A STUDY OF THE INHERITANCE OF RESISTANCE IN SORGHUMS TO THE ROOT, CROWN, AND SHOOT ROT DISEASE

by

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B. S., Kansas State College
of Agriculture and Applied Science, 1933

A THESIS

submitted in partial fulfillment of the

requirements for the degree of

MASTER OF SCIENCE

KANSAS STATE COLLEGE
OF AGRICULTURE AND APPLIED SCIENCE

1935

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INTRODUCTION

In the southwestern states, where grain sorghums are grown extensively, a relatively new disease, the root, crown, and shoot rot of milo, called the "milo disease," is seriously affecting the yield of milos in certain areas. This disease is of recent origin. It has spread each year in localities where established,and in the more severe cases, it has caused complete failure of the crop and is becoming a serious, limiting factor in milo production. It usually produces the greatest loss on land which is continuously cropped to milo. A short-time rotation will not eliminate it from the soil.

The disease is peculiar in that it attacks milos more than any other group of grain or forage sorghums. The kafirs, feteritas, most sorgos, and Sudan grass are apparently immune.

In view of these facts and recognizing in resistant varieties a possible and promising method of combating this disease, a method of study was outlined to determine, if possible, the Mendelian basis on which this disease is inherited in crosses involving milo as one of the parents. The ultimate object of the investigations on this disease is the production of resistant varieties of grain sorghums through hybridization and selection.

The lack of knowledge concerning the causal organism or entity, the identity of which is unknown, is one of the difficulties encountered in the study of this disease. Attempts by various workers to isolate the causal entity have resulted in obtaining various species of both Fusarium and Pythium. Dr. Charlotte Elliott, of the U. S. Dept. of Agriculture, and Dr. C. L. Lefebvre, of the Kansas Agricultural Experiment Station, have found certain species of Pythium to be constantly associated with the diseased roots.

It has been rather definitely established, according to unpublished data by Prof. L. E. Melchers, of Kansas State College, and Dr. Charlotte Elliott, that the entity is soil borne and may live over in the soil for a number of years, even though the host is not grown during that time. Samples of infested soil kept both moist and dry and subjected to the high summer temperatures of the greenhouse were still capable of producing the disease after two years.

REVIEW OF LITERATURE

An attempt has been made to review all the literature pertaining to this disease. There are comparatively few publications since this trouble is of relatively recent origin.

Pammel, King, and Seal (1916) describe a disease on sorghums which they attributed to a Fusarium. It is of interest as specimens were received at the Iowa station from Garden City, Kansas, in 1914.

In some respects this disease is similar to the milo disease, but in all probability is not the same. Sorghum plants attacked by this Fusarium break at the joints which are covered with abundant spores, and diseased heads show the fungus in the seed. Studies in Kansas have shown that the milo disease is not transmitted by means of the seed.

Elliott, Wagner, and Melchers (1932) state that susceptible varieties grown on soil that has produced the disease previously have shown 100 percent diseased plants, while resistant varieties in the same soil have shown few or no disease symptoms. The plants of susceptible varieties reached a height of 10-12 inches before symptoms of the disease were apparent, but the plants remained stunted and eventually died, producing only an occasional, small head. A dark red discoloration of the central cylinder of the roots and the interior of the crown accompanied the yellowing and drying of the aerial parts. These workers made several preliminary tests which indicated that the causal organism may be spread by infested soil or diseased roots and that susceptible plants grown on sterilized soil remained healthy. Soil treatments with potash, phosphate, nitrates, and complete fertilizers have shown no indications that the disease symptoms are due to soil deficiencies. These investigators were not able to demonstrate the pathogenicity of any of the strains of Fusaria or bacteria that were isolated. All varieties of milo and several hybrid derivatives of milo were shown to be very susceptible.

Morgan (1933) described the milo disease as it occurs at Garden City. He observed that in plants infected late in the growing season seed production was not prevented. He found that crop rotation apparently had little effect as a control measure.

