B	86	116	202	4.90*
1D	118	80	198	6.75**
2D	85	118	203	5.85*
3D	99	103	202	.15
4D	103	102	205	.001
5D	116	89	205	3.17
6D	93	110	203	1.68
7D	93	102	195	.56
Rescue x Marquillo- Timstein	305	301	606	.00

\* significant at the 5% level

\*\* significant at the 1% level

7 had an excess of dwarf plants whereas lines deficient for chromosomes 1A, 1B and 1D deviated in the opposite way.

### 2. Chinese Spring Monosomics x Marquillo-Timstein F<sub>2</sub>

The characteristics of the seedling populations were similar to those of the previously described cross but the peculiarities of the dwarf segregants were expressed somewhat later due probably to the higher (65-75°F) growing temperatures. Like the Rescue x Marquillo-Timstein population, classification into three discrete categories: non-heading dwarfs, late heading dwarfs and normal plants was possible (Plate 3). The fact that the dwarf portion of the population is smaller (Fig. 1) is due to the increased temperature which is above the threshold required to permit heading since the Marquillo-Timstein parental checks headed in this case.

The tallest plants within the category of late heading dwarfs were 50 cm. The demarcation between this group and the normal was more pronounced than in the Rescue hybrids (Fig.1). As in the previous cross, non-heading and late heading dwarfs were combined and the ratio of normal to dwarf plants in each deficient line was compared to the ratio obtained from the disomic F<sub>2</sub> population. As is shown in Table 4, five F<sub>2</sub> monosomic lines deviated significantly from the disomic ratio. The critical chromosomes were those of homoeologous group 2, chromosome 1A and 3D all of which had an excess of dwarf plants.

### 3. Chinese Spring Monosomics x Marquillo-Kenya Farmer F<sub>2</sub>

The shorter coleoptile length associated with slower emergence

PLATE 3. Parents,  $F_1$  and typical  $F_2$  segregates from the Chinese Spring x Marquillo-Timstein cross.

1. Chinese Spring,
2.  $F_1$  hybrid,
3. Marquillo-Timstein,
4. Non-heading dwarf,
5. Late heading dwarf,

Remainder normal plants.

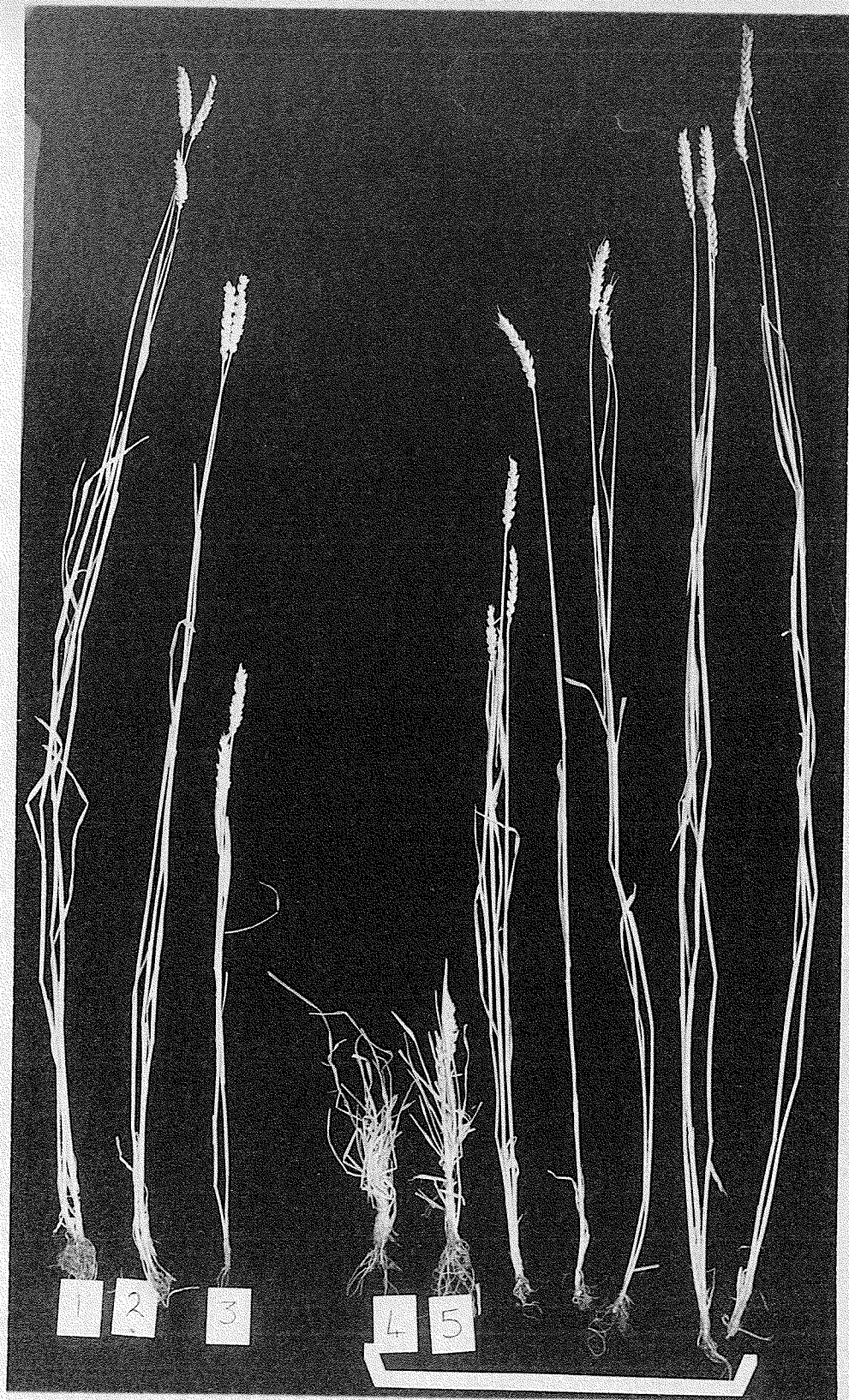


TABLE 4. The ratio of normal to dwarf plants in the  $F_2$  from crosses between the Chinese Spring monosomic series and Marquillo-Timstein.

Line	Number of Plants		Total	$\chi^2$ Value 599:134
	Normal	Dwarf		
1A	177	65	242	11.90**
2A	152	90	242	57.88**
3A	192	51	243	1.19
4A	197	41	238	.18
5A	210	35	245	2.62
6A	193	49	242	.62
7A	198	46	244	.052
1B	166	39	205	.074
2B	184	56	240	4.15*
3B	182	57	239	2.95
4B	85	15	100	.72
5B	195	45	240	.034
6B	192	52	244	1.49
7B	206	39	245	.92
1D	187	55	242	3.19
2D	143	58	201	15.03**
3D	172	60	232	8.91**
4D	191	51	242	1.26
5D	203	37	240	1.32
6D	201	41	242	.29
7D	198	39	237	.53
Chinese Spring x Marquillo- Timstein	599	134	733	.000

\* significant at the 5% level

\*\* significant at the 1% level

of seedlings of grass clump dwarfs was more evident in this cross than in those previously described. Within 10 days after emergence the grass clump segregants started to tiller, became darker and elongation was almost entirely replaced by excessive tillering. The older leaves became stiff and fragile. Although minor variation occurred within the grass clump segregates it was not possible to subdivide this group. The average height of grass clump plants within the 21 monosomic lines varied from 26.7 cm for line 3B to 36.7 cm for 6A whereas the Marquillo-Kenya Farmer parent was 17.5 cm tall.

The  $F_2$  populations of the normal disomics and the 21 deficient lines were classified into two classes: grass clump dwarfs and normal plants, the latter being relatively uniform in height (Plate 4). By comparing the ratios of each monosomic line with the normal disomic population (Table 5) it was found that five critical chromosomes were present: 2A, 4B, 1D, 2D and 7D. Lines 2A, 4B and 2D gave an excess of grass clump plants, whereas lines 1D and 7D had excess of tall plants.

#### 4. Rescue Monosomics x Marquillo-Kenya Farmer $F_2$

The  $F_2$  seedling populations were similar to those of Chinese Spring x Marquillo-Timstein but the grass clump segregates were even less vigorous and usually died prior to the heading of the normal segregates. As in the previous case two discrete classes: normal plants and grass clump dwarfs were established. The data is presented in Table 6. Five deficient lines 2A, 6A, 4B, 1D and 3D deviated sig-

PLATE 4. Parents, F<sub>1</sub> hybrids and F<sub>2</sub> segregates from the cross of Chinese Spring x Marquillo-Kenya Farmer.

