

PLANT HEIGHT INHERITANCE OF A DWARF
MUTANT IN GRAIN SORGHUM,
Sorghum bicolor (L.) Moench

By

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CHAPTER I

INTRODUCTION

The grain sorghum varieties developed through breeding programs before 1930 ranged from 135 to 180 cm. in height and were poorly suited for harvesting with the wheat header or combine. Harvesting was a slow and tedious procedure by hand at that time. At a meeting of sorghum workers at Manhattan, Kansas in 1926, the desirability of a new machine to harvest grain sorghum was discussed, and the development of grain sorghum varieties with a fixed height of about 120 cm. through breeding was suggested. In 1928, the first grain sorghum variety, Beaver, with short-stalk and milo-like grains was selected from the cross between Kafir and Milo and released in Oklahoma. Shortly thereafter, several varieties with such characters were developed and distributed by federal and state experiment stations in the sorghum belt. Combine grain sorghum leaped into importance after the release of the Martin variety in 1941.

The labor for combining grain sorghum is about one-eighth that required by hand heading and threshing. The reduced labor for harvesting resulted in expanded production in the Great Plains and Southwest region. With the development of hybrid varieties utilizing male sterility and other improvement of cultural practices, sorghum now

ranks third among grain crops produced in the United States, exceeded by only wheat and corn. The annual production is over 650 million bushels and the acreage is estimated at close to 13 million acres. More than 95 percent of the sorghum grain is produced on short-stalked varieties.

Both wild and cultivated sorghum species have heights ranging from 50 to 450 cm. The tall varieties are predominantly used as forages. Besides the United States and Australia, dwarfness is not considered advantageous, even in grain varieties, because the stalks are used for other purposes. Dwarf strains of Kafir, Durra, Hegari, Kaoliang and Broomcorn have been selected in the United States from varieties introduced from Africa, Asia and Europe. Several dwarf mutants also have occurred in this country since sorghum was introduced. Certain dwarf mutants have been thoroughly studied and utilized in breeding programs, and some are less well understood than others. Karper and Quinby (1946) stated that "These mutational changes have been of very definite value in producing better adaptation in handling and consistency and surely of yield in this sorghum group. Milo would not have survived in the United States without them."

The purpose of this study was to determine the nature of an abnormal dwarf mutant isolated from the F₅ segregating generations of a natural outcross between Red Kafir and Reed Kafir by Seiglinger in 1933. Preliminary study of this mutant did not reveal any similarity with other known dwarf mutants. In addition, other genetic factors

associated with this mutant were studied. Finally, the genetically known parents used in this study were verified for plant height factors.

The knowledge of plant height inheritance of this mutant will be useful to sorghum breeders and geneticists who may be confronted with a similar mutant.

CHAPTER II

LITERATURE REVIEW

Martin (1936) and Quinby and Martin (1945) reported variation in plant height ranging from 150 to 270 cm. in populations of Standard milo when they were first introduced and grown in the United States. Occasionally natural hybrids grew even taller than this. It was postulated that at some undetermined time, the varieties mutated and plants 90 to 180 cm. tall could be spotted within the populations. The first Dwarf milo was isolated and grown on a few farms in Texas and Oklahoma as early as 1905. Within a few years this more advantageous Dwarf type spread and largely replaced the taller Standard type. About 15 years later the Double Dwarf or Extra Dwarf milo, 50 to 75 cm. tall, was isolated in Arizona in 1918. Quinby and Martin suggested the Dwarf milo plant had lost part of its height, apparently through mutation and had become Double Dwarf milo.

Karper (1932) recognized that a series of plant heights known as standard, dwarf and extra dwarf had occurred in each of the groups of Kafir, Milo, Feterita, Kaoliang and Broomcorn. The data obtained from milo populations indicated that a single factor was responsible for the height difference between standard and dwarf type and another factor was responsible for the difference between dwarf and extra

dwarf. He further stated that the reduction in plant height at each step was undoubtedly the result of natural recessive mutation. These two genes were designated as the first and second height genes (Dw_1 and Dw_2).^{1/}

Sieglinger (1932) crossed two dwarf broomcorn varieties, Western Dwarf and Whisk Dwarf, and found the F_1 plants were as tall as the standard type. The F_2 population segregated for height in a dihybrid ratio and the new plant height, double dwarf type, was discovered. These two alleles were apparently independent.

Karper (1932) discovered the third height factor (Dw_3) in Kafir varieties by observing the frequent occurrence of tall plants in homozygous standard-height populations. In his refined study, he found the tall plants were dominant to normal type and differed by a single gene. He concluded that this gene was unstable and the reversion to the dominant condition occurred at the rate of 1 in 1,200 gametes.

Laubscher (1945) studied an F_2 population segregating for both height and duration of growth and concluded that the inheritance of plant height in sorghum was complex.

Quinby and Karper (1954) reported the fourth height factor (Dw_4) after studying the segregation of F_2 and F_3 progenies of numerous crosses. They concluded that there were only four independently

^{1/} The gene symbols Dw_1 , Dw_2 , Dw_3 and Dw_4 were designated to the first, second, third and fourth height factors respectively, according to the priority of being identified by Quinby and Karper (1954) and Schertz and Stephens (1966).

Inherited genes with approximately equal effects plus a modifier complex controlling the elongation of internodes in sorghum. These genes have no visible manifestations other than shortening internodes in the recessive conditions, since leaf number and size and time of blooming were the same in strains of the same variety of different height. The recessiveness had about the same height reducing effect with each of the four genes. Tallness was partially dominant. They also mentioned that the variations in plant height of some genotypes were largely caused by environmental factors.

According to Quinby and Karper (1954), Ayyangar et al. (1938), reported a case where dwarfness was linked with early maturity, but in this case the segregation was for number of internodes, not for the gene that influenced elongation of internodes.

Quinby and Karper (1945) discovered three genes influencing the time of floral initiation and maturity date as well as the number of internodes. One of these genes was linked with the second height factor at a distance of 8 cross over units. They observed that three types of internode disposition occurred among the four phenotypes of maturity. The early strain had internodes that increased in length from the ground to the peduncle. The intermediate strain has a short internode near the top of the plant with longer internodes above and below it. The late and ultra late strains had two areas of constriction, one close to the ground level and the other close to the top of the plant.

Quinby (1964) stated that multiple alleles had been found at each of four heights and three maturity loci investigated. He also suggested that continuous variation in height, from 60 to 450 cm, and in duration of flowering, from 38 to 100 days, were the result of interaction of dominant and recessive alleles at these seven loci.

The height of sorghum plants is influenced by the number of internodes as well as by the length of internodes. Quinby and Karper (1954) classified those genes that influence time of floral initiation and the consequent number of internodes as maturity genes. Those genes that affect internode elongation were considered to be true height genes.

Hadley (1957) studied the height factors in sorghum and treated them as quantitative characters. Statistical analysis of F_1 , F_2 and F_3 populations of the cross **Double Dwarf White Sooner milo X Durra** was made. Significant genetic variation as well as environmental variation were found. Dominance was incomplete. At least four independent genes, with unequal effects appeared to be segregating in the material used in this study. He admitted his results were in close agreement with those obtained by Quinby and Karper (1945) through essentially Mendelian procedures.

Casady (1967) studied the segregating progenies of a cross between isogenic lines, which differed only in dominant and recessive alleles of the third height factor of three sorghum varieties, **Martin**, **Plainsman** and **Redlan** for three years. The results indicated the interaction of environment X varieties X height factors was statistically

significant for peduncle length and height to top node but not for head length and number of internodes. He concluded that the environment as well as varieties had a differential effect on the performance of plant height and peduncle length. In other words, the same height genotypes would differ in measurement caused by the influence of different environments and varieties. He also reported that Dw genes at least Dw₂ and Dw₃ are pleiotropic, because they also influenced peduncle length, leaf blade length and area.

Kambal and Webster (1966) pointed out that heterosis for plant height was manifested in three components: stem, peduncle and head length. The increase in stem length was due to increase in internodal length rather than increase in number of internodes. The comparison of 190 hybrids with their parents for two years indicated that the average of hybrids was about 12 cm. (4.5 in.) taller than the parental average. Quinby et al (1958) also noticed this similar manifestation.

Quinby and Karper (1954) stated that genes for peduncle and panicle length were independent of those controlling internode length. Short-stalk varieties frequently had peduncles as long as or longer than the part of stem below the base of the peduncle; thus the total height of the plant was not an accurate measurement. They also suggested the most precise measure of stem height would be the height to the top node. However, this measurement was difficult to do because the top node frequently was enclosed within three or four leaf sheaths. The height to the collar of the flag leaf was easily measured and reasonably

accurate. They observed that the leaf sheaths and blades of all except the very late maturing varieties were fully developed before any of the internodes started to elongate. Furthermore, Double Dwarf, Dwarf and Standard Sooner Milo which differ in height had leaves substantially the same size.

Conner and Karper (1917), and Brooks (1967) found that sheath length was relatively constant, and not influenced by internode elongation. Kambal and Webster (1966) also believed that the factors controlling number and length of internodes differed from those determining peduncle and head length.

Brooks (1967) compared several characters among isogenic lines of tall revertant Wheatland, homozygous dominant at the third height locus, and normal Wheatland, recessive at the third locus. He was able to show that there were only slight differences, if any, among these genotypes in flowering date, number of nodes and head and peduncle length. However, the tall allele caused an increase in internode length over the normal plant. The largest increase was at the first internode below the peduncle which contributed almost one-fourth of the total increase. The remaining three-fourths of the increase was due to lesser increases in the length of the remaining internodes. The third internode below the peduncle contributed the least increase in plant height while the fifth internode increased second most.

Freeman et al. (1962) observed similar effects of direct and reversed mutation. They concluded that all "tall revertants" mutated to

normal as well as "normal recovered" mutated to tall, giving the same effect as the original allele when measured for height to collar of flag leaf and days to flowering in 9 varieties studied.

There have been several reports of abnormal dwarf mutations. Ayyangar et al (1938) described a "tiny sorghum", an abnormal dwarf, which occurred in a field of sorghum brought from China and which bred true for 8 years. Then one head segregated and gave a simple 3:1 ratio; the "tiny" mutant was recessive. The height of this mutant was about 18 cm. while the normal plant was 150 cm. tall. The number of internodes was not affected, only the internodal length was reduced to a certain extent.

Quinby and Karper (1942) discovered a "Midget", an extreme dwarf mutant, rarely exceeding 30 cm. in height after treating sorghum seeds with X-rays. The abnormality could be recognized in the seedling stage. The Midget gave smaller seeds and germinated poorly. The line had to be maintained in the heterozygous stage and segregated in a monohybrid ratio.

Haensel et al (1963) mentioned that several types of dwarf mutants occurred following gamma irradiation of colchicine-reactive types of sorghum plants. However, further studies of the nature of these mutants had not been conducted. They also found "Crinkle Leaf" mutant inherited as a simple recessive in this study.

Sieglinger (1933) noticed a dwarf mutant in the F_5 progeny of a cross between Red Kafir and Reed Kafir. The dwarf mutant, 50 cm.

tall, was recessive and differed from the normal plant, 130 cm. tall, by one factor. The progeny segregated only for internode length. He suggested that this dwarf mutant had lost a single height factor.

CHAPTER III

MATERIALS AND METHODS

The dwarf mutant to be studied was isolated by Sieglinger at the Woodward Experiment Station and maintained as a pure line since 1933. The other four genetically known parents, Red Kafir, Redlan, R OK Y8 and SA 3002, were obtained from the seed stocks of the Department of Agronomy, Oklahoma State University. The parents along with height genotypes, measurements of height to the collar of the flag leaf and first blooming dates were given as follows:

TABLE I
GENETIC IDENTIFICATION OF PARENTAL VARIETIES,
HEIGHT AND DAYS TO BLOOM

Parent	Genotype	Height to Flag leaf ^c in cm.		Days to 1st Bloom ^c
		Means	S ^d	
Red Kafir	Dw ₁ Dw ₂ dw ₃ dw ₄ ^a	91.52	8.1	65
Redlan	dw ₁ Dw ₂ dw ₃ dw ₄ ^a	74.68	6.85	58
R OK Y8	dw ₁ Dw ₂ dw ₃ dw ₄ ^b	62.9	5.2	58
SA 3002	dw ₁ dw ₂ dw ₃ dw ₄ ^b	37.74	3.5	55

^a Given by Quinby and Karper (1954)

^b Not identified at that time

^c Data obtained from Agronomy Research Station, Perkins

^d Standard deviations

All possible crosses among the Dwarf Mutant and the four parents including reciprocal crosses of the Dwarf Mutant with the other four parents were made by hand emasculation in 1962 and again in 1963. Thus, there were 14 crosses. F₁ plants of each cross were grown in the field at the Agronomy Research Station, Perkins, in the summer of 1962 and again in 1963. Heads were bagged before blooming to insure self-fertilization, and they were harvested individually.

In the summer of 1967, F₂ populations of each cross and each parent were sown in 2-row plots, 6 meters long, 1 meter apart, and replicated 3 times at the Agronomy Research Station, Perkins. The seedlings were thinned to a spacing of approximately 25 cm. in order to obtain the maximum growth. There were approximately 32 plants per row. Again each head was bagged before blooming. Individual plants in each row were measured and recorded in centimeters for height to the collar of the flag leaf, overall height, height to the base of head and height to the top node before harvesting. By the appropriate subtraction of the above measurement, the following characters were obtained: - Height to the collar of the flag leaf, height to the top node, panicle or head length, peduncle length, and sheath length. Other interesting characters associated with the Dwarf Mutant crosses such as "Crinkle Leaf" and "Sword Leaf" were recorded. Each head was harvested and threshed separately.

The measurements of those five characters of the F₂ populations in each cross and of the parents were grouped into 5 cm. intervals.

The histograms of measurements for parents and F_2 plants were constructed to obtain preliminary knowledge about the nature of inheritance. Some adjustments in classification were necessary in the individual plant groupings for these two height characters based on the peduncle and sheath length.

The form of the histogram of the F_2 population as well as the knowledge of parental inheritance were used to estimate number of height genes segregating in each individual cross. Consequently the number of F_2 rows selected to grow F_3 families was based on the expectation of the number of genes segregating. For the cross that was expected to segregate for one pair of genes, Red Kafir X Dwarf Mutant, only one F_2 row of 32 plants was selected. For those crosses that were supposed to have two different pairs of genes, four rows of F_2 were selected. These crosses were Redlan X Dwarf Mutant, R OK Y8 Dwarf Mutant and Red Kafir X SA 3002. Finally for the cross SA 3002 X Dwarf Mutant, which was expected to have three pairs of genes segregating, six rows of F_2 were chosen to grow F_3 families.

Selection of F_2 plants for F_3 progenies was not on a completely random basis since whole rows of F_2 plants were taken on the basis of those with the most total plants and those with the most mutant type plants in them.

In the summer of 1968, the F_3 families selected were grown in the field at the Agronomy Research Station, Perkins. The experiment was divided into two plots according to the land available. Seed from

each F_2 plant was sown in one row 6 meters long and 1 meter apart. Each range of F_3 families consisted of 32 rows. Thus, each F_3 range represented one of the F_2 rows in the previous year and similarly one F_1 plant. Two rows of each parent were planted along with the F_3 families in that range. Six ranges of the cross SA 3002 X Dwarf Mutant, two ranges each of the crosses Redlan X Dwarf Mutant, R OK Y8 X Dwarf Mutant and Red Kafir X SA 3002, and one range of Red Kafir X Dwarf Mutant were grown at one location at the Agronomy Research Station. The remaining two ranges each of the crosses Redlan X Dwarf Mutant, R OK Y8 X Dwarf Mutant, and Red Kafir X SA 3002 were planted at a separate location. The seedlings were thinned, and individual plant measurements were taken in the same manner as in the F_2 generation.

The F_2 data as well as F_3 data were used to study the nature of inheritance of the Dwarf Mutant.

The means and standard deviations of parental measurements for certain characters were obtained by the method given by Steele and Torrie (1960).

CHAPTER IV

RESULTS AND DISCUSSION

The Measurement of Parents

The measurements of certain parental characters are given in Table II. In 1967, all parental rows were grown in the lower portion of the Perkins Agronomy Research Station, while in 1968 they were planted in two locations, one on the lower portion as in 1967, and the other on the upper portion of the same farm. The effects of year and location on plant characters varied with varieties. In the Red Kafir variety, these effects were most evident and caused variation in every character. Height to the collar of the flag leaf and the top node was greatest in the lower field in 1968, was less in the lower field in 1967, and was shortest for those plants grown on the hill in 1968. For the length of head, peduncle and sheath, the longest ones seemed to be those grown in 1967, and the shortest ones were those grown on the hill in 1968 while those grown in the lower field in 1968 were intermediate.

The variations decreased from Red Kafir to Redlan, R OK Y8 and SA 3002, respectively. The environmental effects caused the least change in the Dwarf Mutant, since all characters were similar in both years and locations.