Melchers and Parker (1934) report that the disease caused the greatest loss on land continuously cropped to milo, but a rotation of three years did not eliminate it from the soil. Kafir, feterita, most sweet sorghums, and Sudan grass are immune. On infested soil plants become infected about 5 to 6 weeks after planting, or when 10-12 inches tall.

Harris and Goss (1934) describe an abnormal condition of young sorghum plants in which the seedlings showed a reddening of the primary roots and of the mesocotyl. This malady apparently has no connection with the "milo disease," although some symptoms seem to be similar.

Myers (1934) studied the influence of soil treatments on the disease and obtained evidence that nitrogen when applied at a fairly heavy rate aids in prolonging the life of milo plants grown on infested soil. It is not fully effective, however, in overcoming the pathological condition. He suggests that the causative organism may influence the nitrogen nutrition of the plant. No other soil treatment tried prolonged the life of the milo plants.

Morgan and Wagner (1935) found that the growth of susceptible Dwarf Yellow milo plants had practically ceased at the time external symptoms of the disease were evident, during the fifth or sixth week after emergence. No differences in the growth rates of Dwarf Yellow milo or resistant Dwarf Yellow milo were observed when both were grown on clean soil.

Wagner (1935) has summarized the results of his tests of the reaction of varieties, selections, and hybrids of sorghums to the milo disease as grown in the milo disease nursery at the Garden City station. He has made several selections of milo, Wheatland, Beaver, and Day milo which are resistant, some of which will probably prove of great value to the sorghum industry of Kansas and other regions.

MATERIALS AND METHODS

During the winter of 1932-1933, C. A. Wismer, graduate assistant in botany, made crosses between Club kafir and resistant and susceptible selections of Dwarf Yellow milo, and between the resistant and susceptible strains of Dwarf Yellow milo. The resistant selection of Dwarf Yellow milo was made by F. A. Wagner, Superintendent of the Garden City Experiment Station. This strain has been given Kansas Botany No. 34342. Club Selection, Kansas Botany No. 33327, came from the Fort Hays Experiment Station in 1932. Seed of the susceptible strain of Dwarf Yellow milo was obtained from the Agronomy Department and is the common Dwarf Yellow milo C.I. 332.

Seed of susceptible Beaver C.I. 871, resistant Beaver C.I. 871 G.C. Sel. 31-2-1, susceptible Wheatland C.I. 918 G.C. Sel. 302-6-2(S)-b(S), and resistant Wheatland C.I. 918 G.C. Sel. 302-8-6(S)-b(S) was secured from F. A. Wagner of Garden City. Dr. John H. Parker furnished seed of White kaoliang C.I. 792 and Sharon kafir, in order to determine the behavior of these varieties when planted on infested soil.

Crosses were made by A. E. Lowe, graduate assistant in agronomy, and the writer, during the winter of 1933-1934, between the resistant selection of Dwarf Yellow milo and the following varieties which were furnished by Dr. John H. Parker: Beaver Row 382, Wheatland Row 368, kafir x milo No. 27317, Kansas Orange x Dwarf Yellow milo Row 381, Custer Row 364, and Early Kalo Row 325. These varieties were chosen for crossing, not only as a means of studying the inheritance of resistance, but also because of the possibility of producing a variety of agricultural value. The F_1 generation and the parents were grown in the botany experimental field in 1934 on clean soil.

The infested soil used in this study was obtained from the milo disease project, field 21, of the Garden City Experiment Station. The same soil was used again in 1934-1935 with the addition of five bags of infested soil from the original source.

The soil was thoroughly screened and mixed and filled in flats to a depth of approximately 2.5 inches. Each flat was divided longitudinally into 8 rows, 1.5 inches apart, and transversely into 22 rows one inch apart. By planting at each intersection, it was possible to grow 176 seedlings in each flat.

During the winter of 1933-1934 the available space in the greenhouse permitted the planting of 13 flats of F_2 material at each sowing. Three flats were divided into three parts each and planted with the seed of the parents, i.e., susceptible and resistant Dwarf Yellow milo and Club.