1. Chinese Spring,
2. F<sub>1</sub> hybrid grown at 80°F,
3. F<sub>1</sub> hybrid grown at 70°F,
4. Marquillo-Kenya Farmer grown at 80°F,
5. F<sub>2</sub> grass clump segregates,
6. F<sub>2</sub> tall segregates.





TABLE 5. The ratio of tall to grass clump plants in the  $F_2$  from the crosses of the Chinese Spring monosomic series and Marquillo-Kenya Farmer.

Line	No. of Plants		Total	$\chi^2$ Value 413:457
	Tall	Grass clump		
1A	98	97	195	.61
2A	58	137	195	24.57**
3A	88	103	191	.15
4A	106	90	196	3.50
5A	94	101	195	.04
6A	94	99	193	.12
7A	97	99	196	.32
1B	103	96	199	1.47
2B	87	100	187	.07
3B	92	98	190	.07
4B	67	137	204	17.50**
5B	93	87	180	1.27
6B	59	53	112	1.22
7B	89	102	191	.06
1D	107	83	190	5.96*
2D	30	66	96	10.20**
3D	90	100	190	.00
4D	67	54	121	3.03
5D	87	100	187	.07
6D	104	89	193	3.18
7D	109	87	196	5.21*
Chinese Spring x Marquillo- Kenya Farmer	413	457	870	

\* significant at the 5% level

\*\* significant at the 1% level

TABLE 6. The ratio of tall to grass clump plants in the  $F_2$  from the crosses of Rescue monosomic series x Marquillo-Kenya Farmer.

Line	No. of Plants		Total	$\chi^2$ Value 318:250
	Tall	Grass clump		
1A	106	93	199	.60
2A	33	56	89	12.82**
3A	87	88	175	2.79
4A	95	93	188	2.27
5A	102	90	192	.64
6A	93	102	195	5.44*
7A	113	101	214	.88
1B	86	60	146	.50
2B	29	29	58	.84
3B	81	68	149	.16
4B	48	75	123	14.36**
5B	93	80	173	.35
6B	104	75	179	.32
7B	115	89	204	.01
1D	89	97	186	4.50*
2D	112	92	204	.10
3D	86	106	192	9.76**
4D	59	39	98	.71
5D	87	82	169	1.39
6D	99	83	182	.19
7D	89	82	171	1.08
Rescue x Marquillo- Kenya Farmer	318	250	568	.00

\* significant at the 5% level

\*\* significant at the 1% level

nificantly from the normal  $F_2$  disomic ratio. Unlike the previous cross all critical lines expressed an excess of grass clump plants. The results from the four series of crosses with respect to dwarfism are summarized in Table 7. A total of 12 different chromosomes proved to be involved.

With respect to crosses with Marquillo-Timstein, lines deficient for chromosomes 2A, 2B and 2D (homoeologous group 2) produced an excess of dwarf plants in both series indicating that both Rescue and Chinese Spring differ from Marquillo-Timstein and that genes for dwarfism are carried on these chromosomes by Marquillo-Timstein.

In the crosses with Rescue two members of homoeologous group 7 (7A and 7B) also gave an excess of dwarf plants whereas these chromosomes were not critical in crosses with Chinese Spring. In crosses with Chinese Spring chromosomes 1A and 3D produced an excess of dwarf plants and with Rescue all members of homoeologous group I deviated by producing a larger number of normal plants.

These differences between the two series may be due to differences between the varieties Rescue and Chinese Spring as compared to Marquillo-Timstein or to the differences in growing conditions particularly temperature which allowed more chromosomes in the Rescue crosses to appear critical due to minor or modifying genes which could not express their effects under warmer conditions.

In the crosses with Marquillo-Kenya Farmer five critical lines were revealed in each series with three being in common namely 1D, 2A, and 4B. Both 2A and 4B produced an excess of grass clump plants

TABLE 7. A summary of the chromosome lines found to be critical in the crosses between the two monosomic series and the dwarf parents.

Crosses	Homoeologous Group I			Homoeologous Group II			Homoeologous Group VII			
	1A	1B	1D	2A	2B	2D	3D	7A	7B	7D
								4B	4B	6A
Rescue x Marquillo-Timstein	+	+	+	-	-	-	-	-	-	-
Chinese Spring x Marquillo-Timstein	-			-	-	-	-			
Rescue x Marquillo-Kenya Farmer				-	-	-	-			
Chinese Spring x Marquillo-Kenya Farmer			+	-	-	-	-			+

+ = more normal plants than expected  
 - = more dwarf plants than expected

whereas 1D with Rescue produced more grass clumps and with Chinese Spring more normal plants. Chromosome 7D with Chinese Spring also gave more normal plants, but had no effect in the Rescue crosses. The remaining chromosomes involved were 2D with Chinese Spring and 6A with Rescue, both producing an excess of dwarfs. It is concluded from the data that Marquillo-Kenya Farmer has major genes for dwarfism in chromosomes 2A and 4B and that Marquillo-Kenya Farmer differs from Rescue for genes in chromosomes 1D, 3D and 6A and from Chinese Spring for genes on chromosomes 1D, 2D and 7D.

The fact that the two normal varieties differ from each other for these particular chromosomes would indicate that these genes may be of a minor or modifying nature.

In crosses involving Marquillo-Kenya Farmer chromosome 4B was critical in both cases whereas it was not implicated in the Marquillo-Timstein crosses. The major difference between the two dwarfs is probably controlled by factors in this chromosome.

With regard to the genetic control of dwarfing in the two dwarf varieties it is apparent that the major genes for dwarfing in Marquillo-Timstein are on chromosomes 2A, 2B and 2D and in Marquillo-Kenya Farmer in chromosomes 2A and 4B. Several modifying genes also probably exist but these cannot be attributed to one parent or the other in these crosses.

(b) PLANT HEIGHT

1. Rescue Monosomics x Marquillo-Timstein F<sub>2</sub>

Comparison of the average height and variability of the normal headed portion of each monosomic F<sub>2</sub> population with the disomic F<sub>2</sub> by means of the "t" test indicated that eight F<sub>2</sub> monosomic populations deviated significantly (Table 8). Six means were significantly below the disomics and two were significantly above. Those significantly shorter were all members of homeologous group 2 and lines 3A, 3D and 5D. The populations which exceeded the disomic mean were 1A and 4B. The F<sub>2</sub> populations deficient for chromosomes 2A, 2B, 2D, 3A, 3D and 5D contained more plants within the shorter ranges than did the disomic population and fewer plants in the Rescue parent range (Table 8). Conversely, lines 1A and 4B had more plants within the taller ranges than the F<sub>2</sub> disomic and a higher percentage of plants within the Rescue parent range.

In addition to causing reduced height in the normal heading plants, the chromosomes of homoeologous group 2 were also critical in producing an excess of dwarf plants as compared to the disomic ratio (Table 1). However, lines 3A, 3D, 4B and 5D deviated significantly from the disomic population in mean plant height but did not deviate from the disomic population in relation to dwarfing.

2. Chinese Spring Monosomics x Marquillo-Timstein F<sub>2</sub>

Sixteen chromosomes were found to influence the height of plants

TABLE 8. Average height and percent of plants in tall parent range for the normal headed portion of three deficient F<sub>2</sub> population.