TABLE II
THE RANGES, MEANS AND STANDARD DEVIATIONS OF THE MEASUREMENTS
IN CENTIMETERS OF THE PARENTAL CHARACTERISTICS FROM
1967 AND 1968

	1967			1968					
	Lower field			Lower field			Upper field		
	Ranges	Means	S ^c	Ranges	Means	S ^c	Ranges	Means	S ^c
<u>Dwarf Mutant (ii Dw₁Dw₁Dw₂Dw₂)^a</u>									
Height to:									
collar of flag leaf	36-60	48.4	4.35	36-60	46.6	5.05	41-60	48.8	4.45
top node	16-35	25.7	3.35	16-35	25.9	4.45	16-35	27.5	3.85
Head length	11-25	18.1	2.35	11-25	16.7	3.05	11-25	16.7	2.75
Peduncle length	6-20	12.7	2.5	6-20	11.6	2.85	6-25	11.4	2.25
Sheath length	11-30	22.4	2.4	16-30	21.9	3.35	16-25	21.9	2.42
<u>Red Kafir (II Dw₁Dw₁Dw₂Dw₂)^b</u>									
Height to:									
collar of flag leaf	81-130	91.5	8.1	101-130	117.4	6.4	71-105	85.8	7.9
top node	61-90	75.4	6.75	71-100	83.1	5.6	41-70	55.9	5.8
Head length	21-40	30.5	3.5	16-35	26.2	3.6	16-30	21.8	3.8
Peduncle length	31-55	47.6	3.8	26-55	38.7	7.3	16-45	27.4	6.05
Sheath length	31-45	37.2	2.15	21-45	32.1	3.15	21-35	31.8	2.85
<u>Redlan (II dw₁dw₁Dw₂Dw₂)^b</u>									
Height to:									
collar of flag leaf	61-90	74.7	6.85	56-80	68.7	5.1	56-75	64.6	4.8
top node	26-55	38.0	5.95	31-45	38.1	3.4	26-40	33.6	3.65
Head length	11-30	21.2	3.0	11-25	17.1	2.15	11-23	17.0	2.55
Peduncle length	26-55	42.6	4.95	26-45	37.5	4.6	21-40	35.4	3.55
Sheath length	26-45	35.1	3.55	26-35	30.2	2.55	26-35	29.9	2.45

TABLE II (CONTINUED)

	1967			1968					
	Lower field			Lower field			Upper field		
	Ranges	Means	S ^c	Ranges	Means	S ^c	Ranges	Means	S ^c
	<u>R OK Y8 (II dw₁dw₁Dw₂Dw₂)^b</u>								
Height to:									
collar of flag leaf	46-80	62.9	5.2	41-60	56.8	3.1	51-65	58.8	5.15
top node	11-30	21.5	4.95	11-30	19.7	4.4	11-25	21.6	3.85
Head length	21-50	39.1	4.15	26-40	31.9	3.65	26-35	31.6	3.8
Peduncle length	41-70	55.6	4.15	46-65	53.4	3.25	31-45	35.1	4.1
Sheath length	31-50	40.3	3.1	31-40	35.1	3.3	31-45	38.0	2.9
	<u>SA 3002 (II dw₁dw₁dw₁dw₁)^b</u>								
Height to:									
collar of flag leaf	26-50	37.7	3.55	26-40	34.6	2.65	31-40	36.0	2.55
top node	1-15	8.9	2.4	6-10	9.6	2.55	6-10	9.0	2.4
Head length	11-20	16.1	2.05	11-20	15.1	2.8	11-20	16.0	2.55
Peduncle length	21-50	31.8	5.75	21-35	26.6	2.9	16-30	24.0	3.15
Sheath length	21-40	28.2	2.15	16-30	24.9	2.45	21-30	25.0	2.55

^a The proposed genotype

^b The known genotype

^c The means and standard deviations S, were obtained by the method given by Steele and Torrie (1960)

Beside the short stature, Sieglinger (1933) described the Dwarf Mutant as having a short and thicker head. However in this study, it was further observed that the Dwarf Mutant also possessed thick, broad and characteristically crinkled leaves, definitely differing from the normal parents. The panicle of this Dwarf Mutant is rarely exerted from its flag leaf sheath. These normal characters disappeared in the heterozygous condition.

For the Redlan variety the measurements of the characters were greater, except for the top node, in 1967 than those in the 1968 lower field, which in turn was greater than the measurements of the characters in the 1968 upper field. Head length differed largely from year to year while the peduncle length differed from location to location. In SA 3002, the least variable variety next to Dwarf Mutant, the effects of year and location could be detected only in the height to the collar of the flag leaf, peduncle and sheath length.

Since all of the parental varieties were considered to be homozygous, environmental effects were largely responsible for the variation as well as the fluctuation of individual plant characters seemed to be solely dependent on the make up of varieties. This was reported by Quinby and Karper (1954), Hadley (1967), Casady (1967) and Brooks (1968).

It was possible to generalize that among these parents, the varieties which were relatively taller such as Red Kafir, Redlan and R OK-Y8 tended to have more variation due to environmental effects. The

shorter varieties, SA 3002 and Dwarf Mutant, seemed to be more stable.

Among the individual plant characters, the larger measurements were subject to more variation. Owing to variety environment interaction, sheath length was least variable, and then the variation progressively increased for head length, height to top node, peduncle length and height to the collar of the flag leaf. Quinby and Karper (1954) have stated that the inheritance of each character studied except the height to the collar of the flag leaf was apparently independent of each other.

The Inheritance of Plant Height in the Dwarf Mutant

Cross between Red Kafir and Dwarf Mutant.

Histograms of the measurements of the F_2 segregating population along with both parents were constructed. Figure 1 shows height to the collar of the flag leaf and Figure 2 shows the height to top node. The distributions indicated the typical bimodal curve of the F_2 population for each measurement. One peak in the curve of the F_2 population coincided with the short parent, the Dwarf Mutant, and the other peak coincided with the tall parent, Red Kafir. The division between the peaks was at 60 to 65 cm. for the height to the collar of the flag leaf and at 35 to 40 cm. for the height to the top node. The number of plants in each group are given in Table III. It should be noted that the counts for both plant height characters were numerically identical. The calculation to test the hypothesis of a 3:1 ratio in F_2 for the two characters gave a Chi-square value of 0.84 with $P^a = .35$ from the total of 381 plants.

In the F_3 population, the number of plants belonging to the tall and short classes were, again identical for both height characters. The Chi-square test of a 3:1 ratio gave value of 0.83 and $P = .35$ from the total of 520 F_3 plants.

^a Chi-square and P, Probability values, were obtained by the method given by Srb et al (1965).

TABLE III

CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO HEIGHT CLASSES WITH CHI-SQUARE AND PROBABILITY VALUES FOR THE CROSS OF RED KAFIR AND THE DWARF MUTANT

Height to	Gen.	Gene Seg.	No. of plants in classes		Total plants	Expt. ratio	X ²	P values
			Tall I-	Short ii				
<u>Collar of Flag leaf</u>								
Red Kafir 81 to 130 cm ^a $\bar{X} = 91.2 \pm 8.1$	F ₂	ii	O ^b 278 E ^c 285.75	103 95.25	381	3:1	0.84	.35
Dwarf Mutant 36 to 60 cm ^a $\bar{X} = 48.4 \pm 4.35$	F ₃	ii	O ^b 397 E ^c 390	123 130	520	3:1	0.83	.35
<u>Top node</u>								
Red Kafir 61 to 90 cm ^a $\bar{X} = 75.4 \pm 6.75$	F ₂	ii	O ^b 278 E ^c 285.75	103 95.25	381	3:1	0.84	.35
Dwarf Mutant 16 to 35 cm ^a $\bar{X} = 25.7 \pm 3.35$	F ₃	ii	O ^b 397 E ^c 390	123 130	520	3:1	0.83	.35

^a Ranges, means and standard deviations respectively

^b Observed values

^c Expected values

This indicated a good fit to the 3:1 ratio in both F_2 and F_3 generations.

Sieglinger (1933) found monogenic segregation in the cross between Red Kafir and the Dwarf Mutant similar to this and the Dwarf Mutant was in recessive condition. This study definitely confirmed his report. He also suggested that the Dwarf Mutant arose from Red Kafir by mutation.

Quinby and Karper (1954) gave the genetic height symbol, $Dw_1 Dw_2 dw_3 dw_4$ for Red Kafir. The homozygous recessive for either Dw_1 , Dw_2 or both in grain sorghum plants were described by Karper (1932), Sieglinger (1932) and Quinby and Karper (1954) but none of them gave a morphological description of the effect of these genes similar to the appearance of the Dwarf Mutant. Accordingly, it seemed unreasonable to suspect the occurrence of the Dwarf Mutant was due to the abnormality of these two genes. Moreover, the third and fourth height genes were likely not to be responsible for this expression, since Red Kafir was already homozygous recessive for these two genes, i. e. dw_3, dw_4 . Besides these facts Karper (1932) indicated dw_3 often mutated to tall dominant Dw_3 . Also he reported that Dw_4 existed only in broomcorn, and had never been reported being found in grain sorghum varieties. From the foregoing discussion it was speculated that the new height factor, not resembling any of those four known genes, had occurred undoubtedly by mutation and was responsible for the expression of the Dwarf Mutant. The symbol "I" for dominance and normal appearance along with its allele "i" for recessiveness and dwarfness

was proposed for that phenotype. Thus, by this assumption, the genotypes for Red Kafir and Dwarf Mutant should be written as $I Dw_1 Dw_2 dw_3 dw_4$ and $i Dw_1 Dw_2 dw_3 dw_4$, respectively.

Since all four known parents as well as the Dwarf Mutant, for the reasons given above, were homozygous recessive at the third and fourth height genes in common, these two genes will be omitted in later discussion.

Cross between Redlan and Dwarf Mutant

The data from the F_2 and F_3 populations of this cross are given in Table IV. Unlike the cross between Red Kafir and Dwarf Mutant, the number of F_2 and F_3 plants counted for plant height to the collar of the flag leaf did not resemble the counts for height to the top node, so the results of each height were reported and discussed separately.

The Height to the Collar of the Flag leaf: - The histogram of the F_2 population measured for this height indicated transgressive segregation and a continuous distribution. Some of the F_2 plants were shorter than 36 cm. which was the lower range of the Dwarf Mutant. In contrast, a number of plants also exceeded 90 cm. in height, the upper range of the tall parent, Redlan. The genotype of Redlan as given by Quinby and Karper (1954) was $dw_1 dw_1 Dw_2 Dw_2$, and differed from Red Kafir at the first height factor. By the previous nomenclature, the genotype of Redlan should be $II dw_1 dw_1 Dw_2 Dw_2$ compared to $ii Dw_1 Dw_1 Dw_2 Dw_2$ for the Dwarf Mutant. Digenic segregation could

be expected from this cross.

Three height classes for the F_2 plants were arbitrarily set up based on two criteria. The first one was the division point observed from the histogram of the F_2 population and the other was the range of the parents for height to the collar of the flag leaf. (See Figure 3)

The F_2 plants that belonged to the short class were those that had the height to the collar of the flag leaf less than the lower range of the short parent, the Dwarf Mutant, i. e., less than 36 cm. The genotype of the double homozygous recessive, $ii\ dw_1dw_1(Dw_2Dw_2)$ was assigned to this class.

The height to the flag leaf of the Dwarf Mutant, $ii\ Dw_1Dw_1(Dw_2Dw_2)$ ranged from 36 to 60 cm. while in Redlan, $II\ dw_1dw_1(Dw_2Dw_2)$ it ranged from 61 to 90 cm. In reality, it was quite impractical to separate one from another, so they were grouped together in the intermediate height class. This class had the height interval from 36 to 80 cm. The genotype of one dominant and one homozygous recessive gene, i. e., $I - dw_1dw_1$ or $ii\ Dw_1 -$ were proposed for those plants falling in this class.

The tall class included the plants having height to the collar of the flag leaf exceeding 80 cm. It was believed that the plants falling in this class had two dominant genes, $I - Dw_1 - (Dw_2Dw_2)$ and a range for plant height quite similar to Red Kafir.

However, some adjustments in classification of F_2 plants were necessary in the individual plant groupings for those that fell at the

border of classes. The justifications for each F_2 plant were based on its peduncle and sheath length, and in some cases on its F_3 progeny performance.

The use of F_3 progenies to verify F_2 genotypes was conducted as follows. Since all plants within an F_3 row came from one F_2 plant, the performance of each F_3 row would indicate the condition of its F_2 parent. If all F_3 plants within a row were uniform for one class of height, the F_2 plant was considered homozygous for that class. The tall F_2 plants would be designated double heterozygotes if their F_3 progenies segregated for three height classes. In the case of the tall F_2 plants giving tall and intermediate height classes in F_3 rows, it was believed to be dominant homozygous for one gene and segregating for another. The intermediate F_2 plant should have F_3 plants in both intermediate and short height classes if in the heterozygous stage and all intermediate F_3 plants if in the homozygous condition. However, the intermediate F_2 plants were assigned double heterozygous genotypes if they segregated for three height classes in the F_3 progenies. This F_3 verification was applied to determine F_2 genotypes throughout this study.

The calculation to fit the expected digenic ratio of 9 tall : 6 intermediate : 1 short gave a Chi-square value of 2.75 with $P = .25$ from the total of 377 F_2 plants. (Table IV)

Since the F_2 plants were not randomly selected to grow the F_3 families as stated in Chapter III (Material and Methods), it was

TABLE IV

CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO HEIGHT CLASSES WITH CHI-SQUARE AND PROBABILITY VALUES FOR THE CROSS OF REDLAN AND DWARF MUTANT

Height to	Gen.	Gene Seg.	No. of plants in classes			Total plants	Expt. ratio	X ²	P. values	Lines		
			Tall I-Dw ₁ -	Intermed. I-dw ₁ dw ₁ iiDw ₁ -	Short iidw ₁ dw ₁							
<u>Collar of Flag leaf</u>			<u>>81 cm</u>	<u>36 to 80 cm</u>	<u><36 cm</u>							
Redlan 61 to 90 cm ^a X̄ = 74.7 ± 6.85	F ₂	IiDw ₁ dw ₁	O ^b	198	157	22	377	9:6:1	2.755	.25	1	
			E ^c	212	141.4	23.6						
Dw. Mut. 36 to 60 cm ^a X̄ = 48.4 ± 4.35	F ₃	IiDw ₁ Dw ₁	O ^b	659	231		890	3:1	.433	.50	3	
			E ^c	667.5	222.5							
		Iidw ₁ dw ₁	O ^b	-	478	167		645	3:1	.273	.60	5
			E ^c	-	483.75	161.25						
		IiDw ₁ dw ₁	O ^b	446	323	52	821	9:6:1	1.685	.45	7	
			E ^c	464.1	309.4	51.5						
<u>Top node</u>			<u>≥46 cm</u>	<u>16 to 45 cm</u>	<u><16cm</u>							
Redlan 26 to 55 cm ^a X̄ = 38 ± 5.95	F ₂	IiDw ₁ dw ₁	O ^b	203	152	22	377	9:6:1	1.289	.55	9	
			E ^c	212	141.4	23.6						
Dw. Mut. 16 to 35 cm ^a X̄ = 25.7 ± 3.35	F ₃	IiDw ₁ Dw ₁	O ^b	661	229		890	3:1	.273	.60	11	
			E ^c	667.5	222.5							
		I-dw ₁ dw ₁	O ^b	-	483	162		645	3:1	.0047	.90	13
			E ^c	-	483.5	161.25						
		IiDw ₁ dw ₁	O ^b	451	318	52	821	9:6:1	.896	.65	15	
			E ^c	464.1	309.4	51.5						

^a Ranges, means and standard deviations respectively ^b Observed values ^c Expected values

advisable not to combine all F_3 data together. The F_2 plants which were represented by an individual F_3 row, were again divided into three groups according to the segregation of plant heights within the F_3 row. The F_3 rows that had all uniform plants within the row were used to verify their F_2 parents' genotypes, but were not counted in the F_3 data.

The first F_2 groups were those having plants within the F_3 row segregating for two height classes; the tall and intermediate height. The genotypes of plants in this group were believed to be either I - Dw_1Dw_1 (Dw_2Dw_2) or II $Dw_1 - (Dw_2Dw_2)$ since they could not be distinguished from one another. The F_2 genotype I - Dw_1Dw_1 would segregate for I Dw_1Dw_1 and ii Dw_1Dw_1 in the F_3 generation in a 3:1 ratio as well as genotype II $Dw_1 -$ for II $Dw_1 -$ and II dw_1dw_1 . The F_3 plants within each row were tabulated according to their height. The Chi-square tests for F_3 plants in this group are given in line 3 and 4 in Table IV.

The second F_2 group consisted of those plants of intermediate height which segregated for two height classes in the F_3 generation, intermediate and short. The genotypes of this group were either I - dw_1dw_1 (Dw_2Dw_2) or ii $Dw_1 - (Dw_2Dw_2)$. Again F_2 genotype I - dw_1dw_1 would segregate for I - dw_1dw_1 and ii dw_1dw_1 in a 3:1 ratio as well as ii $Dw_1 -$ for ii $Dw_1 -$ and ii dw_1dw_1 . The F_3 plants of short and intermediate height were recorded in their respective groups. The number of F_3 plants and the Chi-square tests to fit a 3:1 ratio are given in line 5 and 6 in Table IV, respectively.

The third F_2 group consisted of those tall plants which segregate into three height classes; tall, intermediate and short in the F_3 generation. The genotype of this group was given as $I i Dw_1 dw_1 (Dw_2 Dw_2)$ and believed to segregate for $I - Dw_1 - : I - dw_1 dw_1$ and $ii Dw_1 - : ii dw_1 dw_1$ in a ratio of 9:6:1. The observed number of F_3 plants belonging to each height class is shown in Table VI, line 7 and line 8 shows the expected number, Chi-square and probability values of the total 821 F_3 plants in this group.

It was observed that the F_2 plants that belonged to the short class always gave all uniform, and short F_3 plants. The proposed genotype, $ii dw_1 dw_1 (Dw_2 Dw_2)$ for the plants in this class seemed to be acceptable.

Height to Top node: - The approach and methods of analysis of F_2 and F_3 data for the height to the top node were similar to those used for the height to the collar of the flag leaf. The height to the top node was shorter than the height to the collar of the flag leaf, as shown in the histogram of the F_2 population. (See Figure 4) These two height measurements are attempts to determine the same characteristic in the parents of the segregation populations, but slightly different frequencies in the classes were obtained. The tall class of the expected genotype $I - Dw_1 - (Dw_2 Dw_2)$ consisted of those plants which had the height to the top node exceeding 45 cm. The intermediate height class consisted of those plants which had one dominant gene, either $I - dw_1 dw_1 (Dw_2 Dw_2)$ or $ii Dw_1 (Dw_2 Dw_2)$ and had heights ranging from 16 to

45 cm. The short class of the double recessive genotype, $ii\ dw_1dw_1$ (Dw_2Dw_2), measured less than 16 cm. to the top node. After some adjustments and verification by the performance of F_3 progenies of F_2 plants as mentioned in a previous section, the F_2 data were fit to a ratio of 9:6:1. The data and the Chi-square test revealed a good fit as shown in line 9 and 10 of Table IV.

Again, three groups of F_2 plants represented by F_3 rows were established. The number of F_3 tall and intermediate plants segregating from the tall F_2 plants are given in line 11 along with Chi-square test in line 12 of Table IV. The records of F_3 intermediate and short plants derived from F_2 intermediate populations and the Chi-square test are in line 13 and 14 of Table IV. Similarly the number of tall, intermediate and short F_3 plants arising from the tall F_2 plants and the Chi-square test for 9:6:1 ratio are shown in line 15 and 16 of Table IV, respectively.

The short F_2 plants of the genotype $ii\ dw_1dw_1$ (Dw_2Dw_2) produced all uniform and short plants in the F_3 generation, measuring less than 16 cm. to the height of top node.

It was noted that the height to the top node gave a more accurate estimation of F_2 and F_3 segregating populations than did the height to the collar of the flag leaf as judged by Chi-square and P values in Table IV. Quinby and Karper (1954) indicated this fact in their study of plant height inheritance in sorghum. However, they concluded that the measurement of height to the collar of the flag leaf could be done more easily and gave reasonable precision.