The greenhouse temperature varied between 75-85° F., and sufficient water was supplied so that optimum conditions prevailed for rapid growth of the plants.

During the winter of 1934-1935, the available space permitted the planting of 28 flats at each sowing. Plantings in each flat were arranged in a manner similar to that of the previous year. Only 6 rows however, were planted with hybrid seed, thus reducing the possible number of seedlings in one flat to 132. The two outside rows of each flat were planted with the parents of the cross, hence flats containing only parental material were not necessary. This arrangement eliminated any possibility that the parents and hybrids were grown under different environmental conditions.

No parents were included in the last planting of F_3 plants as it was thought that a sufficient number had been grown to determine their reaction to the disease.

The first year (1933-1934) 48 flats were planted with F_2 hybrid and parental seed. Data were collected on a total of 4613 hybrid seedlings, representing three crosses and including reciprocals. In addition 9 flats, representing a total of 971 seedlings of different varieties or selections, were tested in the agronomy greenhouse. Half of these were kept in the north section of the greenhouse, which had a temperature range of approximately 65-70° F. The remainder were kept in the south section with a temperature range of approximately 75-80° F. It was thought that this arrangement would show whether a temperature difference of 10 degrees would have any effect upon the manifestation of the disease. It was also desired to determine the reaction of these varieties and selections to the disease.

The second year (1934-1935) readings were taken on 25 flats containing F_2 generation plants and on 29 flats containing F_3 generation plants. The studies of this material include a total of 2306 F_3 seedlings and 1963 F_2 seedlings.

Final notes were not taken until the plants of the susceptible parent had been killed, and it was thought that sufficient time had elapsed to permit an accurate classification. The plants were divided into three classes: dead (susceptible), apparently diseased but not dead (intermediate), and healthy (resistant). Plants falling in the first class could easily be determined by observation, but a more careful examination was necessary to classify the plants in the other two classes. The three methods by which this was done are (1) the unthrifty appearance of the plant, (2) an examination of the roots, noting the dead roots and the presence of red coloring in the central cylinder of infected roots, and (3) by splitting the crown and subcrown internode of questionable plants. The presence of a deep reddish brown color in the crown and subcrown was considered as indicating that infection had taken place. This condition was never found in healthy plants, hence those showing none of the above symptoms were classified as resistant. In practically all cases the diseased plants were smaller than the healthy plants and one or two of the lower leaves and the tips of the remaining leaves were dried. The size of the plant was not, however, an indication of disease, as some small plants which were evidently stunted by some other cause seemed to be entirely free from infection. Some of the roots of the resistant plants showed a pinkish color, but the color did not develop further and the roots appeared healthy. Roots coming from the discolored portion of the crown of susceptible plants were almost always dead or dying and were dark red. The observation was made several times during the course of the experiments that the red coloring first appeared in the central cylinder, and as the root died, the color spread through the remainder of the root. The intermediate plants were kept alive by one or more new roots emerging from above the discolored area. These plants were not so vigorous as the resistant plants, and by permitting the last planting of 1934 to grow for a longer period, it was shown that most of them eventually die. This fact seems to support the grouping of diseased and intermediate plants as one class for contrast with the healthy or resistant plants. It appears likely that plants classed as intermediate in the greenhouse tests may often reach maturity under field conditions, producing small, poorly filled heads.

The first planting was made in the greenhouse on November 11, 1933. The seed was dusted with copper carbonate and planted in soil in the flats about one fourth of an inch deep. The flats were soaked in water at the time of planting. They were watered from the top whenever necessary during the course of the tests.

Germination was very uneven in most of the flats, and after three weeks they were replanted with seed previously germinated in the laboratory. Dusting with Semesan Jr. was found to give better results than dusting with copper carbonate. Both of these seed treatments gave better stands than the untreated seed. The advantage in using Semesan Jr. lies in its fungicidal action toward molds and fungi present on the seed, which are usually saprophytic but may become parasitic under some conditions. Semesan Jr. dust did not seem to influence the reaction of the plants to the milo disease.