Line	Rescue x Marquillo-Timstein		Chinese Spring x Marquillo-Timstein		Chinese Spring x Marquillo-Farmer	
	Average Height cm.	% in tall parent range	Average Height cm.	% in tall parent range	Average Height cm.	% in tall parent range
1A	74.6 ± 1.86*	78.2	83.4 ± 1.66**	44.5	108.6 ± 1.98**	74.5
2A	59.6 ± 2.75**	57.8	85.2 ± 1.56**	47.1	103.0 ± 3.02	63.9
3A	57.6 ± 1.54**	47.0	90.5 ± 1.41**	62.2	115.6 ± 1.49**	94.3
4A	68.4 ± 2.17	68.5	99.2 ± 1.16	74.5	109.6 ± 2.03**	78.2
5A	72.0 ± 1.89	71.5	103.1 ± 1.24**	81.9	115.1 ± 1.83**	90.1
6A	65.9 ± 1.99	64.6	97.6 ± 1.07	73.4	94.7 ± 2.10**	62.5
7A	72.5 ± 1.92	77.3	99.8 ± .99	80.2	97.2 ± 1.72*	54.5
1B	66.2 ± 1.52	66.5	86.6 ± 1.50**	45.1	104.4 ± 1.66	71.4
2B	56.1 ± 1.76**	36.0	90.1 ± 1.02**	50.5	93.3 ± 2.52**	54.2
3B	66.9 ± 1.62	74.6	80.4 ± 1.84**	42.9	97.6 ± 2.47	63.7
4B	75.6 ± 1.79**	79.5	89.4 ± 1.95**	50.6	113.1 ± 2.43**	85.2
5B	73.1 ± 1.76	74.7	96.8 ± 1.02*	69.5	121.1 ± 1.86**	92.7
6B	68.2 ± 1.69	74.0	89.9 ± 1.13**	55.1	102.1 ± 1.56	64.0
7B	69.4 ± 1.77	78.2	84.5 ± 1.01**	42.5	114.9 ± 1.66**	89.4
1D	65.5 ± 1.42	60.9	86.7 ± 1.68**	57.3	107.3 ± 1.55**	79.8
2D	64.9 ± 1.34*	70.9	94.6 ± 1.44**	61.2	88.7 ± 2.86**	15.0

continued

TABLE 8 CONTINUED

Line	Rescue x Marquillo-Timstein		Chinese Spring x Marquillo-Timstein		Chinese Spring x Marquillo-Farmer		parent range
	Average Height cm.	% in tall	Average Height cm.	% in tall	Average Height cm.	% in tall	
3D	63.7 ± 1.73*	62.0	97.3 ± 1.35	74.6	93.9 ± 2.04**	45.3	
4D	71.3 ± 1.26	84.2	101.6 ± 1.37	79.7	100.3 ± 2.09	68.6	
5D	62.8 ± 1.31**	57.4	96.6 ± 1.03*	72.8	101.9 ± 1.80	67.9	
6D	65.9 ± 1.35	70.4	92.9 ± .83**	64.2	102.2 ± 1.57	63.6	
7D	69.0 ± 1.21	79.1	87.4 ± 1.08**	45.5	97.7 ± 1.66	55.1	
Dis.F <sub>2</sub>	68.9 ± 1.33	70.4	99.9 ± .97	77.1	101.4 ± 1.34	76.5	
Tall parent	88.3 ± .88	100.0	113.7 ± .62	100.0	131.5 ± 1.22**	100.0	

\* significant at the 5% level

\*\* significant at the 1% level



in the Chinese Spring series x Marquillo-Timstein when the means of monosomic  $F_2$  populations were compared with the  $F_2$  disomic mean (Table 8). The only deficient line which attained greater average height than the disomic was 5A. This line also had the highest percentage of plants within the Chinese Spring height range. The remaining 15 lines were significantly shorter. The percentage of plants within the Chinese Spring height range varied from 42.5% (7B) to 81.9% (5A); the  $F_2$  disomic having 77.1 percent.

The B genome had the most influence on the height of plants since all deficient lines of this genome significantly decreased the mean height. Of the 9 remaining lines, 5 were members of the D genome and 4 of the A genome. All lines which gave an excess of dwarfs as compared to the disomic ratio (Table 4) were also significantly shorter except for 3D which did not differ significantly from the  $F_2$  disomic.

### 3. Chinese Spring Monosomic Series x Marquillo-Kenya Farmer $F_2$

Unlike the crosses involving Marquillo-Timstein, eight of the deficient  $F_2$  lines of Chinese Spring x Marquillo-Kenya Farmer had a significantly taller mean height (1A, 1D, 3A, 4A, 4B, 5A, 5B and 7D).

Five other lines were significantly shorter (2B, 2D, 6A, 7A, 3D). Of the 5 deficient lines influencing the ratio of tall to grass clump plants (Table 5) 3 also influenced height of the normal portion of the  $F_2$  population. Lines 2D and 6A were significantly shorter, whereas 4B increased the height.

The comparison of chromosome effects on height of plants of Chinese Spring x Marquillo-Timstein monosomic  $F_2$  populations with those of Chinese Spring x Marquillo-Kenya Farmer showed that 4 chromosomes produced similar results; 5A increased significantly the average height of plants, 2B and 2D sharply reduced and 4D did not show any difference in the height as compared to their respective  $F_2$  disomic means. Dissimilar effects were found for most of the remaining chromosomes. This suggests that the genetic control of the height in the Marquillo-Timstein and Marquillo-Kenya Farmer is greatly dissimilar and may differ by many factors. This indicates that more genes influence plant height than are involved in the inheritance of dwarfism.

In general chromosomes which were critical for dwarfing also influenced the height but several chromosomes influenced height which were not implicated in the inheritance of dwarfism. Of the 18 chromosomes involved in dwarfism inheritance in the three series 7 did not affect plant height as regards variability in the headed portion of the  $F_2$  population. This shows that while some factors which control these two traits may be either pleiotropic or closely linked, other independent factors must be present.

### $F_3$ MONOSOMIC ANALYSES

$F_3$  lines from individual normal  $F_2$  plants from crosses of the Rescue monosomics x Marquillo-Timstein were grown in the field in 1965.

The ratio of segregating to non-segregating families in each line was compared to the ratio occurring in the disomic  $F_3$  lines (Table 9). Nine lines deviated from the disomic ratio. Of these only three were found to be critical in  $F_2$ . This apparent disagreement can only be explained by differential selection of dwarf genotypes in  $F_2$  caused by the abnormally cool growing conditions.

For example, lines 1B and 1D which were critical in  $F_2$  and produced an excess of tall plants had an excess of segregating families in  $F_3$ . This may mean that these chromosomes in Marquillo-Timstein possess modifying factors which permit a wider range of genotypes to head under cool conditions. This postulation was substantiated by the fact that segregation occurred in  $F_3$  lines derived from normal  $F_2$  plants of all height classes whereas only the  $F_3$  lines derived from  $F_2$  plants in the shorter height classes segregated in most other lines.

#### CONVENTIONAL ANALYSIS OF DISOMIC CROSSES

##### 1. Dwarfing in Marquillo-Timstein x Sonora 64 and Marquillo-Timstein x Norin 10.

The average height of the  $F_1$  plants exceeded that of the taller parents (Plate 5) indicating that the genotypes for dwarfing in the parents differed and that heterosis existed.

The ratio of tall to dwarf plants in the 6  $F_2$  progenies of Marquillo-Timstein x Sonora 64 (608 tall 110 dwarf) and 4 progenies of Marquillo-Timstein x Norin 10 (673 tall 114 dwarf) were established

TABLE 9. The ratios of segregating to non-segregating families in the  $F_3$  from the  $F_2$  heading plants of Rescue monosomic series x Marquillo-Timstein.

Line	No. of families		Total	$\chi^2$ Value 14:70
	Segregating	Non-Segregating		
1A	11	32	43	2.403
2A	2	12	14	0.019
3A	19	26	45	10.493**
4A	2	38	40	3.963*
5A	0	37	37	-
6A	7	42	49	0.149
7A	3	45	48	3.745
1B	10	20	30	5.250*
2B	10	35	45	0.999
3B	0	31	31	-
4B	13	41	54	2.132
5B	4	32	36	0.793
6B	3	8	11	0.952
7B	1	41	42	6.170*
1D	15	28	43	10.150**
2D	2	29	31	2.365
3D	13	29	42	6.168*
4D	3	30	33	1.363
5D	5	30	35	0.131
6D	6	34	40	0.087
7D	0	14	14	-
Disomic $F_3$	14	70	84	0.000

\* significant at the 5% level

\*\* significant at the 1% level

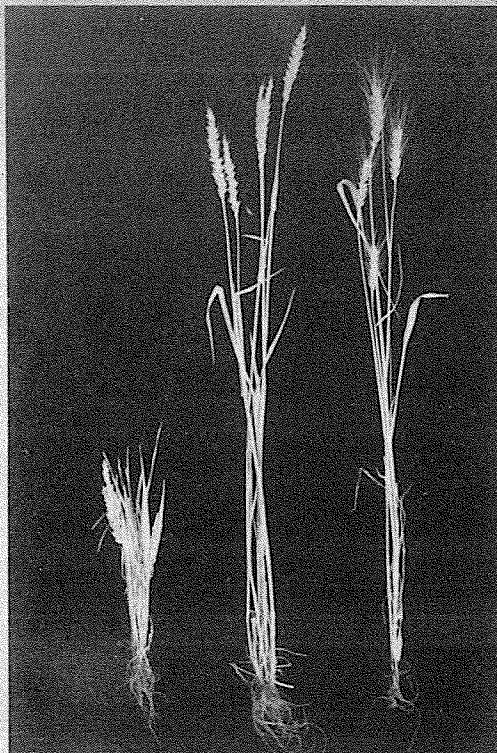
103<sup>a</sup>

PLATE 5. Parent and  $F_1$  plants of the crosses.