Cross between R OK Y8 and Dwarf Mutant

The genotype of R OK Y8 is assumed to be like Redlan having only one dominant height factor, $II\ dw_1dw_1Dw_2Dw_2$. Thus the cross R OK Y8 X Dwarf Mutant was expected to segregate for two genes, $IiDw_1dw_1$. The data from F_2 and F_3 populations were obtained by the same procedure as in the cross Redlan X Dwarf Mutant. The means as well as the ranges of both height to the flag leaf and to the top node in R OK Y8 seemed to be shorter than those for Redlan. The revisions were made for the height classes in both characters. These differences are reflected in the histograms of the F_2 and parental populations shown in Figures 5 and 6.

Height to Collar of the Flag leaf: The height of this character ranged from 46 to 80 cm. in R OK Y8 and from 36 to 60 cm. in Dwarf Mutant. The three classes of plant height were established as follows: The tall class exhibited plant height greater than 75 cm; and the short class measured less than 36 cm. The ratio 9 tall : 6 intermediate : 1 short plants was expected for the F_2 population. The number of F_2 plants, after adjustment and verification, are given in line 1 and the Chi-square and P values in line 2 of Table V.

The F_3 plants within each row were used to identify each F_2 plant and also were counted into three separate groups according to the pattern of segregation as in the previous cross. The F_3 data of each group along with their respective Chi-square tests and P values

TABLE V
CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO HEIGHT CLASSES WITH CHI-SQUARE
AND PROBABILITY VALUES FOR THE CROSS OF R. OK Y8 AND THE DWARF MUTANT

Height to	Gen.	Gene Seg.	No. of plants in classes			Total plants	Expt. ratio	X ²	P. values	Line
			Tall IiDw ₁ -	Intermed. I-dw ₁ dw ₁ iiDw ₁ -	Short iidw ₁ dw ₁					
<u>Collar of Flat leaf</u>			<u>≥ 76 cm</u>	<u>36 to 75 cm</u>	<u>< 36 cm</u>					
R Ok Y8 46 to 80 cm ^a $\bar{X} = 62.9 \pm 5.2$	F ₂	IiDw ₁ dw ₁	O ^b 219	172	19	410	9:6:1	4.49	.10	1
			E ^c 230.63	154.75	25.62					2
Dw. Mut. 36 to 60 cm ^a $\bar{X} = 48.4 \pm 4.35$	F ₃	IiDw ₁ Dw ₁	O ^b 603	234		837	3:1	3.81	.05	3
			E ^c 627.75	209.25						4
		Iidw ₁ dw ₁	O ^b -	335	95	430	3:1	1.94	.15	5
			E ^c -	322.5	107.5					6
		IiDw ₁ dw ₁	O ^b 544	406	67	1017	9:6:1	3.15	.20	7
E ^c 572.06	381.38	63.56	8							
<u>Top node</u>			<u>≥ 41 cm</u>	<u>16 to 40 cm</u>	<u>< 16 cm</u>					
R OK Y8 11 to 30 cm ^a $\bar{X} = 21.5 \pm 4.95$	F ₂	IiDw ₁ dw ₁	O ^b 231	156	23	410	9:6:1	.30	.85	9
			E ^c 230.63	154.75	25.62					10
Dw. Mut. 16 to 35 cm ^a $\bar{X} = 25.7 \pm 3.35$	F ₃	IiDw ₁ Dw ₁	O ^b 616	221		837	3:1	.88	.35	11
			E ^c 627.75	209.25						12
		Iidw ₁ dw ₁	O ^b -	333	97	430	3:1	1.38	.25	13
			E ^c -	322.5	107.5					14
		IiDw ₁ dw ₁	O ^b 551	403	63	1017	9:6:1	1.89	.35	15
E ^c 572.06	381.38	63.56	16							

^a Ranges, means and standard deviations respectively

^b Observed values

^c Expected values

are given in lines 3 to 8 of Table V.

Height to Top node: The height to the top node of R OK Y8 ranged from 11 to 30 cm. and of Dwarf Mutant from 16 to 35 cm. The tall height class for the F_2 and F_3 progenies of this cross were taller than 40 cm., the intermediate height class ranged from 16 to 40 cm. and the short class ranged less than 16 cm. The number of F_2 plants belonging to each of the three classes is given in line 9 and the Chi-square tests with P values in line 10 of Table V.

The number of F_3 plants along with their Chi-square tests and P values of the three segregating groups are given in lines 11 to 16 of Table V.

Cross between SA 3002 X Dwarf Mutant

The SA 3002 variety was known as "4-dwarf" having all four genes in the recessive condition. Therefore the genotype $l_1d_{w_1}d_{w_2}$ was assigned. The height to the collar of the flag leaf varied from 26 to 50 cm. with a mean of 37.7 cm., and the height to the top node ranged from 1 to 15 cm. with a mean of 8.9 cm. Three gene segregation was expected from this cross. The height to the collar of the flag leaf of the F_2 populations varied from 21 to 135 cm. and the height to the top node from 6 to 95 cm. This covered the range of height of one, two and three dominant genes, i. e., the well understood Dw_1 and Dw_2 , and the proposed I locus.

The attempt to group the F_2 plants into three classes based on the height to the collar of the flag leaf as in the previous crosses was not successful. The F_2 plants seemed to vary greatly for this height character. (See Figure 32. B) The number of F_2 plants from an arbitrary classification did not fit the expected ratio even after some adjustments were made. (See Figure 7)

Consequently, only two height classes could be established based on the height to the top node. (See Figure 8) The tall class exceeded 45 cm, which was supposed to be the height of Red Kafir and the phenotype of $I-Dw_1-Dw_2$ was given to it. The intermediate and short class had height less than 46 cm. It included phenotypes $I-Dw_1-dw_2dw_2$, $I-dw_1dw_1Dw_2-$, $iiDw_1-Dw_2-$, $iiDw_1-dw_2dw_2$, $iidw_1dw_1Dw_2-$, $I-dw_1dw_1dw_2dw_2$ and $iidw_1dw_1dw_2dw_2$. The F_2 plants from this cross were expected in a ratio 27:37. The Chi-square test gave an acceptable fit with a P value of .3 from a total of 390 plants as shown in Table VI, lines 1 and 2.

Only the F_3 plants within the rows segregating for plant height were counted. Again, the height to the collar of the flag leaf did not give results to support the three-gene expectation. The data of the height to the top node of the F_3 plants were again grouped into two classes, the tall and the intermediate and short classes as in the F_2 generation. From the total of 2135 F_3 plants, the Chi-square test to fit expected ratio of 27:37 gave an acceptable result with $P = .25$ as shown in Table VI, lines 3 and 4.

TABLE VI
 CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO HEIGHT CLASSES WITH CHI-SQUARE
 AND PROBABILITY VALUES FOR THE CROSS OF SA 3002 AND THE DWARF MUTANT

Height to Top node	Gen.	Gene Seg.	No. of plants in classes		Total plants	Expt. ratio	X ²	P. values
			Tall I-Dw ₁ -Dw ₂ -	Inter and Short. (the rest)				
			≥ 46 cm	< 46 cm				
SA 3002 1 to 15 cm ^a $\bar{X} = 8.9 \pm 2.4$	F ₂	IiDw ₁ dw ₁ Dw ₂ dw ₂	O ^b 154 E ^c 164.54	236 225.46	390	27:37	1.12	.30
Dw. Mut. 16 to 35 cm ^a $\bar{X} = 25.7 \pm 3.35$	F ₃	IiDw ₁ dw ₁ Dw ₂ dw ₂	O ^b 930 E ^c 900.7	1205 1234.	2135	27:37	1.65	.25

^a Ranges, means and standard deviation respectively

^b Observed values

^c Expected values

Quinby and Karper (1954) stated that there was no indication in literature about cytoplasmic inheritance controlling plant height in grain sorghum. In this study, the histogram of the F_2 population of the reciprocal between Red Kafir and Dwarf Mutant segregating for height to the collar of the flag leaf and to the top node were constructed. (See Figures 9 and 10) It was found that the bimodal distribution of both crosses were very similar for these two height characters.

To summarize the findings of plant height inheritance in the Dwarf Mutant, the knowledge obtained from the study of F_2 and F_3 segregating populations of the cross between Red Kafir and Dwarf Mutant indicated clearly that the new height factor seemed to exist in the Dwarf Mutant as Sieglinger (1933) reported. This factor drastically reduced the height of the normal plant in the homozygous recessive condition. The expectation of single gene action was definitely proved in the cross Red Kafir X Dwarf Mutant. However, in the crosses involving two and three gene differences, i. e., Dwarf Mutant crossed with Redlan, R OK Y8, and SA 3002, variation seemed to play a big role. The causes of variation have been discussed by several workers. Quinby and Karper (1954) concluded that a modifier complex, incomplete dominance, and environmental effects were responsible for the sources of variation. Hadley (1957) suggested that a number of minor genes and unequal effects of the four major height genes contributed to the variation in plant height in addition to those mentioned by

Quinby and Karper. Casady (1967) noticed that the interaction between environment, height genes and varieties was statistically significant for height to the top node. Considering the influence of variation, the difficulty of classifying plants into individual genotypes can be understood, and the need for combining classes for analysis justified. However, the results obtained from this study indicated that the hypothesis for the inheritance of the Dwarf Mutant seemed to be acceptable.

The depression of height by the mutant gene seemed to depend on the number of the normal height genes present. The genotypes that possessed one dominant height gene differed in height from those with two dominant height genes in combination with the mutant gene. This was clearly shown in the comparison of two genotypes $iiDw_1Dw_1Dw_2Dw_2$ and $iidw_1dw_1Dw_2Dw_2$. The first genotype would have height to the top node the same as the Dwarf Mutant, i. e., less than 36 cm., while the second genotype would be similar to SA 3002, i. e., less than 16 cm. In other words the normal height genes could express their effects to only a limited degree.

By some unknown method the factor in the Dwarf Mutant prevented them from reaching the normal goal. Since the term "Repressor" has been given for the other phenomena in modern Genetics, the term "Height Inhibitor" was proposed for the expression of this gene in the Dwarf Mutant.

Other Characters Associated with the Dwarf Mutant

An attempt was made to associate other characters with the dwarf mutant gene. The segregation of peduncle and sheath length and "Crinkle Leaf" were observed in F_2 and F_3 generations in every cross involving Dwarf Mutant. In addition a special form of leaf, "Sword leaf" was noticed only in F_2 and F_3 populations of the cross between Redlan and Dwarf Mutant. These four characters will be discussed separately.

Peduncle Length

The measurement of peduncle length were grouped into 5 cm. class intervals and the histograms of the F_2 populations of every cross involving the mutant were constructed along with their appropriate parents to obtain preliminary knowledge of segregation. (See Figures 11, 12, 13 and 14) It was quite evident that every cross gave the typical bimodal distribution with a definite breaking point. The F_2 plants were then dividing into two classes according to the length of their peduncle. The long peduncle class was made up of those plants having peduncle lengths greater than 25 cm. while the short class was made up of those plants with peduncle length of less than 26 cm. This criteria was applied to the F_2 plants of Dwarf Mutant with Red Kafir, Redlan and R OK Y8, because the histograms of parental peduncle length were similar to those of the F_2 population.

For the cross of Dwarf Mutant and SA 3002, the breaking point was 21 cm. Again, the histograms of the parents showed peaks similar to those in the bimodal F_2 population.

The F_3 plants within the row were used to determine the genotype of their F_2 parents for this character. It was observed that the long peduncle plants gave rise to two types of F_3 rows. The first type was all uniform with long peduncle, while the other type segregated for long and short. The short peduncle plants always gave short peduncle plants in the F_3 generation. Only the F_3 plants within the rows that segregated for peduncle length were counted to support the F_2 data. The two classes of this character were established by the same criteria given in the F_2 generation. Since the peduncle length was relatively more constant than height to collar of flag leaf and to top node, tabulation and analysis were easier for this character.

The number of F_2 and F_3 plants counted for each class of peduncle length along with Chi-square and probability values of these four crosses are given in Table VII. The hypothesis that only one inherited factor in homozygous recessive condition depressed the elongation of peduncle seemed to be reasonable in this study.

Sheath Length

The measurement of this character was the distance from the top node to the collar of the flag leaf. Like the study of segregation for peduncle length, the sheath lengths of F_2 plants were grouped into

TABLE VII
 CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO PEDUNCLE LENGTH CLASSES
 WITH CHI-SQUARE AND PROBABILITY VALUES FOR CROSSES OF DWARF MUTANT
 WITH RED KAFIR, REDLAN, R OK Y8 AND SA 3002

Dwarf Mutant crossed with	Gen.	No. of plants in peduncle classes		Total plants	Expt. ratio	X ²	P Values	
		≥ Long	< Short					
Red Kafir 31 to 55 cm ^a $\bar{X} = 47.6 \pm 3.8$	F ₂	O ^b 288	94	382	3:1	.0314	.9+	
		E ^c 286.5	95.5					
	F ₃	O ^b 400	135	535	3:1	.0155	.9+	
		E ^c 401.25	133.75					
	Redlan 26 to 55 cm ^a $\bar{X} = 42.6 \pm 4.95$	F ₂	O ^b 268	101	369	3:1	1.106	.35
			E ^c 276.75	92.25				
F ₃		O ^b 1279	418	1697	3:1	.123	.75	
		E ^c 1272.75	424.25					
R OK Y8 41 to 70 cm ^a $\bar{X} = 55.6 \pm 4.15$		F ₂	O ^b 302	101	403	3:1	.00021	.9+
			E ^c 302.25	100.75				
	F ₃	O ^b 1368	460	1828	3:1	.0085	.9+	
		E ^c 1371	457					
	SA 3002 21 to 50 cm ^a $\bar{X} = 31.8 \pm 5.75$	F ₂	O ^b 288	103	391	3:1	.443	.5
			E ^c 293.25	97.75				
F ₃		O ^b 2485	812	3297	3:1	.0082	.9+	
		E ^c 2472.75	814.25					
Dw. Mut. 6 to 20 cm ^a $\bar{X} = 12.7 \pm 2.5$			≥ 21 cm	< 21 cm				

a Ranges, means and standard deviation respectively
 b Observed values
 c Expected values

5 cm. class intervals. Histograms of every cross involved with Dwarf Mutant were constructed along with the parents. The sheath length of 26 cm. was selected to separate the short and the long sheaths for all four crosses. Only in the cross of Dwarf Mutant and SA 3002 did the histogram not show a typical bimodal distribution. (See Figures 15, 16, 17 and 18)

The determination of genotypes in the F_2 generation was done by the pattern of segregation in F_3 progenies as usual. F_3 plants in the rows that segregated for sheath length were recorded to support F_2 data.

The number of F_2 and F_3 plants belonging to the short and long sheath classes in all crosses involved with Dwarf Mutant along with the Chi-square and P values are given in Table VIII. The result of this study indicated that the reduction of sheath length as well as the peduncle length was controlled by one genetic factor.

Crinkle Leaf

This peculiar leaf character was observed in the Dwarf Mutant and among all of its F_2 populations. The leaf blades seemed to be thicker and broader than the normal ones. The most typical appearance was the wrinkling or twisting of the leaf blade which looked less than fully expanded. (See Figure 31. B) This character could be recognized from the fifth leaf up to the last leaf or the flag leaf, which partially covered the panicle.

TABLE VIII
 CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO SHEATH LENGTH CLASSES WITH
 CHI-SQUARE AND PROBABILITY VALUES FOR CROSSES OF THE DWARF MUTANT
 WITH RED KAFIR, REDLAN, R OK Y8 AND SA 3002

Dwarf Mutant crossed with	Gen.	No. of plants in sheath classes		Total plants	Expt. ratio	X ²	P value
		Long ≥26 cm	Short <26 cm				
Red Kafir 31 to 45 cm ^a \bar{X} = 37.2 ± 2.15	F ₂	O ^b 276	106	382	3:1	1.539	.25
		E ^c 286.5	95.5				
	F ₃	O ^b 389	142	531	3:1	.8604	.40
		E ^c 398.25	132.75				
Redlan 26 to 45 cm ^a \bar{X} = 35.1 ± 3.55	F ₂	O ^b 283	83	366	3:1	1.0528	.30
		E ^c 274.5	91.5				
	F ₃	O ^b 1306	423	1729	3:1	.2638	.60
		E ^c 1296.75	432.25				
R OK Y8 31 to 50 cm ^a \bar{X} = 40.3 ± 3.1	F ₂	O ^b 301	101	402	3:1	.0027	.90+
		E ^c 301.5	100.5				
	F ₃	O ^b 1406	461	1867	3:1	.0732	.80
		E ^c 1400.25	466.75				
SA 3002 21 to 40 cm ^a \bar{X} = 28.2 ± 2.15	F ₂	O ^b 291	100	391	3:1	.068	.80
		E ^c 293.25	97.75				
	F ₃	O ^b 2509	842	3351	3:1	.0286	.90+
		E ^c 2513.25	837.75				
Dw. Mut. 11 to 30 cm ^a \bar{X} = 22.4 ± 2.4							

^a Ranges, means and standard deviation respectively

^b Observed values

^c Expected values

The number of plants possessing crinkled leaves in the F_2 and F_3 populations are given in Table IX along with the Chi-square test and P values. It was noticed that the Chi-square and P values to fit the expected 3:1 ratio did not fall in the acceptable limit while those of the F_3 populations seemed to be more reliable. The difference in the results between these two years was apparently due to the inability to recognize all plants with crinkled leaves in the various degrees of expression. In 1967 when the F_2 population was grown, only the plants showing very prominent characteristics were recorded. It was believed that the number of plants with these abnormal leaves were underestimated.

In 1968, more attention was given to this leaf character and all F_3 plants were examined carefully and repeatedly. It was found that some variation in the expression of crinkle leaf existed. There were a number of F_3 plants possessing only slightly wrinkled leaves which could be distinguished from normal plants with great care. Therefore, all F_3 plants with either slight or prominent expressivity were grouped together as crinkle leaf. The Chi-square and P values obtained in the F_3 generation were considered statistically reliable. Again, the appearance of this strange leaf character seemingly was under the control of a simple recessive factor.

The normal F_2 plants when verified in the F_3 generation produced either normal or segregating F_3 rows while the crinkled leaf F_2 plants gave rise to all crinkled leaf F_3 plants.