Disease symptoms became evident the latter part of December and advanced rapidly during the next two weeks, permitting final notes to be taken about six weeks after planting.

The first indication of infection in the seedling stage is the limp, ashy-grey condition of the leaves, which appear as if they had been scalded. A few days later an orange tinge around the outer margin of the first leaf may be detected. This color gradually advances over the entire plant, the last leaf to be developed being the last one to lose its normal green color and die. The leaves dry up and die a short time after they turn yellow. Finally, the plants turn a light brown color but remain upright for some time, not falling over as they do when killed by the damping-off fungus. Final notes were taken on this planting the latter part of January, 1934.

Several pictures were taken of flats in this planting to show the typical differences between susceptible and resistant plants. A flat of parental varieties, Club, Dwarf Yellow milo, and resistant Dwarf Yellow milo is shown in Plate I. A flat containing resistant and susceptible selections of Wheatland is shown in Plate II. The clear-cut differences between resistant and susceptible plants shown in these plates are typical of the reaction of susceptible and resistant plants to milo disease.

F_2 individuals of the cross resistant Dwarf Yellow milo x Dwarf Yellow milo are shown in Plate III. The segregation shown here is typical of that which occurs in crosses between resistant and susceptible varieties of sorghum.

The same plants as in Plate III are shown in Plate IV after they have been removed from the flat and classified. The relative growth produced by a group of 60 susceptible plants, 15 intermediate plants, and 20 resistant plants is clearly shown. The resistant plants, although numbering only 5 more than the intermediate plants, have produced almost twice as much growth. They also show a great deal more vigor and fewer withered leaf tips.

In a second planting, a pronounced red color developed in all the plants when they were only a few inches tall. This color was noted especially in crosses having milo as a parent. Ammonium sulphate was applied at the rate of 300 pounds per acre, or about 6 grams per flat. This was scattered on the surface and then washed into the soil. The plants developed normal green color soon after this treatment, which apparently did not interfere with infection. Final notes on the second planting were taken the last week in March, 1934.

The flats were prepared for a third planting, and a nitrogenous fertilizer was applied. Final notes on this planting were not taken until June, 1934, in order to determine if the plants classified as intermediate would die if left for a longer time. The number of plants placed in the intermediate class was smaller than usual, and the number of dead plants was larger, indicating that at least a large percentage of the plants classed as intermediate were susceptible, though not so susceptible as those which died earlier and which were classed as susceptible. These observations indicate that it is logical to combine the intermediate and susceptible classes and to contrast this group with the resistant class.

EXPERIMENTAL RESULTS

Various groupings were made of the data obtained in seeking a satisfactory Mendelian explanation of the results. It has been pointed out that the diseased (intermediate) and dead (susceptible) plants could be considered as one group for comparison with the healthy (resistant) plants. This grouping seems to be more in accord with observations made than one contrasting the dead plants with the intermediate and resistant plants. The data fit the simple 3:1 ratio fairly closely in most cases. The observed numbers of susceptible and intermediate plants and of resistant plants closely approach the calculated numbers in nearlyall cases. Deviations in the ratios are to be expected because of injuries by sow bugs, damping-off, poor germination, and the variation due to chance.

Studies of F_2 Populations, 1933-1934

Detailed data collected for each cross studied are shown in table 1. No plants of the cross, Club x resistant Dwarf Yellow milo, and its reciprocal, resistant Dwarf Yellow milo x Club, showed any indication of susceptibility but remained healthy and vigorous. In the first series of plantings, 21 F_2 seedlings of the cross, Club x resistant Dwarf Yellow milo, were recorded as intermediate, probably because of inexpeience in classifying the plants and because of the previously mentioned pink color which has occasionally been found on the roots of healthy plants. Crosses between Club and Dwarf Yellow milo and between the resistant and susceptible selections of Dwarf Yellow milo show rather clear-cut segregation into the three classes, resistant, intermediate, and susceptible. These results indicate that no factor responsible for susceptibility to the milo disease is carried by either Club or resistant Dwarf Yellow milo.