1. Redman Federation x Norin 10,
2. Marquillo-Timstein x Norin 10,
3. Sonora 64 x Redman Federation,
4. Norin 10 x Senora 64.

Sonora  
-----

The  $F_1$  is placed between the parents.



1.



2



3



4

on the basis of plant morphology. The dwarf segregates had the characteristics of Marquillo-Timstein such as low stature and excessive tillering and were easy to separate from the normal segregates which in some cases were shorter than the taller of the dwarfs. The height expression in the  $F_2$  of Marquillo-Timstein x Sonora 64 and Marquillo-Timstein x Norin 10 are presented in Figures 2 and 3 respectively. Comparison of the  $F_2$  tall:dwarf ratio for the two populations indicated no significant difference ( $\chi^2 = 1.465$ ,  $P = .20 - .30$ ). This means that the genotype of Sonora 64 and Norin 10 are similar with respect to their interaction with the common parent Marquillo-Timstein. The distribution also reveals that Marquillo-Timstein may be a source of genes for short stature that could complement the genes in the other two varieties for plant breeding purposes.

## 2. Dwarfing in Redman x Federation

A third dwarf used in this study was obtained in an advanced generation of the cross Redman x Federation. This cross was repeated in order to study the inheritance of dwarfism in this hybrid. Both Redman and Federation are normal, tall varieties. The  $F_1$  plants were all normal and dwarf plants appeared in the  $F_2$  generation. Of the 394  $F_2$  plants 327 were tall and 67 dwarf showing agreement to a 13:3 ratio ( $\chi^2 = .787$  and  $P = .30 - .50$ ).

To account for this ratio the assumption was made that the parents

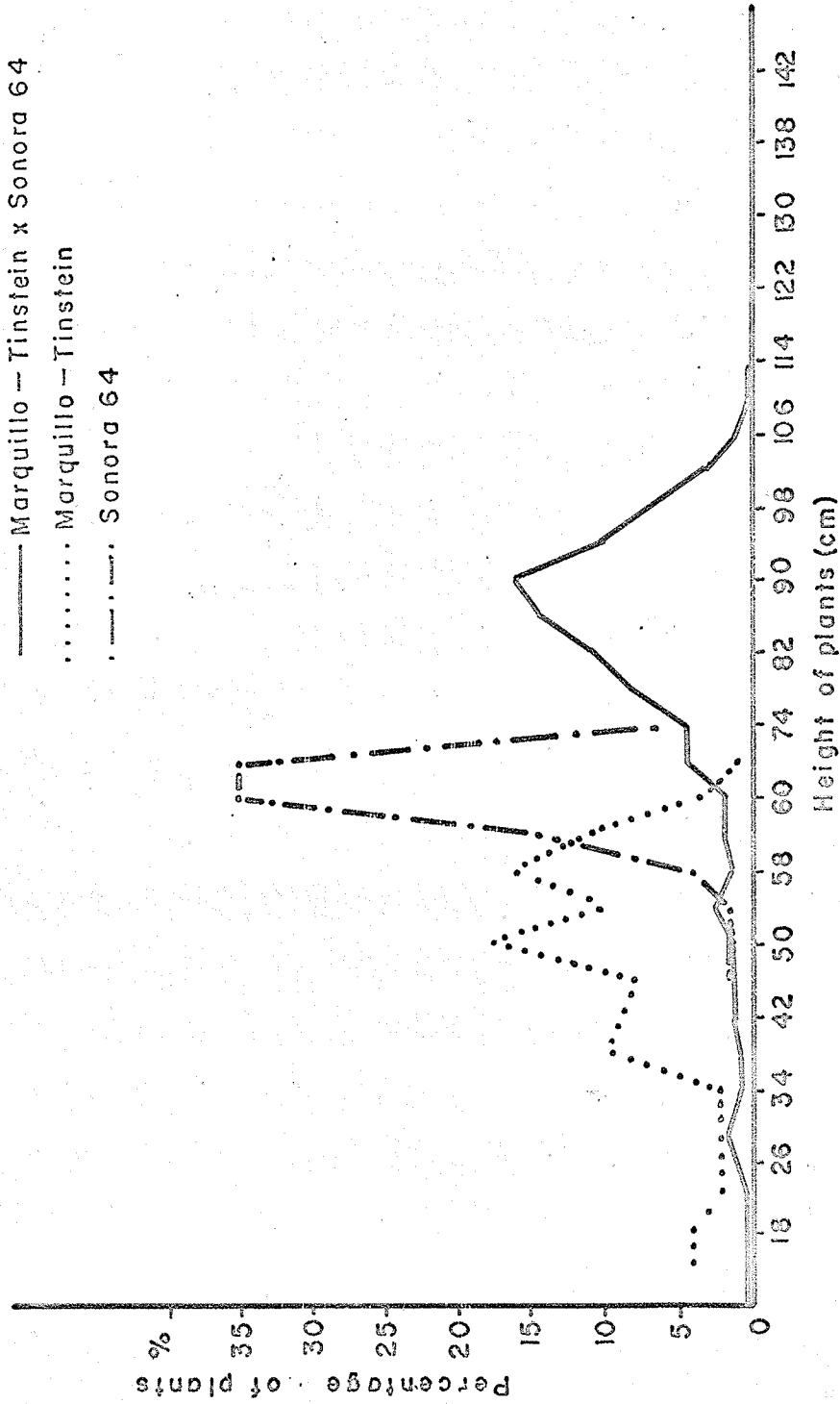


FIGURE 2. Plant height distribution of the parents and the F<sub>2</sub> population from the cross Marquillo-Tinstein x Sonora 64.