TABLE IX
 CLASSIFICATION OF F₂ AND F₃ POPULATIONS BASED ON CRINKLE LEAF WITH
 CHI-SQUARE AND PROBABILITY VALUES FOR CROSSES OF DWARF MUTANT
 WITH RED KAFIR, REDLAN, R OK Y8 AND SA 3002

Dwarf Mutant crossed with	Gen.	No. of plants in leaf classes		Total plants	Expt. ratio	X ²	P value
		Normal	Crinkle				
Red Kafir	F ₂	O ^a 318	64	382	3:1	13.885	.01
		E ^b 286.5	95.5				
	F ₃	O ^a 408	130	538	3:1	.2006	.65
		E ^b 403.5	134.5				
Redlan	F ₂	O ^a 311	58	369	3:1	16.955	.01
		E ^b 276.75	92.25				
	F ₃	O ^a 797	256	1053	3:1	.2633	.6
		E ^b 789.75	263.25				
R OK Y8	F ₂	O ^a 337	74	411	3:1	10.726	.01
		E ^b 308.25	102.75				
	F ₃	O ^a 943	332	1275	3:1	.7344	.4
		E ^b 956.25	318.75				
SA 3002	F ₂	O ^a 322	71	393	3:1	10.077	.01
		E ^b 294.75	98.25				
	F ₃	O ^a 943	332	1275	3:1	.734	.4
		E ^b 956.25	318.75				

^a Observed values

^b Expected values

Sword Leaf

Another kind of leaf form was observed in, and only in, the segregating generations of the cross between Redlan and Dwarf Mutant. The plants with this type of leaves looked somewhat more slender and had fewer leaves than normal. The leaves were somewhat erect. The leaf blades were abnormally long and narrow with prominent midribs giving a more or less "Sword-like" appearance. (See Figure 32A) The stem as well as the leaves were pale green in color and easily broken down. The heads were small in size and poorly set with seeds. The number of F_2 and F_3 plants with the Chi-square and P values are given in Table X. The number of F_3 plants came from those rows that segregated for sword leaf only. The inheritance of this character will be discussed later.

TABLE X

CLASSIFICATION OF F_2 AND F_3 POPULATIONS BASED ON SWORD LEAF WITH CHI-SQUARE AND PROBABILITY VALUES FROM THE CROSS OF DWARF MUTANT AND REDLAN

Cross	Gen.	No. of plants with leaf classes		Total plants	Expt. ratio	X^2	P value
		Normal	Sword				
Dw. Mutant X Redlan	F_2	O ^a 314	57	371	13:3	2.76	.08-.1
		E ^b 301.44	69.56				
	F_3	O ^a 1399	209	1608	13:3	36.62	.01
		E ^b 1306.5	301.5				

^a Observed values

^b Expected values

According to the results derived from the above studies of these four characters, only one factor beside the height genes in the Dw series could be detected. In the studies of the inheritance of plant height to the flag leaf and height to the top node from the crosses between Dwarf Mutant and other parents, it was reasonable to assume that this dwarfing character also depressed the elongation of peduncle and sheath length as well as the normal expansion of the leaves. In support of this assumption was the fact that these suppressions were not observed in the progenies of other crosses excluding the Dwarf Mutant. Moreover, the segregation of F_2 and F_3 progenies undoubtedly indicated the suppression occurred in a simple recessive condition for all three characters. These expressions were rather unique because there was no evidence that the other four parents differed genetically for peduncle and sheath length. In the cross between Red Kafir and Dwarf Mutant, it was observed that the plants with the short height to the flag leaf and to the top node always had short peduncle and sheath lengths and crinkled leaves. The genotype $iiDw_1Dw_1Dw_2Dw_2$ was already assigned to this type of plant. Again in the cross Redlan X Dwarf Mutant and R OK Y8 X Dwarf Mutant, about half of the plants in the intermediate height class showed the crinkle leaf character along with short peduncle and sheath length. This group of plants was supposed to have a genotype of $iiDw_1-Dw_2-$ as did their dwarf parent. For the short height class of genotype $iidw_1dw_1Dw_2-$, all plants seemed to possess the short peduncle and sheath length and crinkled leaves. It

might be logical to assign the gene symbol *ii* to the expression of all three characters.

However, the data from this study did not indicate the effect of the Dwarf Mutant on the suppression of the head length elongation. The F₂ population of all crosses involving the Dwarf Mutant showed the typical continuous distribution for this character. (See Table XI)

The nature of the sword leaf seemed to be more complex than those of peduncle and sheath length and crinkle leaf. The studies of segregating progenies indicated that this expression was the result of interaction of the genes from Redlan and Dwarf Mutant. No sword leaf plant occurred in crosses other than Redlan X Dwarf Mutant. Part of this expression was contributed by Redlan and part by the Dwarf Mutant, but both parts had to be together in order to obtain the sword leaf character.

The second finding from the study of this cross was that this gene seemed to be independent of the four height factors in the Dw series especially Dw₁ and Dw₂. The plants with the sword leaf character varied considerably in height. Furthermore, some F₂ plants with the sword leaf character were found which bred true for sword leaf but segregated for height in the F₃ population.

Possibly the responsible gene from Dwarf Mutant was the *ii* factor, since it was the only factor found to be different from the other four parents in this study. Thus, the crosses of Redlan with Red Kafir, R OK Y8 and SA 3002 did not give any sword leaf progeny.

TABLE XI
 CLASSIFICATION OF PARENTS OF F₂ POPULATIONS INTO 5-CM. INTERVALS
 FOR HEAD LENGTH OF ALL CROSSES INVOLVING THE DWARF MUTANT

Parents and F ₂	Length of head (panicle) in cm.											
	5	10	15	20	25	30	35	40	45	50	55	
Dwarf Mutant			36	107	42							
Red Kafir					16	60	92	6				
Redlan			7	55	111	4						
R OK Y8					1	6	9	87	47	6	1	
SA 3002			74	116								
<u>F₂ of Dwarf Mutant</u>												
X Red Kafir			8	21	23	63	40	4				
X Redlan	2	3	30	83	92	101	24	8				
X R OK Y8			13	48	61	99	119	45	8	6		
X SA 3002	2	4	17	56	63	39	11	2	1			

However, the possible complementary gene from the Redlan parent was undetermined. Several speculations were made as to the nature of the inheritance in Redlan, but according to available data none of them was considered an adequate explanation.

The most likely hypothesis was to designate one dominant factor in Redlan with the gene symbol SwSw for the sword leaf character.

Thus, the Redlan genotype for this purpose would be IISwSw and iiswsw would be for the Dwarf Mutant. The F₁ plants with IiSwsW genotype would have normal leaves. So in the F₂ and F₃ generation the plants with genotypes of iiSwSw and iiSwsW were supposed to have sword leaf, while I-Sw-, I-swsW and iiswsw were normal or crinkle leaf plants.

The expected ratio for this assumption would be 13:3 of non-sword leaf to sword leaf plants. From a total of 371 F₂ plants this expectation gave a Chi-square value of 2.56 and a P value of .08 - 0.1 which was barely acceptable. However, in the F₃ generation, a total of 1608 plants were counted from those rows segregating for the sword leaf character. This gave a Chi-square value of 36.62 and a P value of less than 0.01 which would reject the hypothesis.

Lethality was frequently observed from early seedling up to the flowering stage in this cross. This could alter the true nature of the inheritance to some degree.

Since Quinby and Karper (1954), Casady (1967) and Brooks (1967) indicated that the height genes in Dw series were independent of those genes controlling peduncle and sheath length, the expression of the

dwarf mutant factor was apparently not similar to any of those. The data showed that once it suppressed the internodal elongation, it further reduced the peduncle and sheath length and also was responsible for the production of the crinkle and the sword leaf character. Except in the case of the sword leaf, the inhibitor seemed to show a typically simple Mendelian pattern of segregation and expressed its suppressing effect in the homozygous recessive condition. Sieglinger (1933) observed this pattern and mentioned that the sudden occurrence of this Dwarf Mutant was due to the loss of one factor.

One may speculate that the loss of one functional genetic unit could give rise to this Dwarf Mutant. This functional unit could be responsible for the process of elongation of internodes, peduncle and sheath as well as the expansion of leaf blade in the later stage of development. In support of this speculation was the difference in plant height of the two genotypes, $iiDw_1Dw_1Dw_2Dw_2$ and $iidw_1dw_1Dw_2Dw_2$. The genes Dw_1 and Dw_2 would direct internode elongation to some extent. At a certain period of time the i gene interrupted this elongation and caused the plant height of $iiDw_1Dw_1Dw_2Dw_2$ to differ considerably from $iidw_1dw_1Dw_2Dw_2$. Another evidence was the occurrence of crinkle leaf. The young leaf was allowed to develop almost to full structure, however, the process of expansion was lacking. Since the developing leaf could not attain its maximum growth, the crinkle appearance resulted.

However, this was purely speculation. If the reasoning given above were validated, it should lead to the conclusion that all of the expressions were the result of multiple effects, pleiotropism, from a single gene *i*, rather than separate and closely linked genes.

Plant Height Inheritance in Other Crosses

Excluding the Dwarf Mutant

All possible crosses between the four parents excluding the Dwarf Mutant were made and the data were used to reaffirm Quinby and Karper's work on plant height inheritance. The crosses of Red Kafir X Redlan, Red Kafir X R OK Y8, Redlan X SA 3002 and R OK Y8 X SA 3002 were assumed to differ by only one height factor, so only F_2 plants were grown for the purpose of this study. On the other hand, the cross of Red Kafir and SA 3002 was believed to have two genes different. Consequently, it was necessary to have both F_2 and F_3 populations for more reliable confirmation. Four F_2 rows were selected as mentioned in Chapter III to produce the F_3 generation.

The procedures for the measurements of the height characters in the classification of the F_2 plants and for the calculations of the Chi-square tests for each cross were essentially the same as in the study of plant height inheritance of the Dwarf Mutant. Each cross will be reported separately and will be discussed together in a later section.

Cross between Red Kafir and Redlan

According to the list of parents given on page 12, the Red Kafir genotype was $Dw_1Dw_1Dw_2Dw_2$ while the Redlan genotype was $dw_1dw_1Dw_2Dw_2$ and the first height factor Dw_1 was expected to segregate in this cross. (See Figures 19 and 20) Two height classes were established, the tall and intermediate height classes, by arbitrarily dividing the frequency distribution at 90 cm. for height to the collar of the flag leaf and at 60 cm. for the height to the top node. The data for both height characters, the Chi-square tests and P values are given in Table XII. The results were considered an acceptable fit to a monohybrid segregation.

Cross between Red Kafir and R OK Y8

The R OK Y8 genotype was $dw_1dw_1Dw_2Dw_2$ which was similar to the Redlan genotype. Thus, segregation was expected for the first height factor, Dw_1 . The tall and intermediate height classes of plants in the F_2 population were separated at 80 cm. for the height to the collar of the flag leaf, and at 45 cm. for the height to the top node, on the basis of the measurements of the parents and the histogram of the F_2 populations. (See Figures 21 and 22) In Table XIII, the numbers of plants in each class, their Chi-square tests and P values indicated that the fit to the expected one gene segregating ratio was acceptable.

TABLE XII

CLASSIFICATION OF F₂ POPULATION INTO HEIGHT CLASSES WITH CHI-SQUARE
AND PROBABILITY VALUES FOR THE CROSS OF RED KAFIR AND REDLAN

Height to	Gen.	Gene Seg.	No. of plants in classes		Total plants	Expt. ratio	X ²	P. values
			Tall Dw ₁ -Dw ₂ Dw ₂	Intermed. dw ₁ dw ₁ Dw ₂ Dw ₂				
<u>Collar of Flag leaf</u>			<u>≥ 91 cm</u>	<u>< 91 cm</u>				
Red Kafir 81 to 130 cm ^a $\bar{X} = 91.5 \pm 8.1$	F ₂	Dw ₁ dw ₁	O ^b 143 E ^c 147.75	54 49.25	197	3:1	.61	.40
Redlan 61 to 90 cm ^a $\bar{X} = 74.7 \pm 6.85$								
<u>Top node</u>			<u>≥ 61 cm</u>	<u>< 61 cm</u>				
Red Kafir 61 to 90 cm ^a $\bar{X} = 75.4 \pm 6.75$	F ₂	Dw ₁ dw ₁	O ^b 152 E ^c 150	48 50	200	3:1	.11	.75
Redlan 26 to 55 cm ^a $\bar{X} = 38 \pm 5.95$								

^a Ranges, means and standard deviation respectively

^b Observed values

^c Expected values

TABLE XIII

CLASSIFICATION OF F₂ POPULATION INTO HEIGHT CLASSES WITH CHI-SQUARE
AND PROBABILITY VALUES FOR THE CROSS OF RED KAFIR AND R OK Y8

Height to	Gen.	Gene Seg.	No. of plants in classes		Total plants	Expt. ratio	X ²	P. values
			Tall Dw ₁ -Dw ₂ Dw ₂	Intermed. dw ₁ dw ₁ Dw ₂ Dw ₂				
<u>Collar of Flag leaf</u>			<u>≥ 86 cm</u>	<u>< 86 cm</u>				
Red Kafir 81 to 130 cm ^a $\bar{X} = 91.5 \pm 8.1$	F ₂	Dw ₁ dw ₁	O ^b 140 E ^c 135	40 45	180	3:1	.74	.35
R OK Y8 46 to 80 cm ^a $\bar{X} = 62.9 \pm 5.2$								
<u>Top node</u>			<u>≥ 46 cm</u>	<u>< 46 cm</u>				
Red Kafir 61 to 90 cm ^a $\bar{X} = 75.4 \pm 6.85$	F ₂	Dw ₁ dw ₁	O ^b 139 E ^c 138	45 46	184	3:1	.029	.95
R OK Y8 11 to 30 cm ^a $\bar{X} = 21.5 \pm 4.95$								

^a Ranges, means and standard deviation respectively

^b Observed values

^c Expected values

Cross between Redlan and SA 3002

The genotype of SA 3002 was believed to have all four dwarf genes in the recessive condition, so in this cross the F_2 populations were expected to segregate for the second height gene, Dw_2 . Two classes of F_2 plants, the intermediate and short height classes were separated at 50 cm. for height to the collar of the flag leaf and at 15 cm. for the height to the top node according to the previous criteria. (See Figures 23 and 24) The F_2 plants recorded for each class, their Chi-square tests and P values are presented in Table XIV. Again, the hypothesis of the 3:1 ratios were apparently acceptable for both height characters.

Cross between R OK Y8 and SA 3002

Since R OK Y8 and Redlan genotypes were symbolically similar for height factors, one gene segregation, Dw_2 , was expected among the F_2 plants of this cross. (See Figures 25 and 26) F_2 plants were grouped into the intermediate height class if their height to the collar of the flag leaf exceeded 45 cm. and remaining plants were put in the short height class. Similarly, F_2 plants were put into the intermediate class if their height to the top node was greater than 15 cm., and the rest were included in the short height class. In Table XV, the F_2 data of this cross, their Chi-square tests and P values revealed an acceptable fit to a one gene segregation.

TABLE XIV

CLASSIFICATION OF F₂ POPULATION INTO HEIGHT CLASSES WITH CHI-SQUARE
AND PROBABILITY VALUES FOR THE CROSS OF REDLAN AND SA 3002

Height to	Gen.	Gene Seg.	No. of plants in classes		Total plants	Expt. ratio	X ²	P. values
			Intermed. dw ₁ dw ₁ Dw ₂ -	Short dw ₁ dw ₁ dw ₂ dw ₂				
<u>Collar of Flag leaf</u>			<u>≥ 51 cm</u>	<u>< 51 cm</u>				
Redlan 61 to 90 cm ^a $\bar{X} = 74.7 \pm 6.85$	F ₂	Dw ₂ dw ₂	O ^b 143	47				
SA 3002 26 to 50 cm ^a $\bar{X} = 37.7 \pm 3.55$			E ^c 142.5	47.5	190	3:1	.007	.90+
<u>Top node</u>			<u>≥ 16 cm</u>	<u>< 16 cm</u>				
Redlan 26 to 55 cm ^a $\bar{X} = 38 \pm 5.95$	F ₂	Dw ₂ dw ₂	O ^b 140	40				
SA 3002 1 to 15 cm ^a $\bar{X} = 8.9 \pm 2.4$			E ^c 135	45	180	3:1	.742	.35

^a Ranges, means and standard deviations respectively

^b Observed values

^c Expected values

TABLE XV

CLASSIFICATION OF F₂ POPULATION INTO HEIGHT CLASSES WITH CHI-SQUARE
AND PROBABILITY VALUES FOR CROSS OF R OK Y8 AND SA 3002

Height to	Gen.	Gene Seg.	No. of plants in classes		Total plants	Expt. ratio	X ²	P. values
			Intermed. dw ₁ dw ₁ Dw ₂ -	Short dw ₁ dw ₁ dw ₂ dw ₂				
<u>Collar of Flag leaf</u>			<u>≥ 46 cm</u>	<u>< 46 cm</u>				
R OK Y8 46 to 80 cm ^a $\bar{X} = 62.9 \pm 5.2$	F ₂	Dw ₂ dw ₂	O ^b 136	56				
SA 3002 26 to 50 cm ^a $\bar{X} = 37.7 \pm 3.55$			E ^c 144	48	192	3:1	1.777	.15
<u>Top node</u>			<u>≥ 16 cm</u>	<u>< 16 cm</u>				
R OK Y8 11 to 30 cm ^a $\bar{X} = 21.5 \pm 4.95$	F ₂	Dw ₂ dw ₂	O ^b 147	45				
SA 3002 1 to 15 cm ^a $\bar{X} = 8.9 \pm 2.4$			E ^c 144	48	192	3:1	.25	.60

- ^a Ranges, means and standard deviations respectively
^b Observed values
^c Expected values

Cross between Red Kafir and SA 3002

From the list of parents on page 12, a two height gene difference, Dw_1 and Dw_2 , was expected between these two parents. (See Figures 27 and 28) It was considered more appropriate to grow the F_3 population in order to verify the F_2 parental genotypes. Since Quinby and Karper (1954) stated that the height genes had an approximately equal effect on plant height, three classes of plants were arbitrarily established. The plants in the tall class were supposed to have two dominant genes like Red Kafir, those in the intermediate height class were expected to have one dominant gene like Redlan or R OK Y8, and the plants in the short class, no dominant gene like SA 3002. The methods used to classify F_2 and F_3 plants and to test the expected ratios were essentially similar to those used in the studies of plant height inheritance of the Dwarf Mutant crosses. The measurement of both plant height characters, the numbers of plants in each class, the Chi-square tests and the P values are given in Table XVI. The results obtained from the available data indicated that a two gene segregation apparently existed in this cross.