Table 1.--Reaction of F_2 populations and parental varieties to the milo disease, as tested in the greenhouse, Manhattan, Kansas, 1933-1934.

Name	Observed number of plants: Total	Dead (Susc.)	Inter-mediate (Susc.)	Total Susc.	Resist-ant	Observed ratio	Calculated (3:1) number of plants: Susc.	Res.	Devia-tion from calc. number	PE	Dev. / PE
Club	133	0	0	0	133						
Dwarf Yellow milo	110	101	8	109	1						
Res. Dwarf Yellow milo	123	0	6	6	117						
Club x Res. Dwarf Yellow milo	123	0	21	21	102						
Res. Dwarf Yellow milo x Club	117	0	0	0	117						
Club x Dwarf Yellow milo	247	88	92	180	67	2.68:1	185.25	61.75	5.25	±4.59	1.14
Dwarf Yellow milo x Res. Dwarf Yellow milo	238	135	38	173	65	2.66:1	178.5	59.5	5.50	±4.50	1.22
Res. Dwarf Yellow milo x Dwarf Yellow milo	472	273	92	365	107	3.41:1	354.0	118.0	11.00	±6.41	1.71
Club	114	0	0	0	114						
Dwarf Yellow milo	161	141	20	161	0						
Res. Dwarf Yellow milo	122	0	1	1	121						
Club x Res. Dwarf Yellow milo	145	0	0	0	145						
Res. Dwarf Yellow milo x Club	293	0	0	0	293						
Club x Dwarf Yellow milo	342	100	144	244	98	2.5 :1	256.5	85.5	12.50	±5.40	2.31
Dwarf Yellow milo x Res. Dwarf Yellow milo	200	70	69	139	61	2.3 :1	150.0	50.0	11.00	±4.13	2.66
Res. Dwarf Yellow milo x Dwarf Yellow milo	566	216	163	379	187	2.02:1	424.5	141.5	45.50	±6.95	6.54
Club	143	0	0	0	143						
Dwarf Yellow milo	155	155	0	155	0						
Res. Dwarf Yellow milo	147	1	0	1	146						
Club x Res. Dwarf Yellow milo	140	0	0	0	140						
Res. Dwarf Yellow milo x Club	387	0	0	0	387						
Club x Dwarf Yellow milo	417	213	91	304	113	2.7 :1	312.75	104.25	8.75	±5.96	1.47
Dwarf Yellow milo x Res. Dwarf Yellow milo	439	278	40	318	121	2.63:1	329.25	109.75	11.25	±6.12	1.84
Res. Dwarf Yellow milo x Dwarf Yellow milo	487	342	37	379	108	3.5 :1	365.25	121.75	13.75	±6.44	2.13

Observed ratios for the three plantings of the cross, Club x Dwarf Yellow milo, were 2.68:1, 2.5:1, and 2.7:1. The deviation of the observed number of plants from the calculated number is in each case less than 3 times the probable error. This indicates that the variation is no greater than would be expected due to chance. Ratios of 2.66:1, 2.3:1, and 2.63:1 were obtained for the cross, Dwarf Yellow milo x resistant Dwarf Yellow milo. The deviation from the calculated number of plants is within the limits of variation expected on the basis of chance. In the third cross, resistant Dwarf Yellow milo x Dwarf Yellow milo, the ratios were 3.4:1, 2.02:1, and 3.5:1, respectively. The deviation from the calculated number of plants in the second planting of this cross was more than 2 times that expected on the basis of chance variation. No satisfactory explanation can be given for this wide deviation. It may have been due to failure to distinguish between the intermediate and resistant plants. By totaling the results for the three experiments, a 2.6:1 ratio is obtained. Data on the reaction to milo disease of F_2 plants of each cross and of parental varieties grown during the winter of 1933-1934 are summarized in table 2.