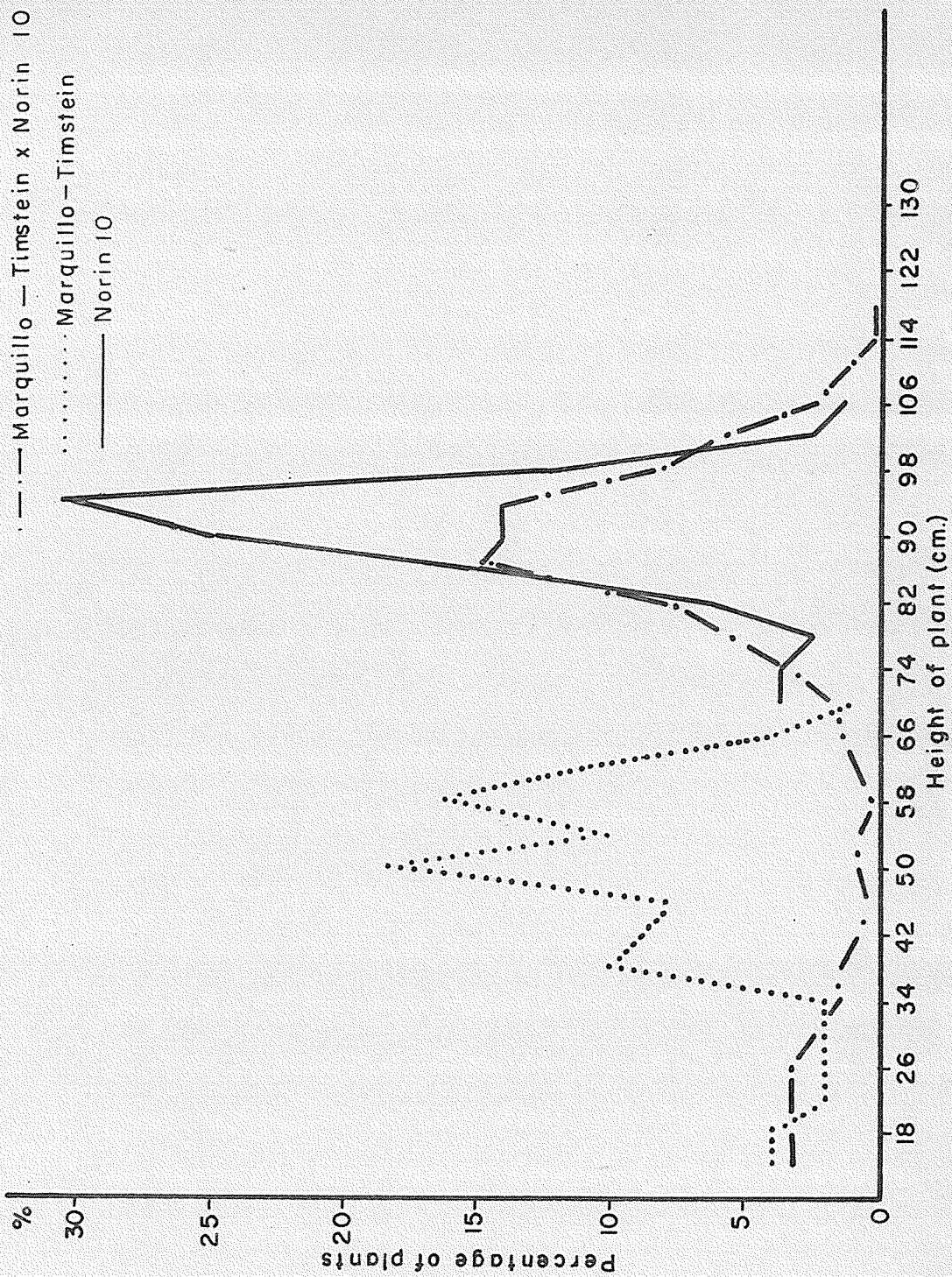


FIGURE 3. Plant height distribution of the parents and the F<sub>2</sub> population from the cross Marquillo-Timstein x Norin 10.

differ by 2 genetic factors; a dominant dwarfing factor (DD) and an inhibiting factor (II). One parent must carry two dominant factors, DDII, the other both recessive factors, ddii.

This hypothesis was verified by studying 132  $F_3$  families from individual  $F_2$  plants. Of these 100 were from normal  $F_2$  plants and 32 from dwarfs. Based on the above hypothesis 7/13 of the  $F_3$  lines from normal  $F_2$  plants should breed true and 6/13 segregate whereas of the  $F_3$  lines from dwarf  $F_2$  plants 2/3 should segregate and 1/3 be dwarfs. Table 10 presents the actual results:

TABLE 10. Segregation occurring in  $F_3$  lines from normal and dwarf  $F_2$  plants of the cross Redman x Federation.

$F_2$	$F_3$	Observed	Calculated	$\chi^2$
Normal	Homozygous normal	54	53.86	0.00036
	segregating 13:3 or 3:1	46	46.14	0.00042
Dwarf	segregating 1:3	11	10.66	0.0108
	homozygous dwarf	21	21.34	<u>0.0054</u>
				$\chi^2$ 0.01698
				P .99

In addition the  $F_1$  was backcrossed to both parents. According to the hypothesis the progeny of one backcross should give the ratio of 3 tall to 1 dwarf, the other only tall plants. From the backcross of Redman x (Redman x Federation  $F_1$ ) a ratio of 25 tall: 6 dwarf plants

was obtained, which is not significantly different from a ratio of 3:1 ( $\chi^2 = 0.537$ ,  $P = 0.50 - 0.75$ ). The backcross of (Redman x Federation  $F_1$ ) x Federation resulted in only tall plants. It was concluded that the proposed 2 factor theory provides a logical explanation for the inheritance of dwarfing in this cross. The backcross results support findings by Stephens (38), McMillan (18) and Tingey (43) that Federation has the constitution of DDII. Redman must therefore be ddii. This result indicates that the 2 dominant genes for "grass clump" located in chromosomes 2A and 4B of Redman by Hurd and McGinnis (16), which proved to have a complementary action with at least one gene for "grass clump" in Kenya-Farmer, showed no interaction with the genes found in Federation.

It may therefore be concluded that the 2 dominant genes for "grass clump" in Redman are not the same genes which are involved in dwarfing in the cross with Federation.

3. Dwarfing in Sonora 64 x Redman - Federation, and Redman-Federation x Norin 10.

The average height of the  $F_1$  plants exceeded that of the taller parents (Table 11, Plate 5), indicating that the genotypes for dwarfing in the parents differed and that heterosis occurred, particularly in the  $F_1$  of Sonora 64 x Redman-Federation.

TABLE 11. Parental and F<sub>1</sub> height and F<sub>2</sub> segregation in the crosses of Sonora 64 x Redman-Federation and Redman-Federation x Norin 10.

Line	F <sub>1</sub> Height cm	F <sub>2</sub> Segregation		Calculated		χ <sup>2</sup>	P
		tall	dwarf	tall	dwarf		
Sonora 64 x Redman-Federation	70.0 ± 1.15	513	99	513.9	98.1	0.0178	.80-.90
Redman-Federation x Sonora 64	72.2 ± 1.59	456	86	455.1	86.9	6.282	.01-.02
Redman-Federation x Norin 10	72.9 ± 1.15	392	110	407.7	94.2		
Sonora 64	56.9 ± 1.31						
Norin 10	68.7 ± 1.16						
Marquillo-Timstein	51.5 ± 2.16						

The segregation in the  $F_2$  of these crosses was established on the basis of plant morphology because the height of dwarf plants differed considerably, often overlapping with normal plants. From the data in Table 11 it is clear that the reciprocal crosses of Sonora 64 and Redman Federation produced very similar  $F_2$  population whereas the  $F_2$  of Redman Federation x Norin 10 was significantly different. This may be due however to environment since the latter was grown in the greenhouse and the former in the field.

The plant height distribution of Sonora 64 x Redman-Federation is presented in Figure 4. Of the  $F_2$  79.3% were taller than the Sonora 64 parent but the overall height range exceeded both parents indicating that Redman-Federation may be another source of different genes for short stature.

#### 4. Dwarfing in the cross of Tom Thumb x Redman Federation

The average height of the  $F_1$  plants was  $53.0 \pm 1.0$  cm as compared to  $22.8 \pm 1.5$  cm for Redman-Federation and  $32.7 \pm .95$  cm for Tom Thumb (Plate 6).

The  $F_2$  population was grown in the greenhouse and the parents and many dwarf segregates failed to head (Plate 6). The normal portion of the population contained plants up to 110 cm in height indicating that heterosis and very different gene control of dwarfism existed between the two parents.