Cross between Redlan and R OK Y8

The parents of this cross possessed the same height genotype, $dw_1dw_1Dw_2dw_2$, and the F_2 population did not indicate any appreciable segregation. The overall height of these two varieties was approximately the same. However, the measurement of Redlan appeared

TABLE XVI
 CLASSIFICATION OF F₂ AND F₃ POPULATIONS INTO HEIGHT CLASSES WITH CHI-SQUARE
 AND PROBABILITY VALUES FOR THE CROSS OF RED KAFIR AND SA 3002

Height to	Gen.	Gene Seg.	No. of plants in classes			Total plants	Expt. ratio	X ²	P. values	Line		
			Tall Dw ₁ -Dw ₂ - dw ₁ dw ₁ Dw ₂ -	Intermed. Dw ₁ -dw ₂ dw ₂ dw ₁ dw ₁ Dw ₂ -	Short dw ₁ dw ₁ - dw ₂ dw ₂							
<u>Collar of Flag leaf</u>			≥ 81 cm	36 to 80 cm	< 36 cm							
Red Kafir 81 to 130 cm ^a X̄ = 91.5 ± 8.1	F ₂	Dw ₁ -Dw ₂ -	O ^b	125	64	9	198	9:6:1	4.002	.15	1	
			E ^c	111.35	74.24	12.38					2	
SA 3002 56 to 50 cm ^a X̄ = 37.7 ± 3.55	F ₃	Dw ₁ -Dw ₂ Dw ₂ -	O ^b	799	258		1057	3:1	.297	.55	3	
			E ^c	792.75	264.25						4	
		Dw ₁ dw ₂ dw ₂ -	O ^b	-	491	175		666	3:1	.579	.45	5
			E ^c	-	499.5	166.5						6
Dw ₁ -Dw ₂	O ^b	584	444	58	1086	9:6:1	5.849	.015	.015	7		
	E ^c	610.9	407.2	67.9						8		
<u>Top node</u>			≥ 46 cm	16 to 45 cm	< 16 cm							
Red Kafir 61 to 90 cm ^a X̄ = 75.4 ± 6.75	F ₂	Dw ₁ -Dw ₁ -	O ^b	114	73	9	196	9:6:1	.250	.90	9	
			E ^c	111.38	74.24	12.38					10	
SA 3002 1 to 15 cm ^a X̄ = 8.9 ± 2.4	F ₃	Dw ₁ -Dw ₂ Dw ₂ -	O ^b	808	249		1057	3:1	1.174	.30	11	
			E ^c	792.75	264.25						12	
		Dw ₁ -dw ₂ dw ₂ -	O ^b	-	490	176		666	3:1	.723	.35	13
			E ^c	-	499.5	166.5						14
Dw ₁ -Dw ₂	O ^b	599	425	62	1086	9:6:1	1.53	.45	.45	15		
	E ^c	610.9	407.2	67.9						16		

^a Ranges, means and standard deviations respectively

^b Observed values

^c Expected values

taller at height to the top node but shorter in head, peduncle and sheath length than R OK Y8. Plants with non-parental combinations, i. e., both high top node and long peduncle and both short top node and peduncle, were observed in the F_2 generation along with plants of the parental types. The histogram of F_2 plants of this cross shows a typical normal distribution in both height characters. (See Tables XVI and XVII) It was suspected that the variation observed might have resulted from modifiers which could not be detected by the Mendelian method being employed.

The above findings confirmed Quinby and Karper's report about the existence of height factors, independent inheritance and relatively equal and cumulative effects of each height gene. However, a number of F_2 and F_3 plants were observed to be taller than the parents to some extent. These might arise from the effects of a modifier complex as suggested by Quinby and Karper (1954) or from minor genes reported by Hadley (1957). Varietal and environmental effects were also believed to cause this variation as pointed out by Casady (1965, 1967), Hadley (1957) and Freeman et al (1962). Heterosis in plant height was reported by Graham and Lessman (1966), Kambal and Webster (1966) and Quinby et al (1958). Undoubtedly, the above suggestions could cause variability in one or more plant characters in F_2 and F_3 generations in this study.

TABLE XVII

CLASSIFICATION OF PARENTS AND F₂ POPULATION INTO 5 CM. INTERVALS FOR HEIGHT TO THE COLLAR OF THE FLAG LEAF FOR THE CROSS OF REDLAN AND R OK Y8

Parents and F ₂	Height to the collar of flag leaf in cm.										
	50	55	60	65	70	75	80	85	90	95	100
Redlan				16	29	55	43	25	3	5	
R OK Y8	2	7	34	78	22	7	2	1	1		
F ₂		3	3	24	41	64	33	23	13	7	3

TABLE XVIII

CLASSIFICATION OF PARENTS AND F₂ POPULATION INTO 5 CM. INTERVALS FOR HEIGHT TO THE TOP NODE FOR THE CROSS OF REDLAN AND R OK Y8

Parents and F ₂	Height to the top node in cm.										
	15	20	25	30	35	40	45	50	55	60	65
Redlan				7	40	64	46	11			
R OK Y8	11	52	56	9							
F ₂		1	16	44	50	41	25	13	4	6	1

The histograms of the segregating populations along with the range and means of parental measurements were very useful in the establishment of progeny classes. However, in certain crosses these measurements were overlapping, and other related characters had to be considered to enable classification.

It was found that the height to the top node gave a better fit in the Chi-square tests of the expected ratio than the height to the collar of the flag leaf in every cross except in the cross Redlan X SA 3002. This was true because the height to the collar of the flag leaf was the sum of height to the top node and sheath length. However, height to the collar of the flag leaf gave reliable results in almost every cross. Quinby and Karper (1954) indicated this.

An attempt was made to analyze the segregation for other characters such as head, peduncle and sheath length among the progenies of all crosses excluding the Dwarf Mutant, but it was unsuccessful. The class intervals of F_2 populations indicated normal distributions, and the ranges of parental measurement of these characters overlapped each other to some extent (See Tables XIX, XX and XXI). It might be concluded that the height genes that controlled the length of internodes were different and independent to those determining the peduncle, head and sheath length as reported by Quinby (1961), Quinby and Karper (1954), Kambal and Webster (1966) and Brooks (1967).

However, Casady (1967) and Graham and Lessman (1966) believed that Dw genes influenced both internodal and peduncle lengths.

TABLE XIX
 CLASSIFICATION OF PARENTS AND F₂ POPULATION INTO 5 CM. INTERVALS FOR
 PEDUNCLE LENGTH OF ALL CROSSES EXCLUDING THE DWARF MUTANT

Parents and F ₂	Length of peduncle in cm.											
	20	25	30	35	40	45	50	55	60	65	70	75
Red Kafir				1	6	38	94	40				
Redlan			4	4	36	83	26	8				
SA 3002		22	67	54	34	11	3					
R OK Y8						3	28	52	33	24	10	
<u>F₂</u>												
Red Kafir X Redlan		3	2	7	12	28	52	55	30	9	1	1
Red Kafir X R OK Y8				1	9	15	37	47	36	33	5	
Redlan X R OK Y8			1	3	9	16	44	57	53	25	3	1
Redlan X SA 3002	3	7	33	53	24	15	3	2	1			
R OK Y8 X SA 3002		3	11	35	41	42	35	14	5	2		
Red Kafir X SA 3002		10	33	44	41	37	26	2	3			

TABLE XX
 CLASSIFICATION OF PARENTS AND F₂ POPULATION INTO 5 CM. INTERVALS FOR
 SHEATH LENGTH OF ALL CROSSES EXCLUDING THE DWARF MUTANT

Parents and F ₂	Length of sheath in cm.							
	20	25	30	35	40	45	50	55
Red Kafir				33	129	6		
Redlan			15	75	84	2		
R OK Y8				3	78	68	5	
SA 3002		11	160	16	3			
<u>F₂</u>								
Red Kafir X Redlan		1	9	46	111	28	1	
Red Kafir X R OK Y8	2	3	4	30	73	63	5	2
Redlan X R OK Y8			3	19	121	60	4	3
Redlan X SA 3002	1	6	52	82	43	4	2	
R OK Y8 SA 3002	1	4	42	85	50	6		
Red Kafir X SA 3002		2	32	107	48	4	1	

TABLE XXI
 CLASSIFICATION OF PARENTS AND F₂ POPULATION INTO 5 CM. INTERVALS FOR
 HEAD LENGTH OF ALL CROSSES EXCLUDING THE DWARF MUTANT

Parents and F ₂	Length of head (panicle) in cm.								
	10	15	20	25	30	35	40	45	50
Red Kafir				16	60	92	6		
Redlan		7	55	111	4				
R OK Y8				1	6	9	87	47	7
SA 3002	74	53							
<u>F₂</u>									
Red Kafir X Redlan		2	14	59	90	28	4	2	
Red Kafir X R OK Y8				8	31	70	63	8	2
Redlan X R OK Y8		1	2	42	100	53	10	1	1
Redlan X SA 3002		14	93	49	12	1	1		
R OK Y8 X SA 3002	1	4	26	73	68	16	2		
Red Kafir X SA 3002		8	50	62	62	14	1		

In this study, the available data and methods employed did not indicate any pleiotropic effects of these height genes.

Quinby (1967) and Quinby and Karper (1954) strongly indicated that a difference in maturity might be the cause of differences in plant height due to the increase in the number of internodes. Fortunately, the parents used in this study were considered uniform in maturity when compared to the materials they used in 1954. The SA 3002 variety took 55 days from planting to first bloom, Redlan and R OK Y8, 58 days, while Red Kafir and Dwarf Mutant required 65 days. The maximum difference of the first blooming date was 10 days at Perkins. Quinby and Karper (1954) also pointed out that June planting showed the least yearly variation. Accordingly, the materials used in this study for 1967 and 1968 were both sown in the month of June. It was believed that both planting date and the difference in maturity between varieties used in this study should not have caused any considerable confusion in identifying plant height and other characters.

CHAPTER V

SUMMARY AND CONCLUSIONS

A study was carried out to determine the nature of plant height inheritance in the abnormal Dwarf Mutant isolated by Sieglinger in 1933. Four genetically known parents, Red Kafir, Redlan, R OK Y8 and SA 3002 were used in this study.

All possible crosses among the Dwarf Mutant and those four parents including four reciprocal crosses were made. Each F_2 population and selected F_3 plants were grown in the field in summer 1967 and again in 1968. The measurement for height to the collar of the flag leaf, to the top node, and the lengths of head, peduncle and sheath were made in centimeters.

The estimates for number of genes segregating were based on individual plant classification which, in turn, were based on the histogram of the F_2 population and the ranges of parental measurement. Variability due to several modifiers was noticed, so it was necessary to make some adjustment for individual plant groupings.

Chi-square tests of segregating populations indicated that the Dwarf Mutant acted as an inhibitor to suppress the elongation of internodes. The magnitude of this inhibition was partly determined by the

number of height genes in Dw series. The Dwarf Mutant also reduced the peduncle and sheath length, and caused leaves to crinkle. By some undetermined factor, this mutant was thought to be responsible for the occurrence of sword leaf in the cross, Redlan X Dwarf Mutant.

The Dwarf Mutant segregated in a simple Mendelian ratio and expressed its inhibiting effects in the homozygous recessive condition. From the available data as well as careful observation, it is possible to assume that the expression is a result of multiple effects, pleiotropism, from a single gene rather than that separate and closely linked genes are involved.

Moreover, the expression of this mutant seems to be independent of the height genes described by Quinby and Karper. The sudden loss of a genetically functional unit responsible for the process of plant elongation and leaf expansion was suggested for these phenomenon.

Finally, the analysis of the height genes in the crosses of the four known parents were evidently confirmed.

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APPENDIX

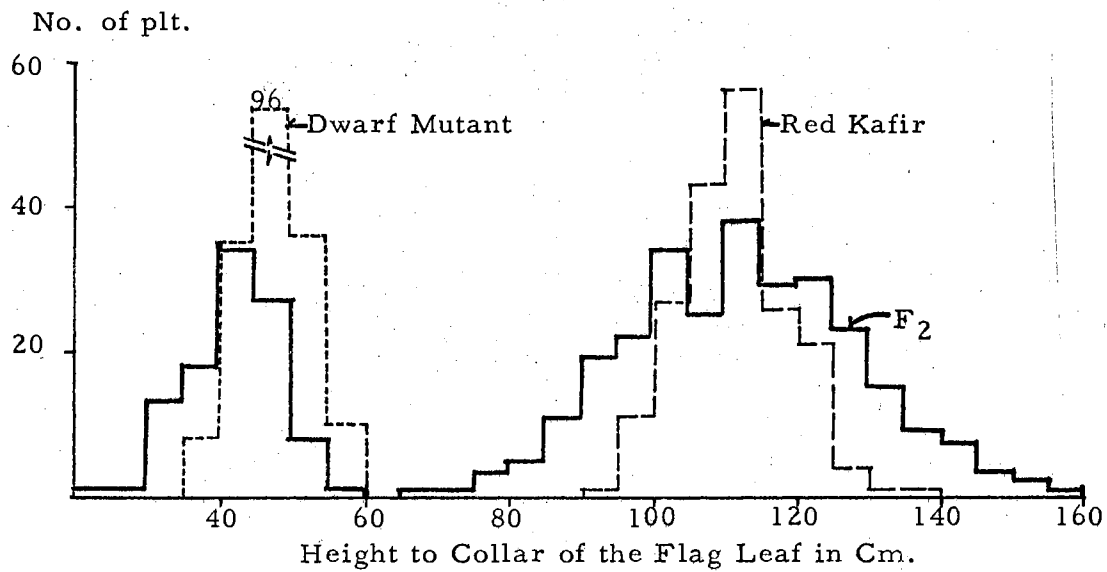


Figure 1. Histogram of Height to the Collar of the Flag Leaf of Parents of the F₂ Population for the Cross of Red Kafir and Dwarf Mutant.

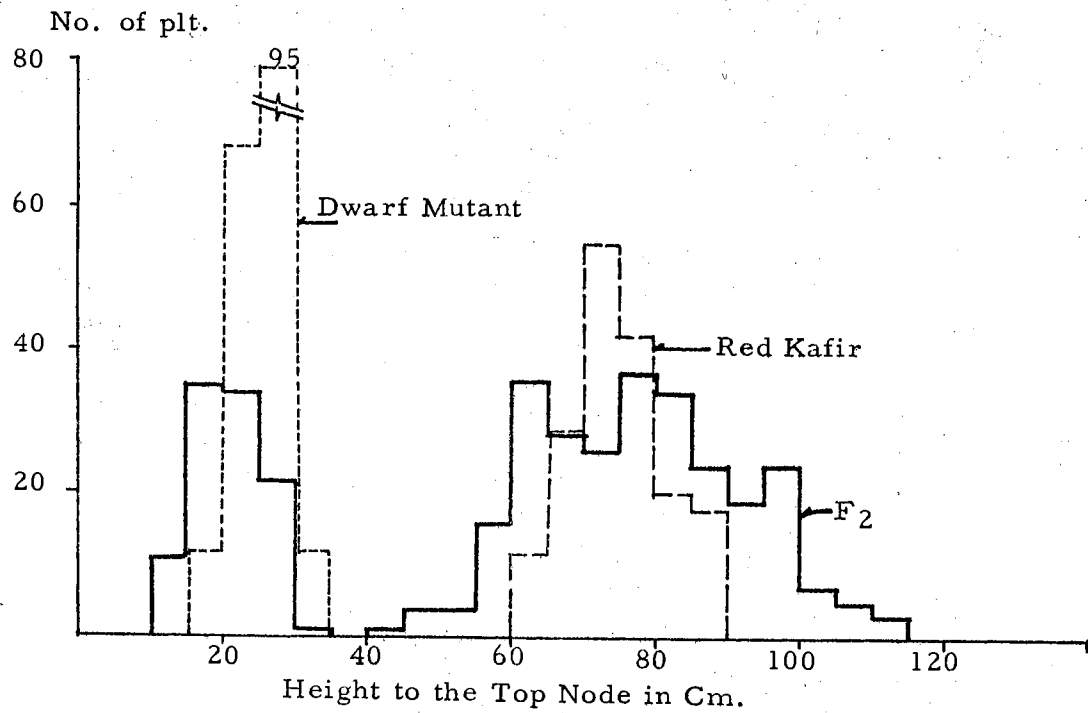


Figure 2. Histogram of Height to the Top Node of Parents and F₂ Populations for the Cross of Red Kafir and Dwarf Mutant.

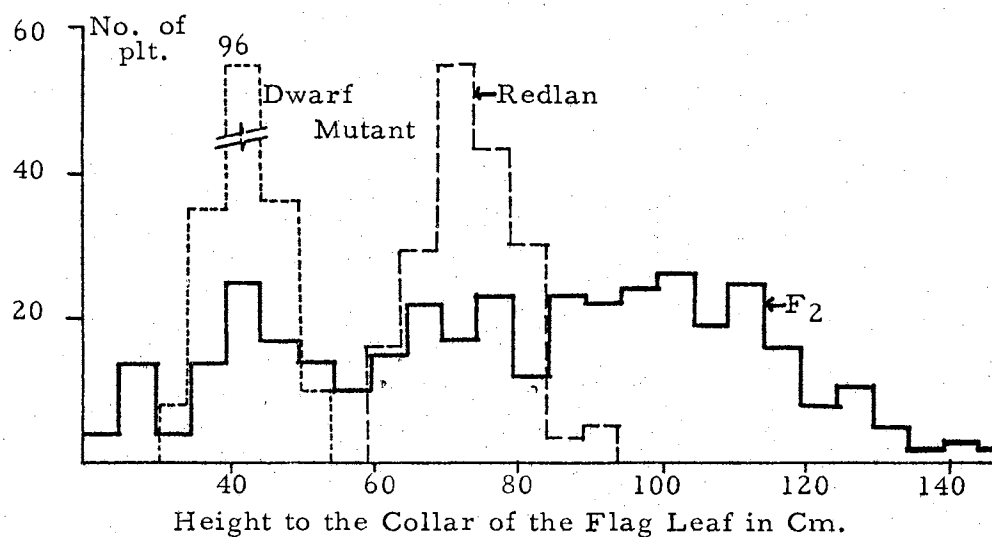


Figure 3. Histogram of Height to the Collar of the Flag Leaf of the Parents and F₂ Population for the Cross of Redlan and Dwarf Mutant.

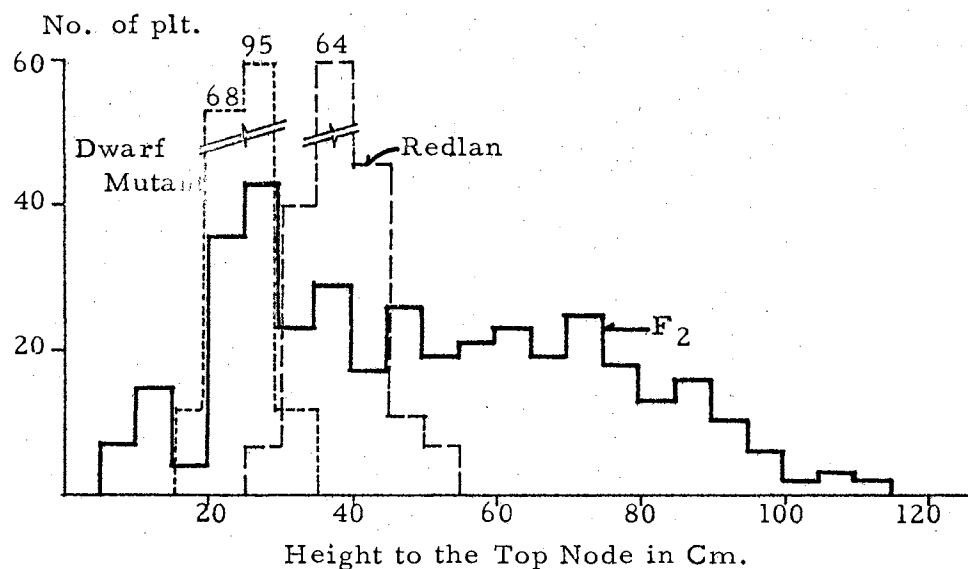


Figure 4. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of Redlan and Dwarf Mutant.