Table 2.--Summary of the reaction of F_2 plants and parental varieties to the milo disease as tested in the greenhouse, Manhattan, Kansas, 1933-1934.

Name	Observed number of plants: Total	Observed number of plants: Susc.	Observed number of plants: Res.	Observed ratio	Calculated (3:1) number of plants: Susc.	Calculated (3:1) number of plants: Res.	Deviation from calc. number	PE	Dev./PE
Dwarf Yellow milo	426	425	1						
Resistant Dwarf Yellow milo	392	8	384						
Club	390	0	390						
Club x Dwarf Yellow milo	1006	728	278	2.62:1	754.50	251.50	26.5	± 9.26	2.86
Club x Res. Dwarf Yellow milo	1205	0	1205						
Dwarf Yellow milo x Res. Dwarf Yellow milo	877	630	247	2.55:1	657.75	219.25	27.75	± 8.65	3.21
Res. Dwarf Yellow milo x Dwarf Yellow milo	1525	1102	423	2.60:1	1143.75	381.25	41.75	±11.40	3.66

The cross, Club x Dwarf Yellow milo, gave a ratio of 2.6:1. The observed number of plants was 728 susceptible and intermediate to 278 resistant, as compared with the calculated number of 754.5:251.5 $\pm$ 9.26. The goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, was 2.86. In the cross, Dwarf Yellow milo x resistant Dwarf Yellow milo, the observed number of plants was 630 susceptible to 247 resistant and the calculated number 657.75:219.25 $\pm$ 8.65. The goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, was 3.21, and the observed ratio 2.55:1. The cross, resistant Dwarf Yellow milo x Dwarf Yellow milo, segregated in a 2.6:1 ratio. The observed number of plants was 1102:423, compared with the expected number, 1143.75:381.25 $\pm$ 11.40. The goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, was 3.66.

These studies of F_2 seedlings show that the inheritance of susceptibility and resistance to the milo disease in these crosses may be interpreted on the basis of the simple 3:1 Mendelian ratio. It is evident that no factor responsible for susceptibility to the milo disease is carried by Club or resistant Dwarf Yellow milo. When Dwarf Yellow milo is crossed with either one of these resistant varieties some factor is introduced which allows the causal organism to attack the plant.

Studies of F_2 Populations, 1934-1935

Unfavorable climatic conditions in the summer of 1934 were responsible for the very small amount of viable seed obtained from the F_1 plants of the crosses made during the winter of 1933-1934. Most of the plants failed to set seed until it was too late for it to mature, although a killing frost was not received until the latter part of October. Sixty-two F_1 heads were collected, but the seed of only a very few germinated more than 5 to 10 percent.

The seed was harvested on October 31, and a series of plantings made in the greenhouse on November 10. The method of planting differed somewhat from that followed the previous year. The flat was marked off to hold 176 plants. The two outside rows of each flat were planted to the parents of the cross, each row containing 22 plants. The remaining 6 rows were planted with hybrid material, giving a population of 132 hybrid plants. The cross resistant Dwarf Yellow milo x (kafir x milo) produced good seed and from all appearances was a true cross. The average height of 6 F_1 plants was 49 inches compared with 29 and 40 inches for the parents, kafir x milo and resistant Dwarf Yellow milo, respectively. Of the 475 F_2 plants tested, however, only six plants were questionable in their reaction to the disease. All others were resistant. This behavior may be explained by the fact that one parent is a cross between a susceptible and a resistant variety. It is thought possible that the particular plant of kafir x milo used as parent may have been a resistant segregate, although the bulk plantings of kafir x milo grown as checks were all susceptible.

The F_2 populations studied in the greenhouse in 1934-1935 were limited by the small amount of viable seed and were further decreased by a freeze in the greenhouse which killed most of one planting. This freeze occurred at a time when the susceptible plants were beginning to die. This made it necessary to take the final notes immediately, so that the susceptible plants would not be confused with those killed by the freeze, hence a large number of plants were classified as intermediates. Under normal conditions some of these would probably have been classed as dead. It is also possible that some of the plants classed as resistant would have later proved to be susceptible, as field observations indicate that some plants may escape infection for a time and later succumb.