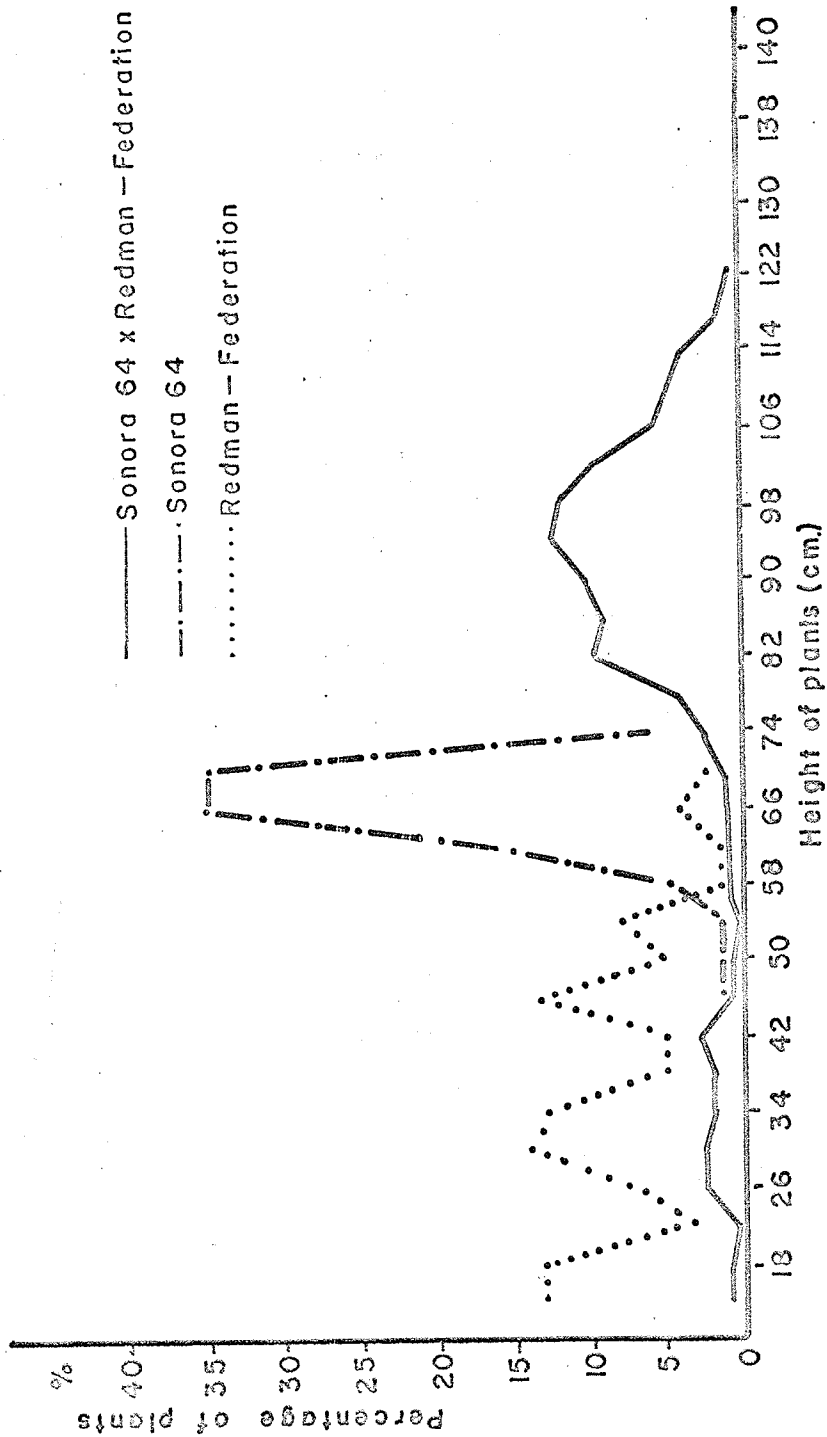
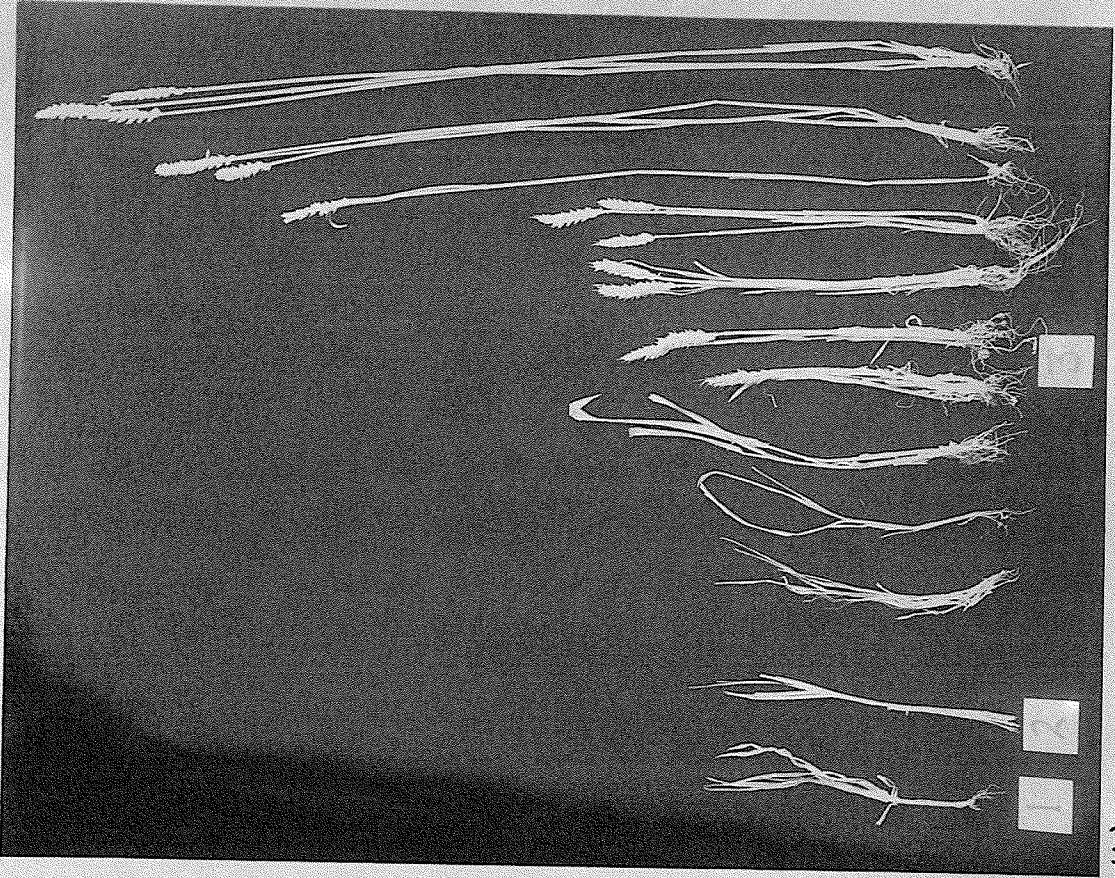
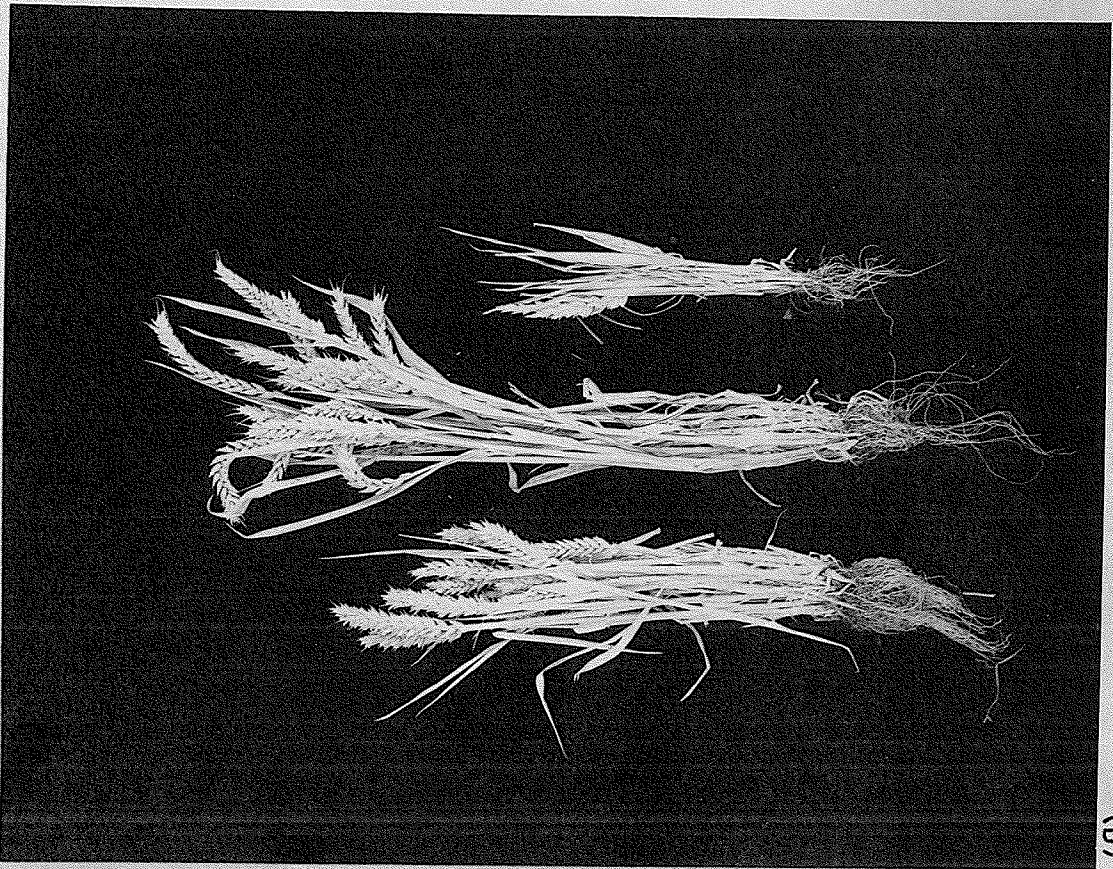


FIGURE 4. Plant height distribution of the parents and the F<sub>2</sub> population from the cross Sonora 64 x Redman-Federation.