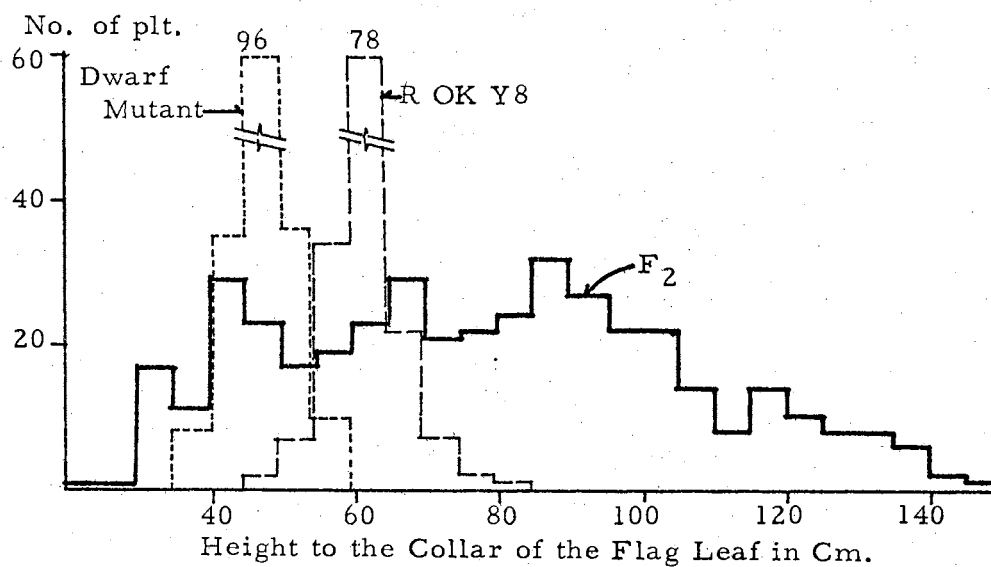


Figure 5. Histogram of Height to the Collar of the Flag Leaf of the Parents of F₂ Population for the Cross of R OK Y8 and Dwarf Mutant.

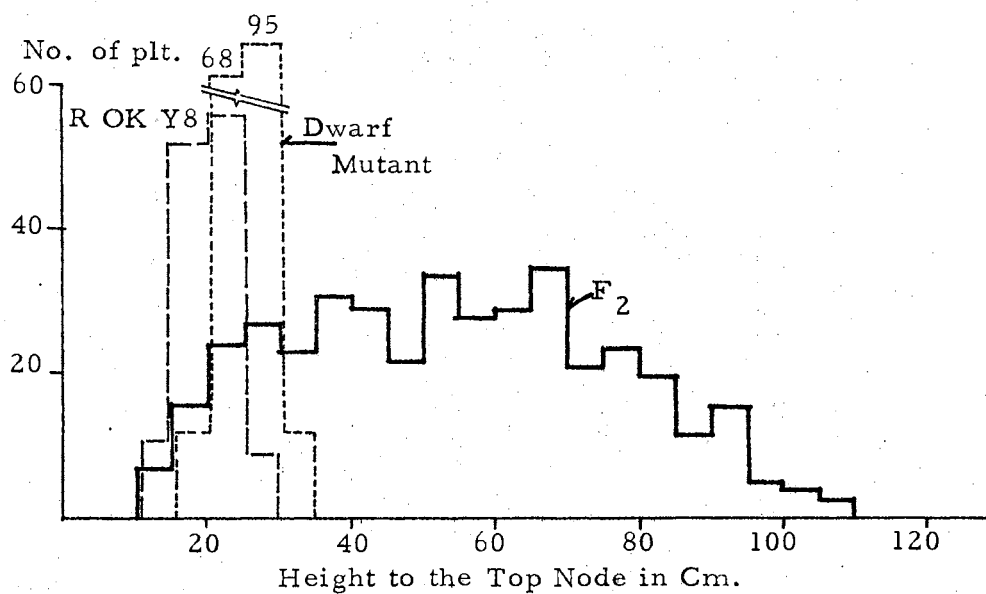


Figure 6. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of R OK Y8 and Dwarf Mutant.

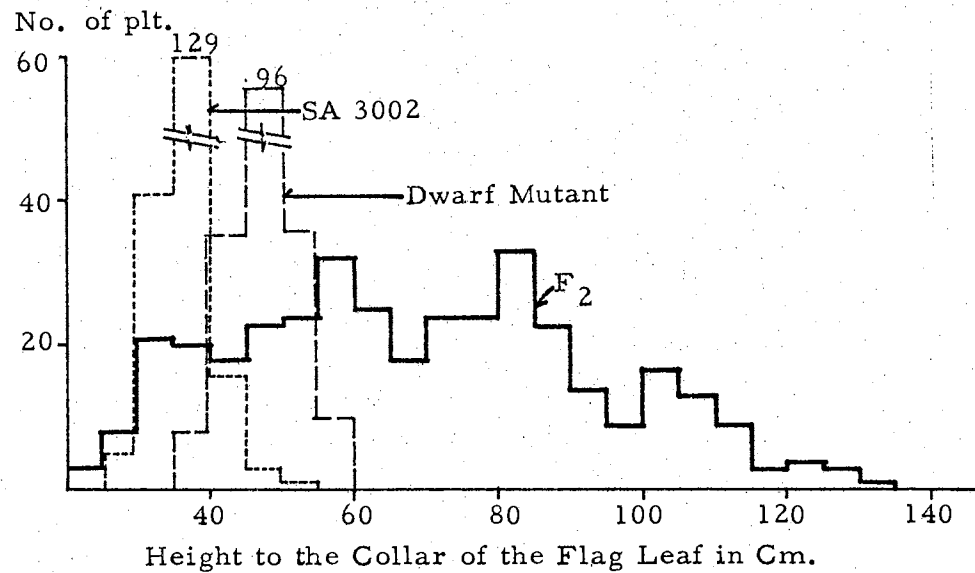


Figure 7. Histogram of Height to the Collar of the Flag Leaf of the Parents and F₂ Population for the Cross of SA 3002 and Dwarf Mutant.

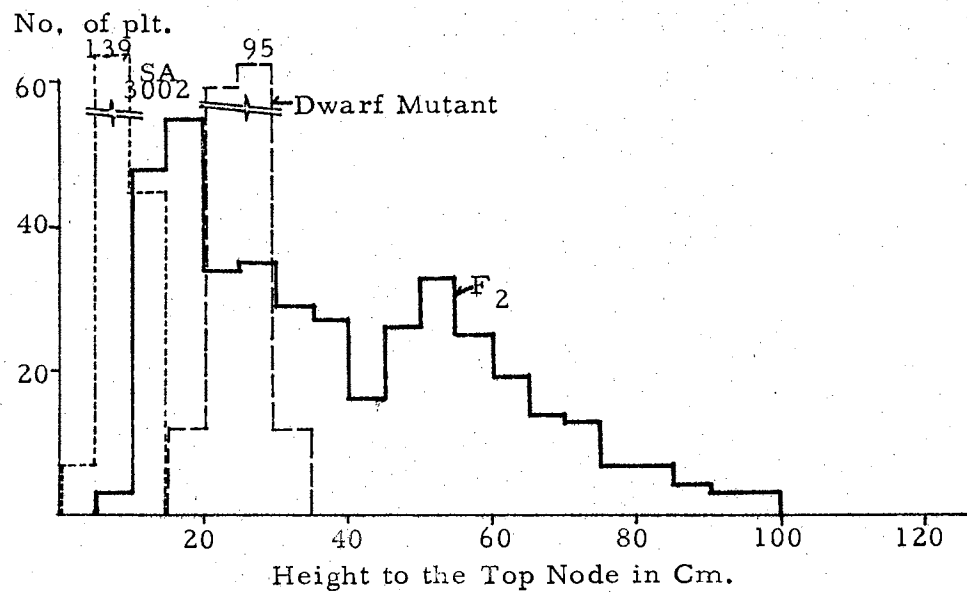


Figure 8. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of SA 3002 and Dwarf Mutant.

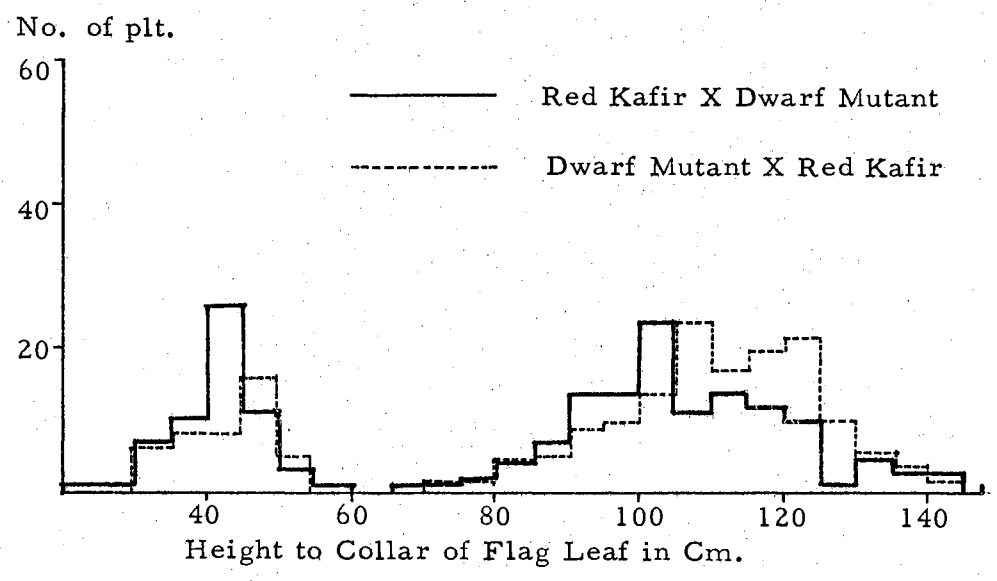


Figure 9. Histogram of Height to the Collar of the Flag Leaf of the F₂ Population for the Reciprocal Crosses of Red Kafir and Dwarf Mutant.

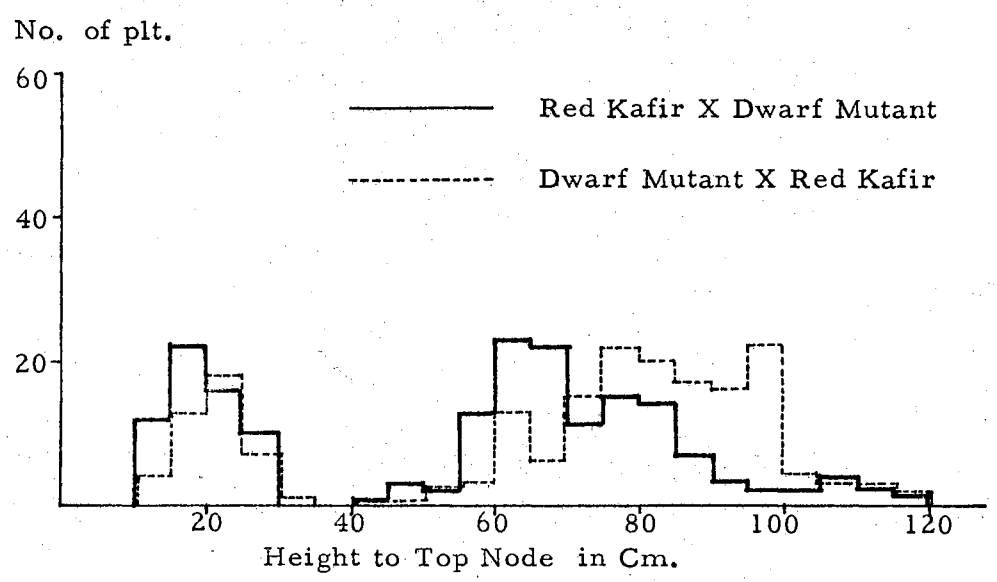


Figure 10. Histogram of Height to the Top Node of the F₂ Population for the Reciprocal Crosses of Red Kafir and Dwarf Mutant.

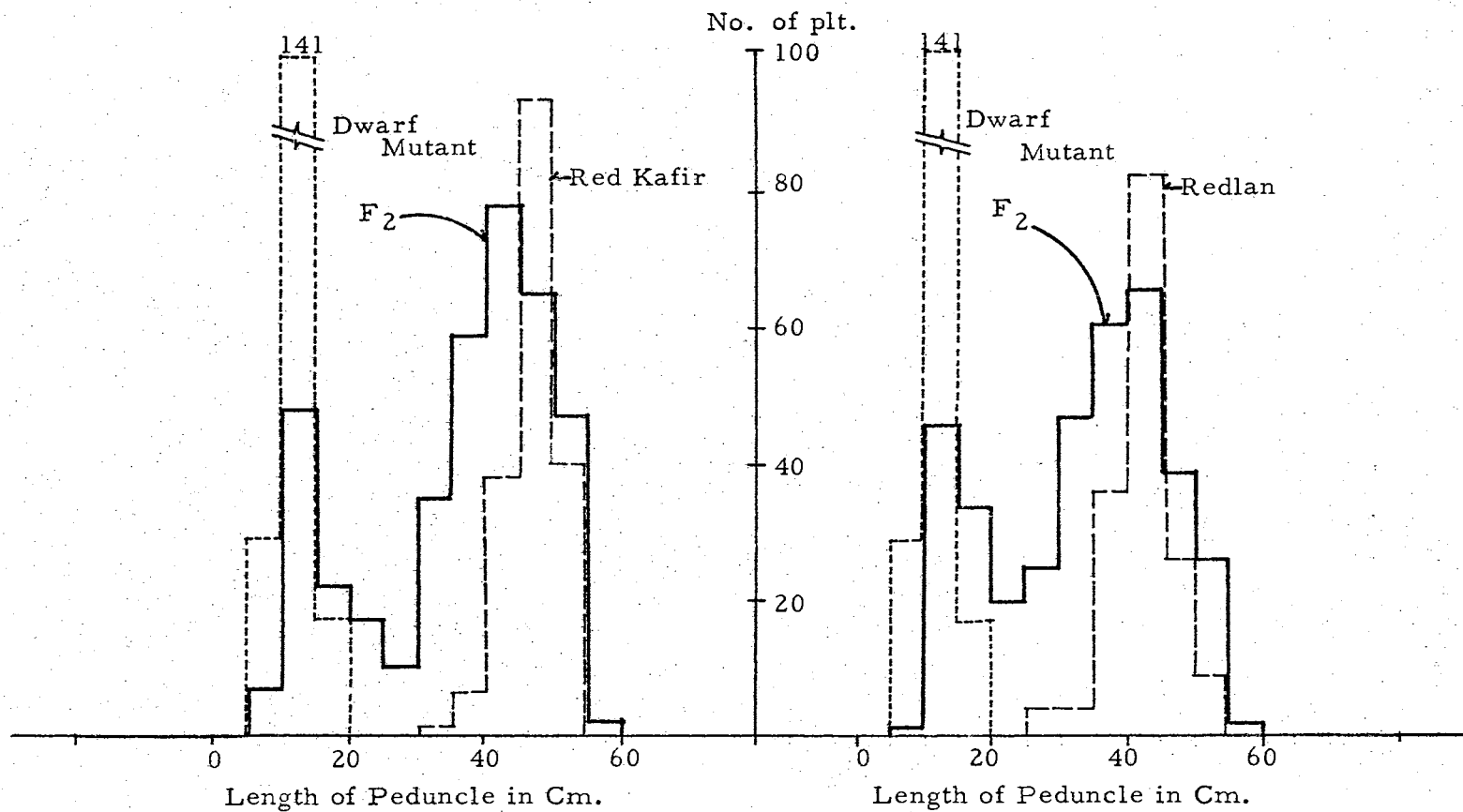


Figure 11. Histogram of the Peduncle Length of the Parents and F₂ Population for the Cross of Red Kafir and Dwarf Mutant.

Figure 12. Histogram of the Peduncle Length of the Parents and F₂ Population for the Cross of Redlan and Dwarf Mutant.

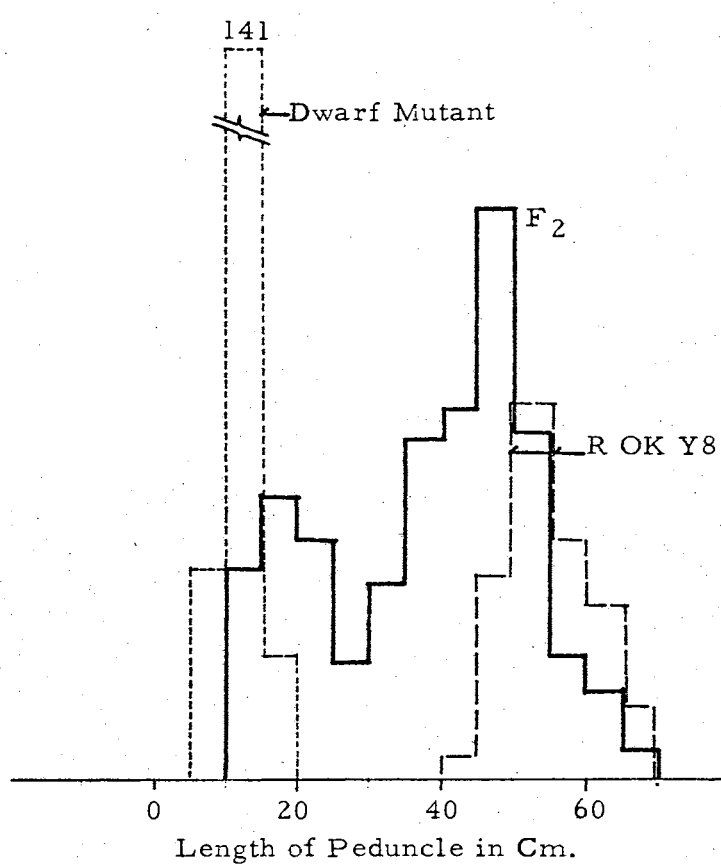


Figure 13. Histogram of the Peduncle Length of the Parents and F₂ Population for the Cross of R OK Y8 and Dwarf Mutant.