(b)



(b)

PLATE 6. (a) The  $F_1$  and the parents,

(b) The  $F_2$  segregates and parents (right) of the cross<sup>2</sup> of Tom Thumb x Redman Federation.

(a) Tom Thumb (left),  $F_1$  (center) Redman-Federation (right)

(b) 1. Tom Thumb,  
2. Redman-Federation  
3.  $F_2$  segregates



5. Dwarfing in the cross of Marquillo-Timstein x Tom Thumb

The average height of  $F_1$  plants was  $49.8 \pm .69$  cm as compared to  $56.7 \pm 1.50$  cm for Marquillo-Timstein and  $32.7 \pm .95$  cm for Tom Thumb. The distribution pattern for  $F_2$  plant height (Fig.5) shows that transgressive segregation occurred in both directions.

6. Dwarfing in the Crosses of Tom Thumb x Sonora 64 and Norin 10 x Tom Thumb.

The average height of the  $F_1$ 's were  $40.4 \pm .95$  cm and  $43.9 \pm .63$  cm respectively. Whereas Sonora 64 was  $56.9 \pm 1.31$  cm, Norin 10  $68.7 \pm 1.16$  cm and Tom Thumb  $32.7 \pm .96$  cm. The  $F_2$  height distributions are illustrated in Plate 7 and Figure 6. In both cases the height range exceeds both parents indicating that the genes for dwarfing in the parents differ.

The results from this series of crosses indicate that the dwarfs; Marquillo-Timstein and Redman-Federation differ genotypically from all other semi-dwarf varieties tested. Norin 10 and Sonora 64 react similarly in all crosses indicating that they differ little in dwarfing genotype as would be expected since Sonora 64 has Norin 10 in its parentage. Crosses between Tom Thumb and Marquillo-Timstein and Redman-Federation indicate that it differs from these two lines and also that these two differ from each other.

The  $F_2$  distribution in all cases indicates that dwarfism is complexly inherited.

Due to the complex nature of the inheritance revealed by the

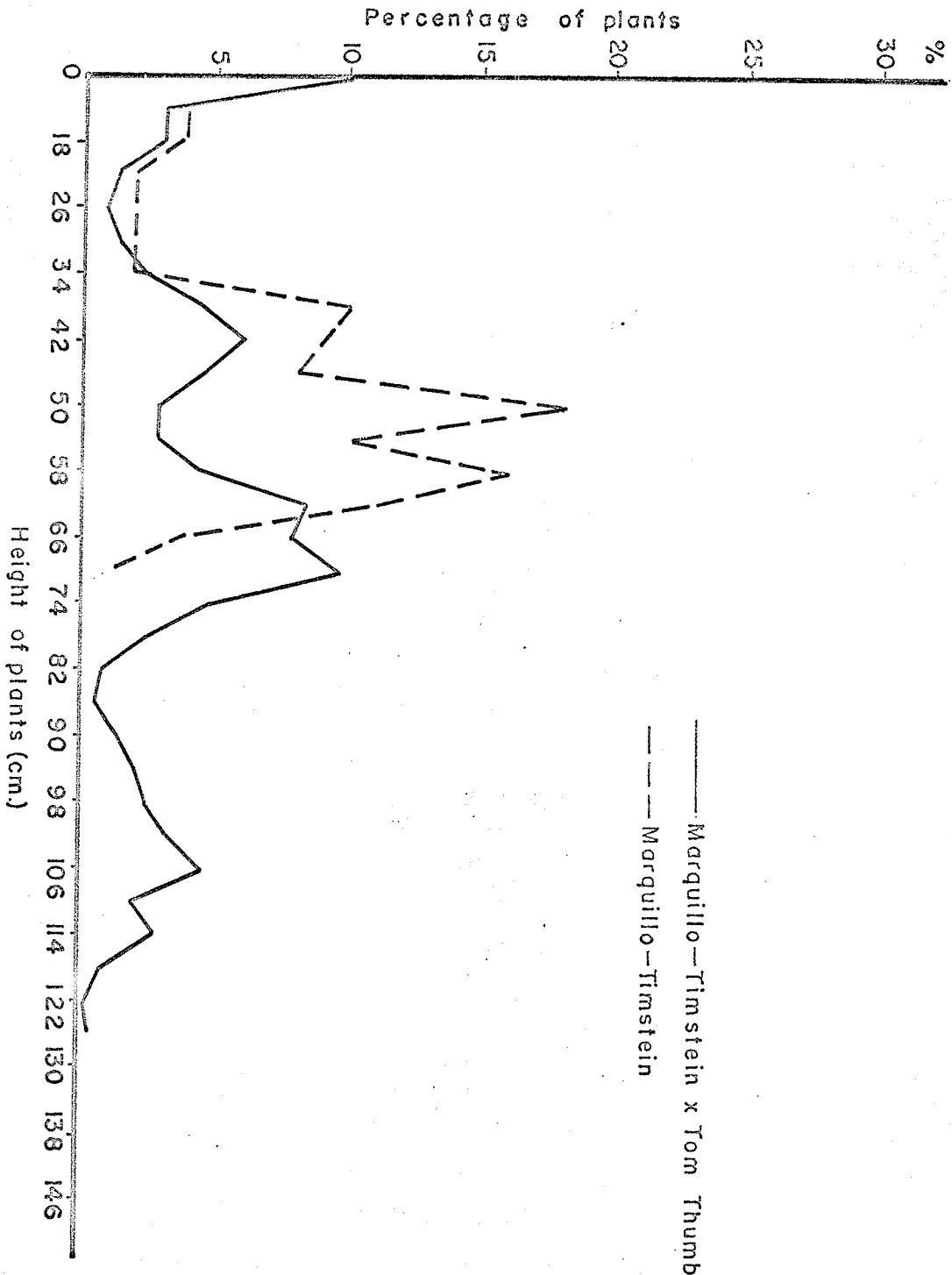


FIGURE 5. Plant height distribution of the Marquillo-Timstein and the F<sub>2</sub> population from the cross Marquillo-Timstein x Tom Thumb.

- PLATE 7. (a) The  $F_1$  and parents (left),  
(b)  $F_2$  segregates and parents (right) of  
the cross of Tom Thumb x Sonora 64.
- (a) Tom Thumb (left),  $F_1$  (center),  
Sonora 64 (right)
- (b) 1. Tom Thumb  
2. Sonora 64  
3.  $F_2$  segregates.

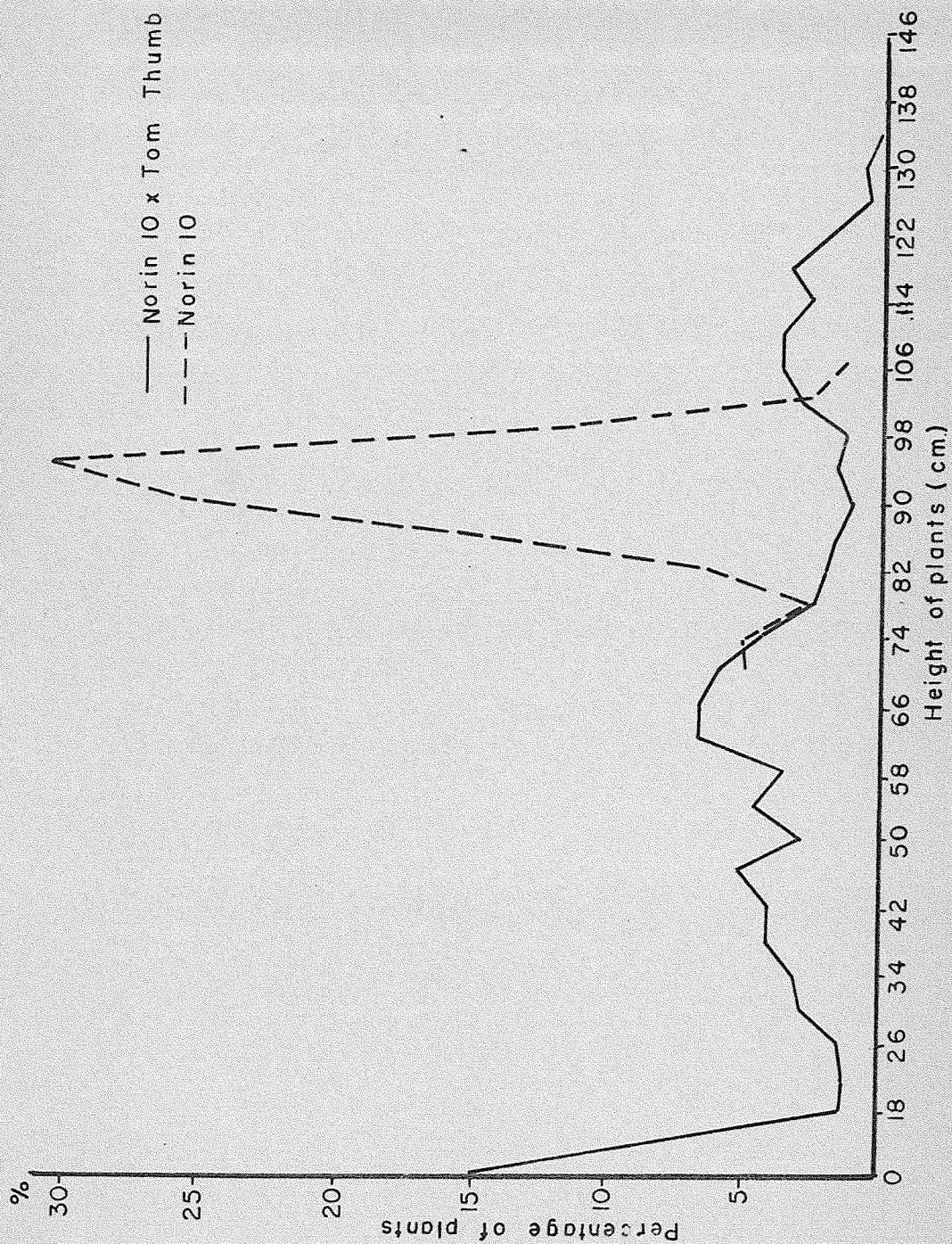


FIGURE 6. Plant height distribution of the Norin 10 and the F<sub>2</sub> population from the cross Norin 10 x Tom Thumb.

monosomic analyses and the transgressive segregation occurring in the disomic crosses no attempt was made to postulate the actual mode of inheritance in the disomic crosses.

## GENERAL DISCUSSION AND CONCLUSIONS

The results of this study show that both the Marquillo-Timstein and Marquillo-Kenya Farmer types of dwarfism are conditioned by several genes. In addition to major genes there are modifying genes which were revealed by the  $F_2$  and  $F_3$  monosomic analysis.

All chromosomes of homoeologous group two of Marquillo-Timstein carry genes for dwarfism, of these 2A and 2D are regarded as major genes since they deviated greatly from the disomic populations in crosses with both monosomic series. Chromosome 2B would appear to carry a major gene since it was critical in both monosomic series but because of very slight deviation from the disomic population it could be regarded rather as a minor gene.  $F_2$  lines deficient for chromosomes 1B and 1D proved to be critical under cool growing conditions and  $F_3$  families deficient for these chromosomes had an excess of segregating lines suggesting that these chromosomes possess modifying genes which reduce the temperature sensitivity of the Marquillo-Timstein. The other lines which were found critical in crosses with one or the other of the monosomic series and Marquillo-Timstein are regarded as being due to modifiers carried by the Chinese Spring or Rescue varieties and not essential to the expression of dwarfism.

The influence of environment on dwarfism has been reported previously by Clark and Hooker (6) and by McMillan (18). Both of whom found that the frequency of grass clumps in a population varied with changes in environmental conditions. McMillan also reported variation in dwarf plant morphology due to variation in environment.

Hermsen (14) reported that the variety Timstein has two genes for dwarfism located on chromosomes 4B and 2D whereas the present study showed Marquillo-Timstein to carry major genes on 2A and 2D.

This indicates that the dwarfism of Marquillo-Timstein is probably due to one major gene from Marquillo and only one from Timstein.

Chromosomes 2A and 4B of Marquillo-Kenya Farmer were found to carry major dwarfism genes in this study. Hurd and McGinnis (16) established in crosses of Redman x Kenya Farmer that these two chromosomes of Redman also carry major genes for dwarfism. The fact that chromosome 2A was critical in both series with Marquillo-Timstein and with Marquillo-Kenya Farmer, and that chromosome 4B proved to be critical in both series with Marquillo-Kenya Farmer only indicates that the major difference between the Marquillo-Timstein and the Marquillo-Kenya Farmer dwarfs is due to gene differences on chromosome 4B. This chromosome probably contains the factor which increases the temperature sensitivity of Marquillo-Kenya Farmer as compared to Marquillo-Timstein.

Conventional genetic analysis of dwarfism in the cross of Redman x Federation revealed it to be controlled by 2 genes. The results from the  $F_2$ ,  $F_3$  and backcross progenies support previous findings (38,18,43) that Federation has one dominant gene for dwarfism and an inhibitor and that Redman must carry the opposite alleles.

Apparent contradiction with Hurd and McGinnis' (16) finding that Redman carries 2 complementary genes for dwarfing on chromosomes 2A and 4B can be explained by assuming that the genes found in Redman and Federation represent independent, nonallelic loci.

It is probable that in cases of  $F_1$  dwarfism such as exists in crosses between Marquillo x Timstein and Marquillo x Kenya Farmer that three major genes exist and that any two in the homozygous condition are sufficient to produce dwarfs but that the genes on chromosome 2A and 4B are more potent than the one on chromosome 2D. Dwarfism such as that between Redman and Federation which occurs in the  $F_2$  and is prevented by an inhibitor gene may either be totally unrelated to the other type or else is due to different gene action.

In crosses between the three above mentioned dwarfs and the varieties Sonora 64, Norin 10 and Tom Thumb the semi-dwarfism of these varieties appears to be superimposed on the dwarf genotype producing transgressive segregation beyond the limits of both parents. This indicates that major gene differences exist between the two types resulting in heterosis.

From the results of the study of dwarf inheritance it was clear that the dwarf varieties also influenced height within the non-dwarf portion of the segregating population. In other words the genes which cause dwarfism appear to influence height of normal plants when the complete genotype required to produce dwarfs is not present.

Studies by Allan and Vogel (1) showed that eleven chromosomes influence height in the cross of the Chinese Spring monosomic series and the semi-dwarf line Norin 10-Brevor 14. Results from the present study do not completely agree with those of Allan and Vogel (1) as



far as the chromosomes involved is concerned but they do confirm the complexity of the inheritance of height.

In most cases chromosomes which carried genes influencing the frequency of dwarfing in the  $F_2$  populations also influenced the range of plant heights in the normal portion of the population. In addition many chromosomes influenced the height patterns which were not involved in the inheritance of dwarfism. On this basis it is probable that the dwarf character is conditioned by genes that in some cases are able to modify plant height and that other genes control the dwarfing mechanism without having any effect on the height of normal plants. In other words some genes have a pleiotropic effect while other influence one or the others but not both characters.

The results from the monosomic crosses indicates that the dwarfs, Marquillo-Timstein and Redman-Federation, express a complementary and non-allelic relationship with the semi-dwarf genotypes resulting in transgressive segregation. The occurrence of plant types that are shorter than either parent indicates that the two new dwarf lines may have potential in plant breeding alone or in combination with other semi-dwarf parental lines.

The results of the present study suggest some shortcomings of monosomic analyses in studying characters of such complexity as dwarfism. Firstly, it is difficult to distinguish chromosomes carrying major factors from those which have minor or modifying effects. Secondly, although this method reveals which chromosomes affect the

inheritance of dwarfing it does not establish whether the effect found is due to the homozygous condition of the chromosome of the variety being tested or whether it is caused by the loss of a chromosome of the other variety.

It is possible that the production of substitution lines of the chromosome found to be critical may give more precise information about the significance of genes on each chromosome.

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