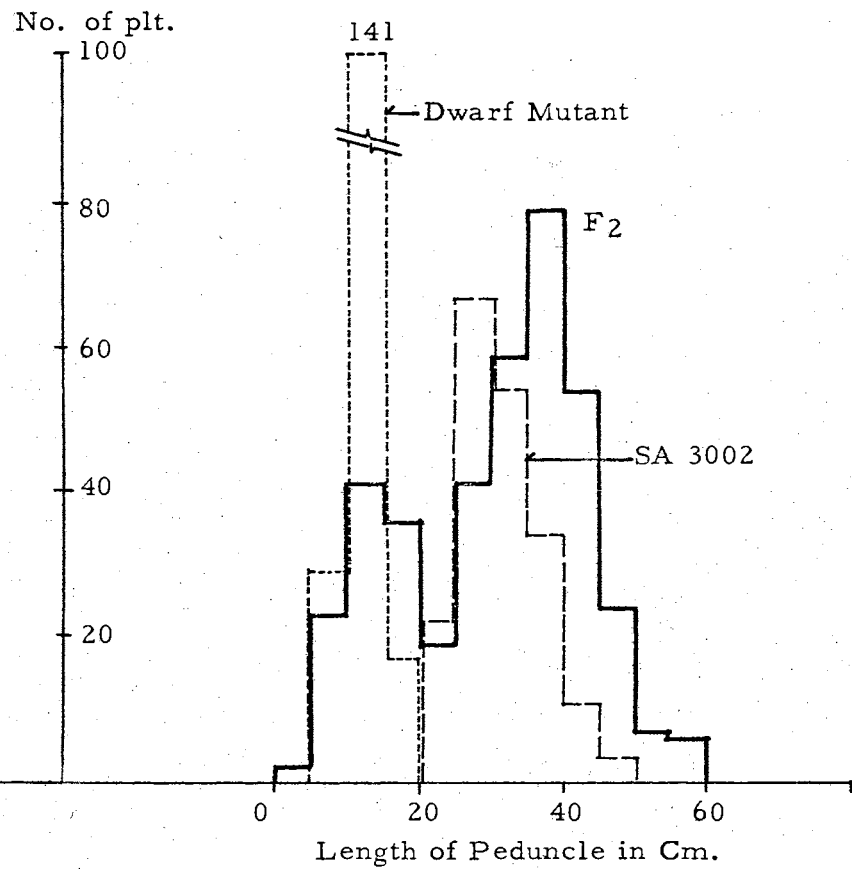


Figure 14. Histogram of the Peduncle Length of the Parents and F₂ Population for the Cross of SA 3002 and Dwarf Mutant.

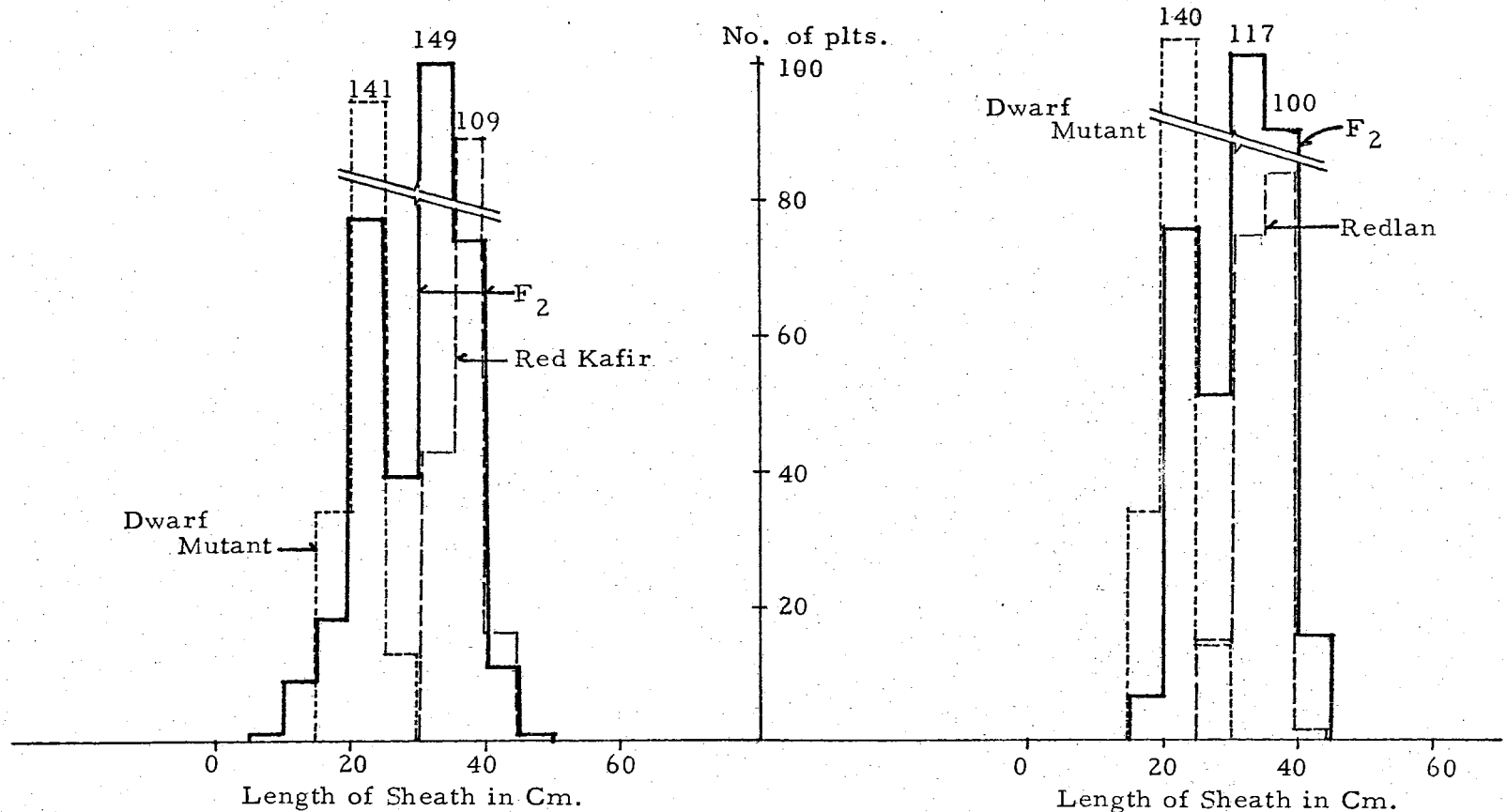


Figure 15. Histogram of the Sheath Length of the Parents and F₂ Population for the Cross of Red Kafir and Dwarf Mutant.

Figure 16. Histogram of the Sheath Length of the Parents and F₂ Population for the Cross of Red Kafir and Dwarf Mutant.

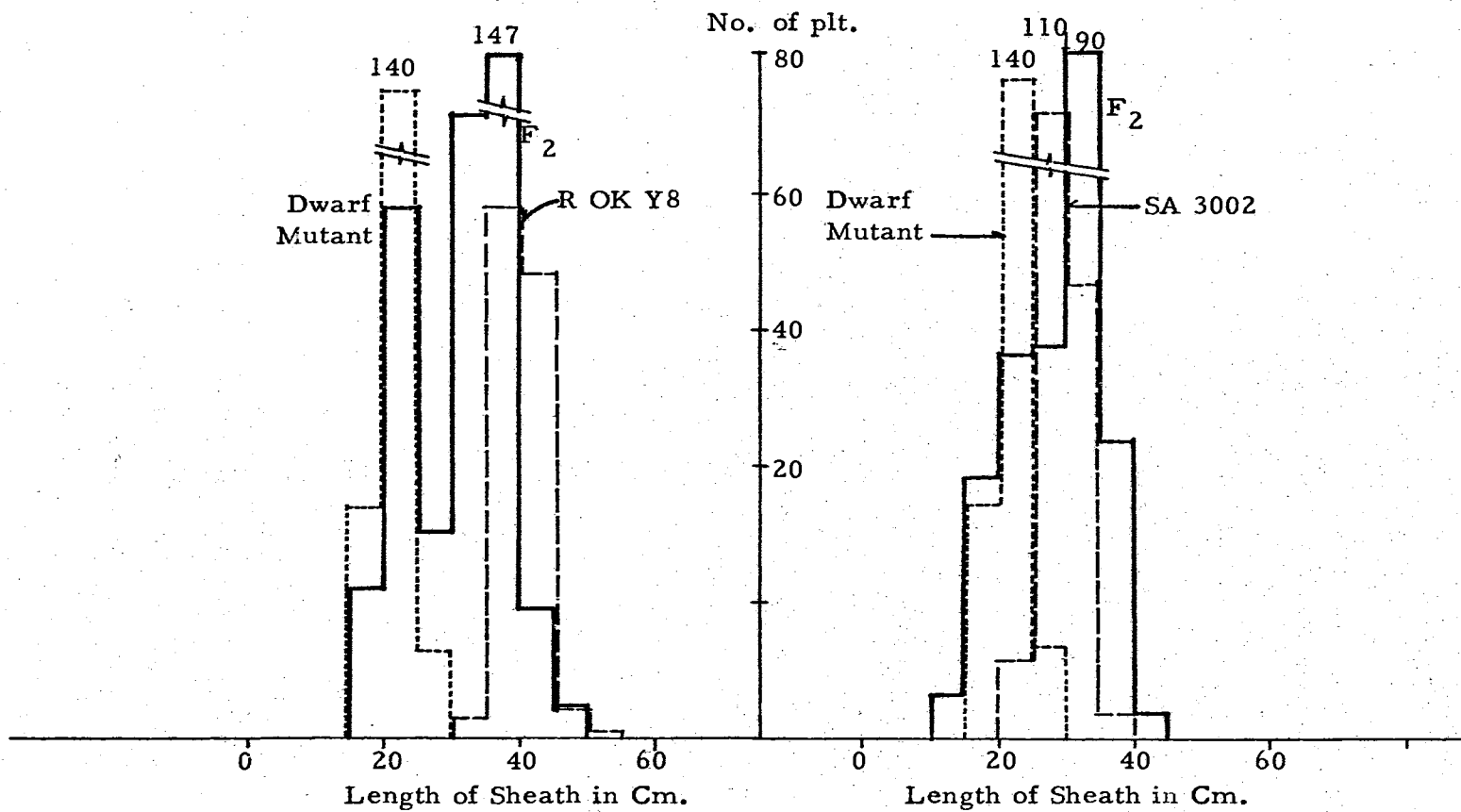


Figure 17. Histogram of the Sheath Length of the Parents and F₂ Population for the Cross of R OK Y8 and Dwarf Mutant.

Figure 18. Histogram of the Sheath Length of the Parent and F₂ Population for the Cross of SA 3002 and Dwarf Mutant.

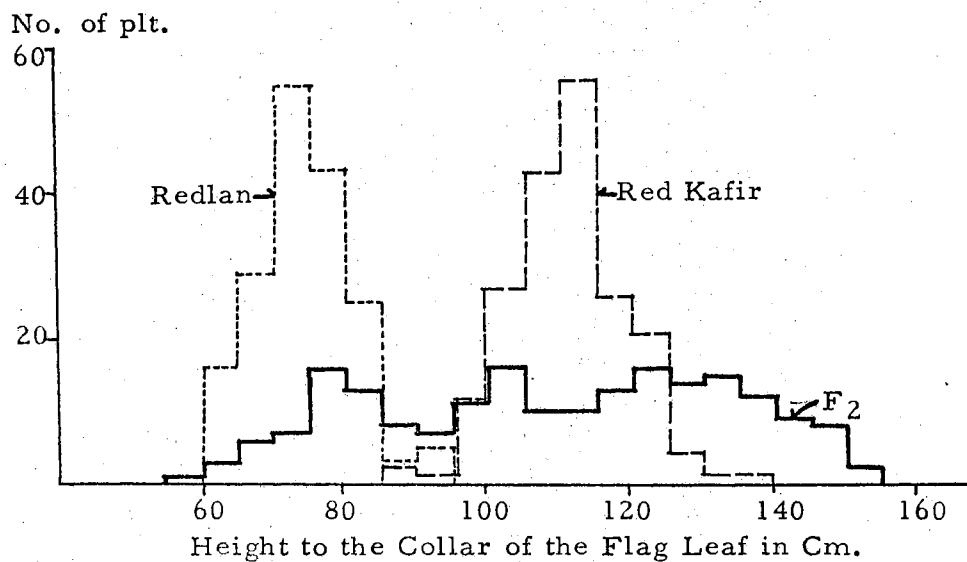


Figure 19. Histogram of Height to the Collar of the Flag Leaf of Parents and F₂ Population for the Cross of Red Kafir and Redlan.

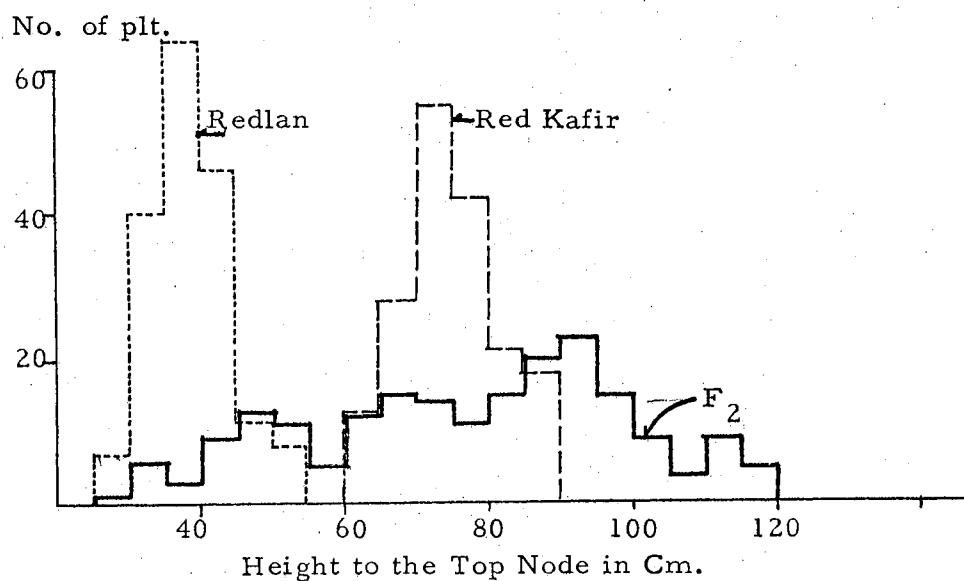


Figure 20. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of Red Kafir and Redlan.

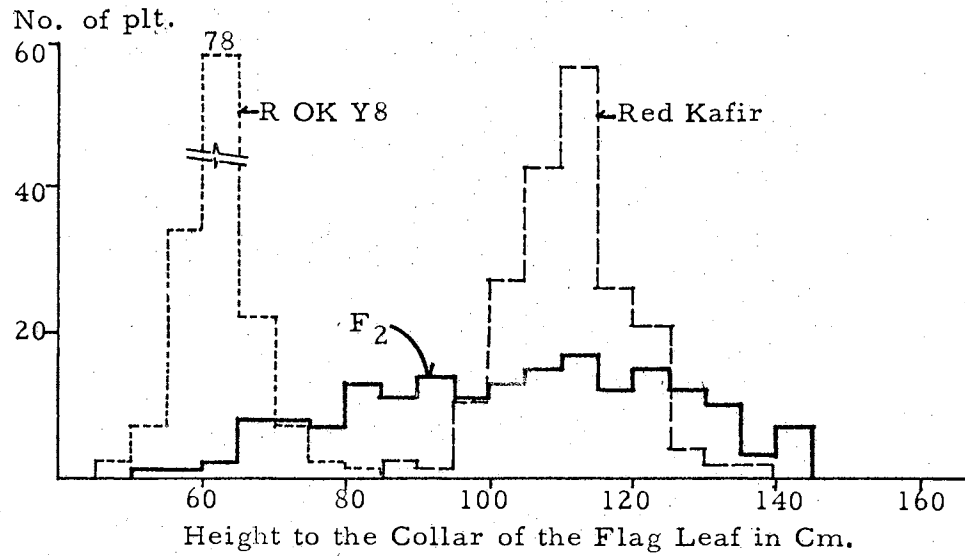


Figure 21. Histogram of Height to the Collar of the Flag Leaf of the Parents and F₂ Population for the Cross of Red Kafir and R OK Y8.

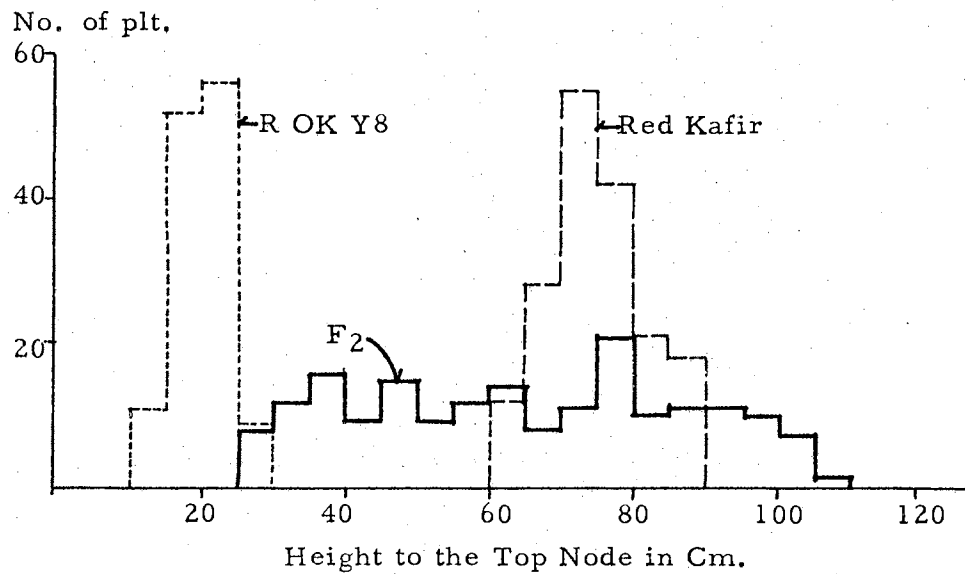


Figure 22. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of Red Kafir and R OK Y8.

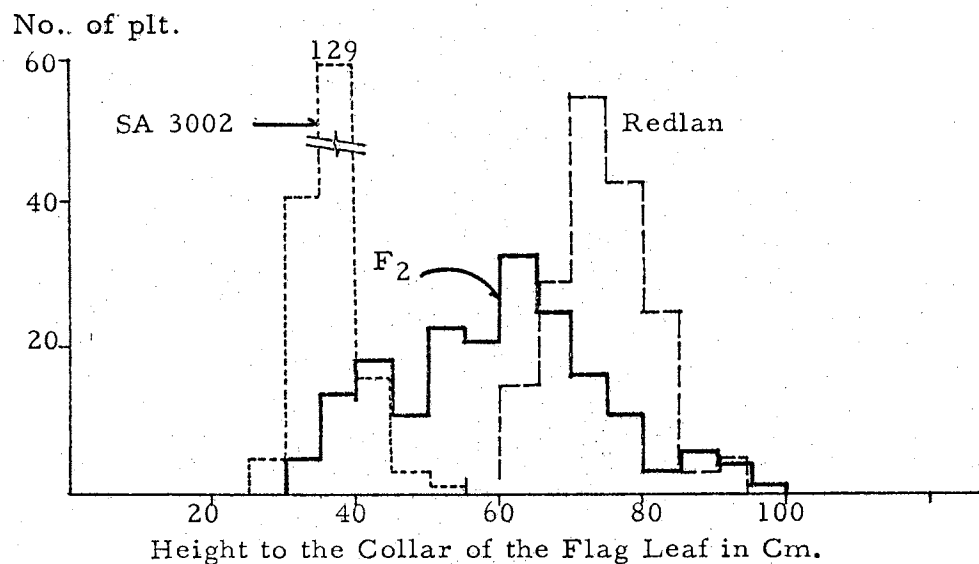


Figure 23. Histogram of Height to the Collar of the Flag Leaf of the Parents and F₂ Population for the Cross of Redlan and SA 3002.

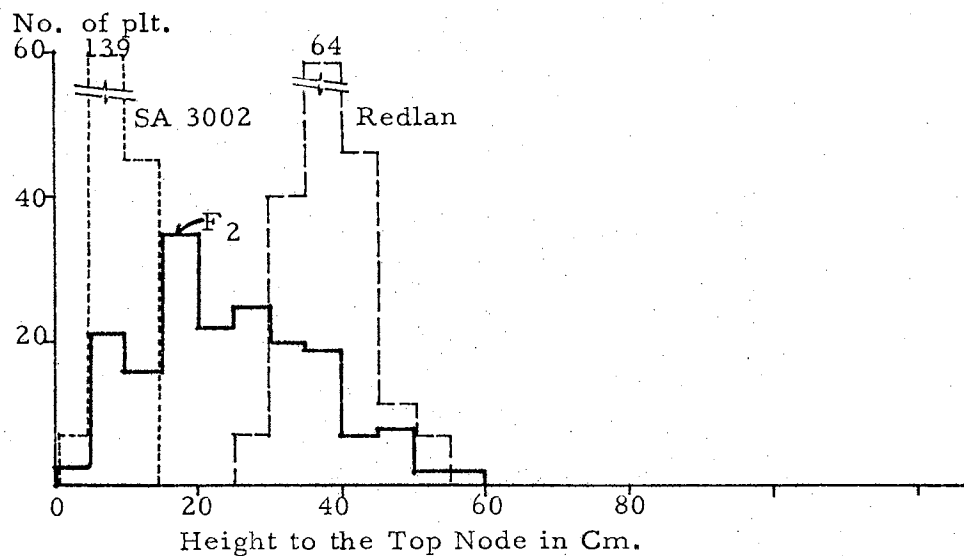


Figure 24. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of Redlan and SA 3002.

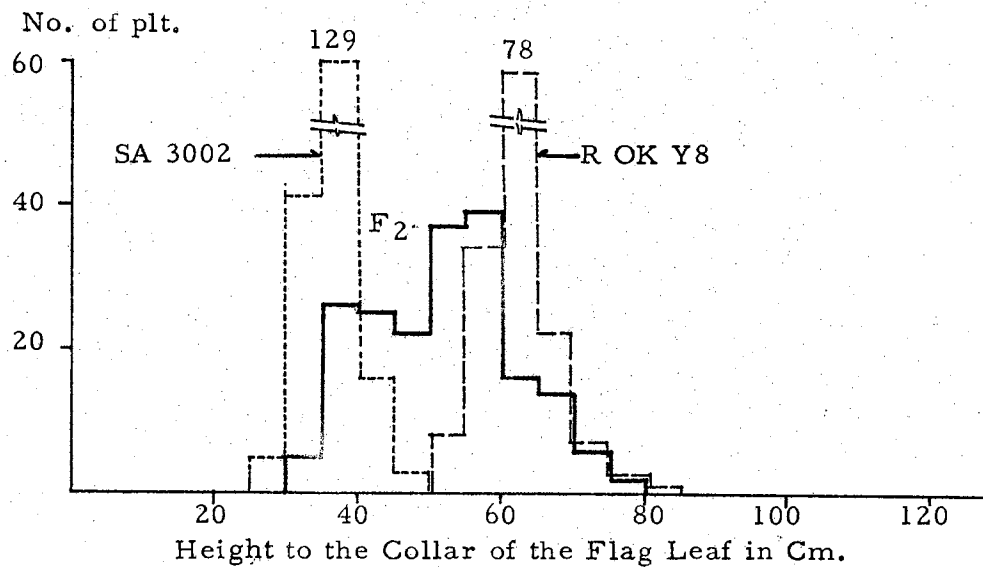


Figure 25. Histogram of Height to the Collar of the Flag Leaf of the Parents and F₂ Population of the Cross Between R OK Y8 and SA 3002.

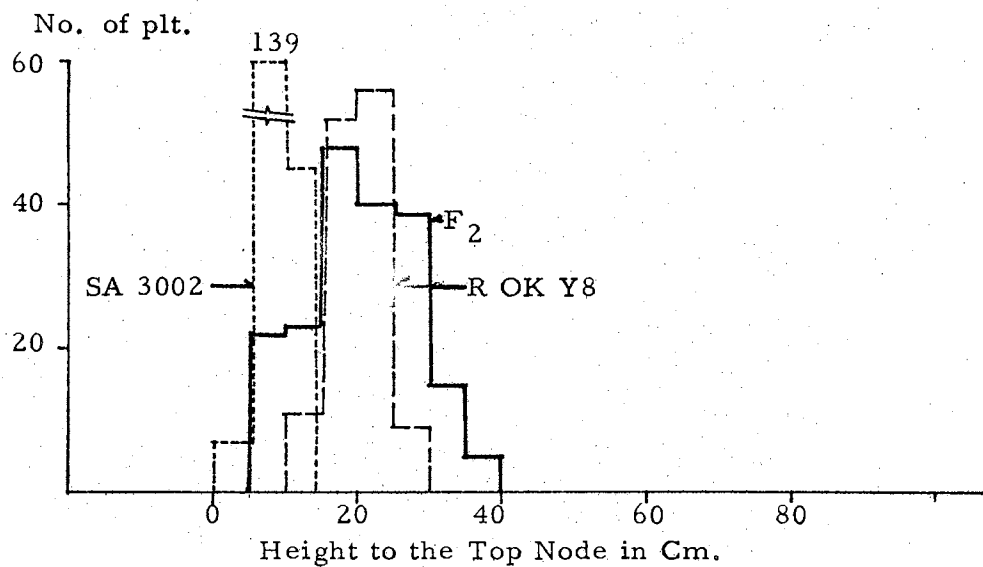


Figure 26. Histogram of Height to the Top Node of the Parents and F₂ Population for the Cross of R OK Y8 and SA 3002.

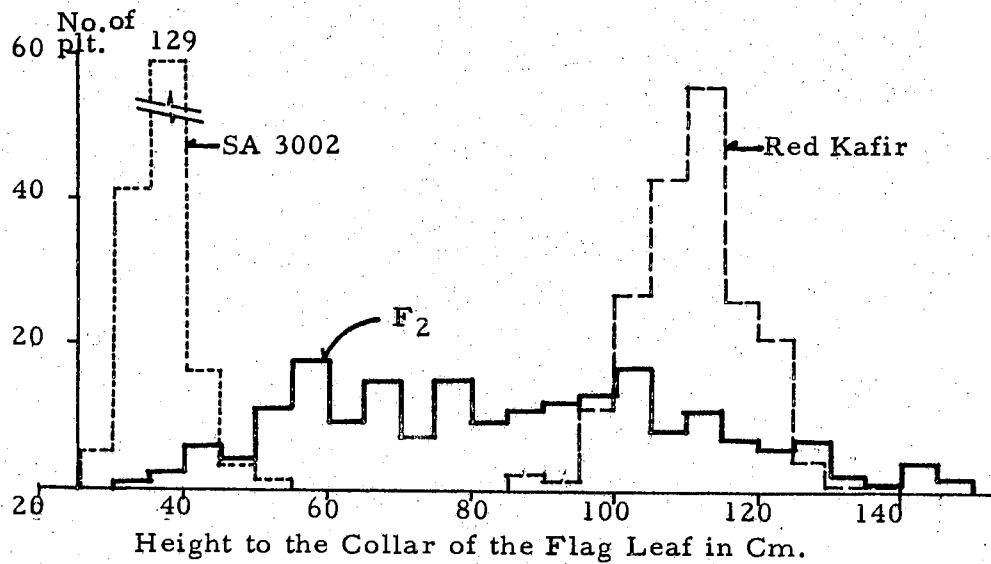


Figure 27. Histogram of Height to the Collar of the Flag Leaf of the Parents and F_2 Populations for the Cross of Red Kafir and SA 3002.

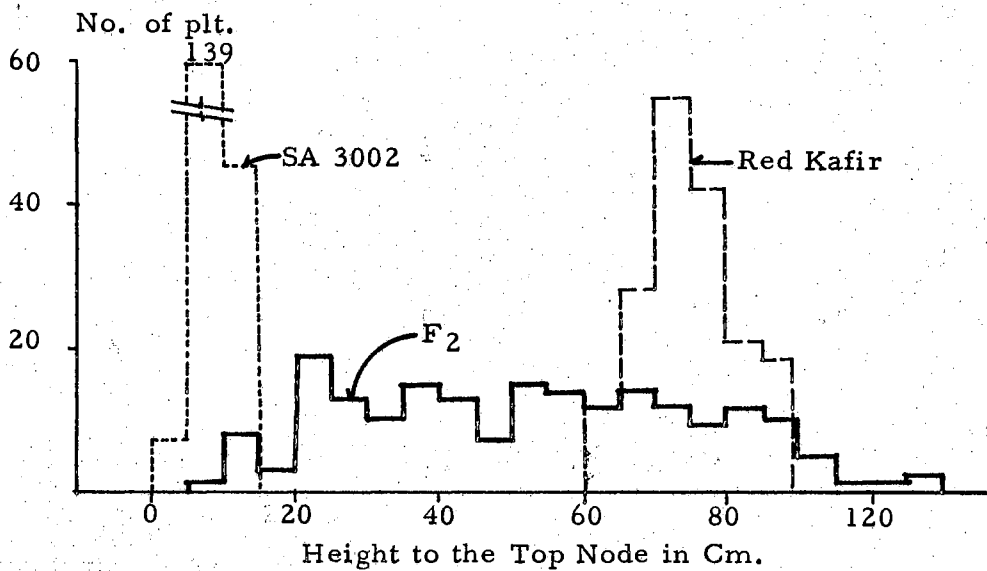


Figure 28. Histogram of Height to the Top Node of the Parents and F_2 Population for the Cross of Red Kafir and SA 3002.

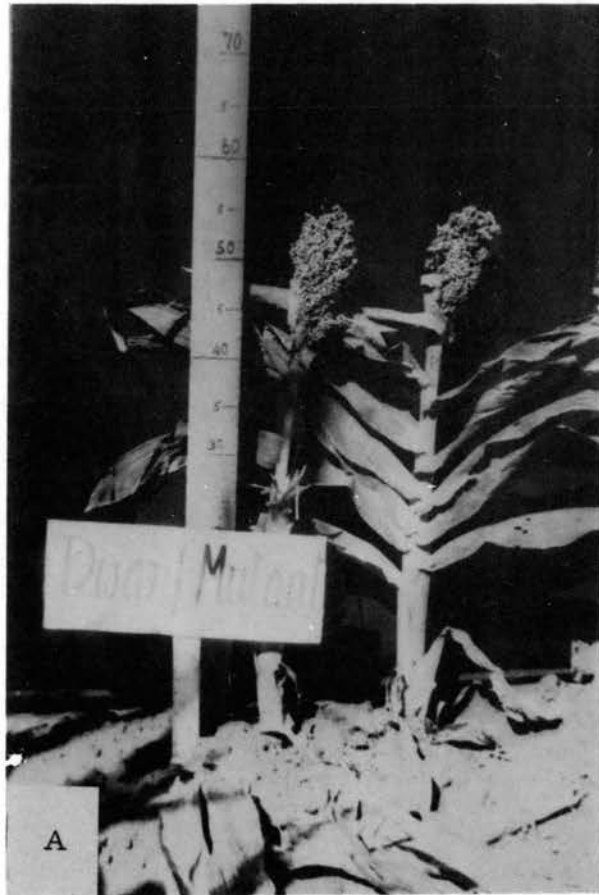


Figure 29. Pictures of (A) the Dwarf Mutant and (B) Red Kafir, two dwarf parents.



Figure 30. Pictures of (A) Redlan and (B) R OK Y8, three dwarf parents.

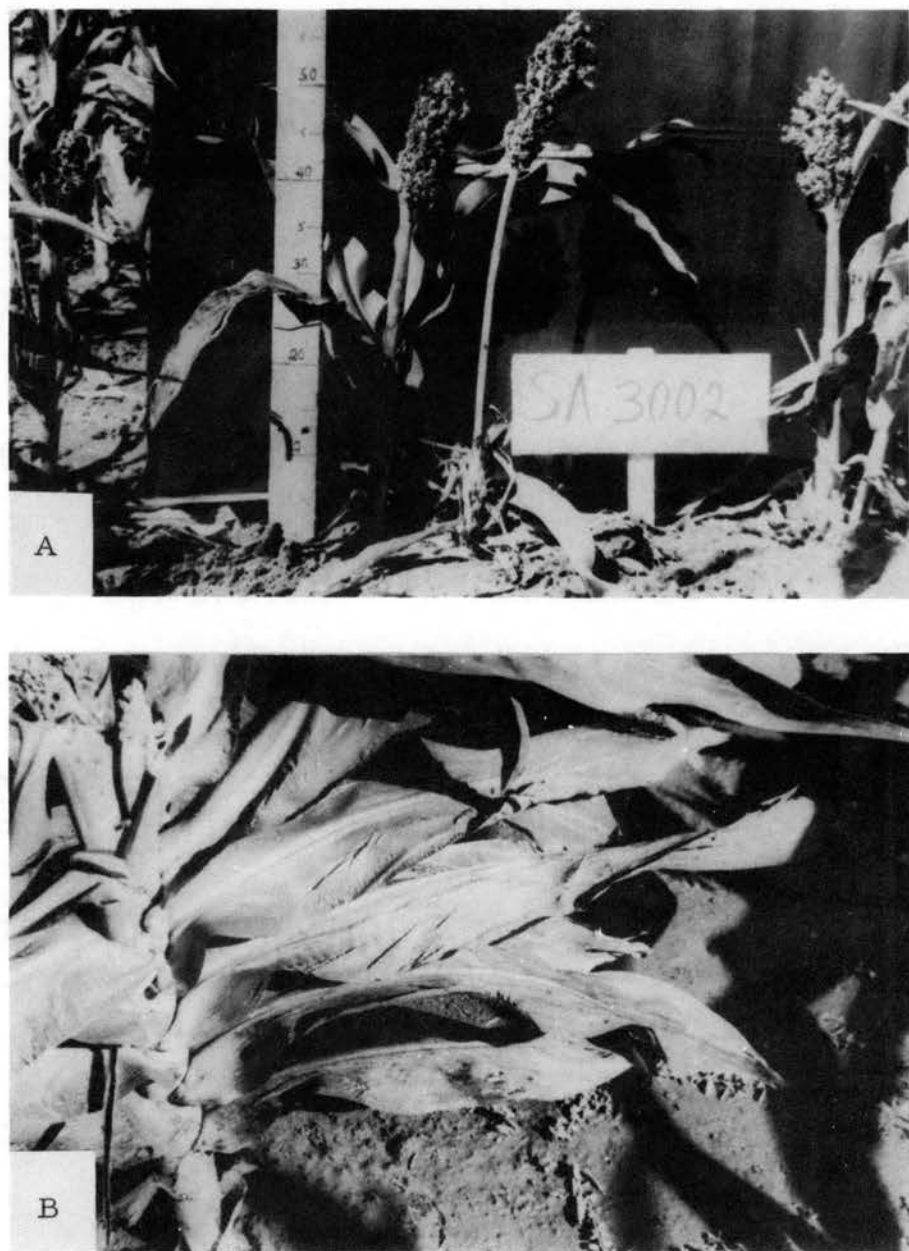


Figure 31. Pictures of (A) SA 3002, four dwarf parents and (B) Crinkle leaves of Dwarf Mutant.

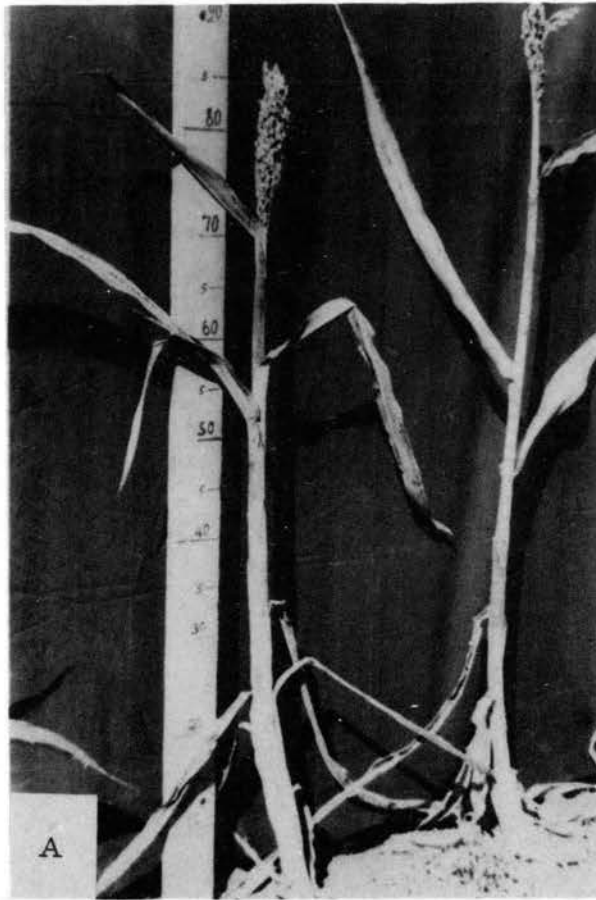


Figure 32. Pictures of (A) Sword leaves, and (B) Variation in height of the F_3 plants in the cross SA 3002 and Dwarf Mutant.

VITA

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Arwooth Na Lampang

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