Seed from three heads of the cross, resistant Dwarf Yellow milo x Custer, was used. The average height of the F_1 plants of this cross was 59 inches, compared with 33 and 40 inches for the parents, Custer and resistant Dwarf Yellow milo, respectively. This manifestation of heterosis, as well as other indications, led to the assumption that these were true F_1 plants. The F_2 progenies from three heads, however, were all resistant, except for two plants. All the parental plants were susceptible, and it is evident that these heads were not from true F_1 plants. Plants from a fourth head of the same cross segregated according to the expected Mendelian fashion, although the size of the population was small. The observed numbers were 139 susceptible and intermediate to 79 resistant. The calculated numbers are $163.5:54.5 \pm 4.25$.

The largest amount of viable seed was obtained in the cross, resistant Dwarf Yellow milo x Beaver, and an F_2 population of reasonable size was grown. The observed ratio was 2.5:1 and the goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, was 3.23. The data are presented in table 3.

Table 3.--Reaction of F_2 populations and parental varieties to the milo disease, as tested in the greenhouse, Manhattan, Kansas, 1934-1935.

Name	Observed number of plants: Total	Dead (susc.)	Intermediate (susc.)	Total susc.	Res.	Observed ratio	Calculated (3:1) number of plants: Susc.	Res.	Deviation from calc. number	PE	Dev./PE
Club	137	0	0	0	137						
Beaver	51	43	8	51	0						
Early Kalo	61	0	0	0	61						
Custer	100	85	15	100	0						
Kafir x milo	92	76	16	92	0						
Dwarf Yellow milo	168	150	18	168	0						
Res. Dwarf Yellow milo	564	0	1	1	563						
Res. Dwarf Yellow milo x Early Kalo	6	0	0	0	6						
Res. Dwarf Yellow milo x (kafir x milo)	475	1	5	6	469						
Res. Dwarf Yellow milo x Custer	254	0	2	2	252						
Res. Dwarf Yellow milo x Custer	218	44	92	139	79	1.7:1	163.5	54.5	24.5	±4.25	5.76
Res. Dwarf Yellow milo x Beaver	1010	414	313	727	283	2.5:1	757.5	252.5	30.5	±9.28	3.28

Studies of F_2 Populations Grown in Milo Disease Nursery at Garden City, Kansas, 1934

Surplus seed of certain crosses, not used for the greenhouse plantings in 1933-1934, was sent to Superintendent F. A. Wagner of the Garden City Experiment Station in the spring of 1934 for planting in the milo disease nursery.

Classification of the plants as either susceptible or resistant was based entirely on the appearance of the aboveground parts. No examination was made of the roots since it was not desirable to destroy any of the plants at the time the notes were taken on October 1, 1934. At this time all the plants of susceptible Dwarf Yellow milo in the check rows were dead. Club was not included in the nursery; however, it is known to be resistant.

In the Club x resistant Dwarf Yellow milo cross no symptoms of disease were evident. This is in agreement with the greenhouse results, indicating that the gene responsible for susceptibility to the milo disease is not present in either of these varieties. The other crosses in which one parent is susceptible segregated in a 3:1 ratio. The data from these field plantings are presented in table 4.

Table 4.--Reaction of F_2 sorghum hybrids to the milo disease. Garden City, Kansas, 1934.

1934 Row No.	Name	Number of plants: Susceptible	Resistant
2	Club x Res. Dwarf Yellow milo	0	all
3	do.	0	all
4	do.	0	all
5	do.	0	all
6	do.	0	all
7	Club x Dwarf Yellow milo	35	13
8	do.	36	18
9	do.	36	11
10	Dwarf Yellow milo	all	0
11	do.	all	0
12	Res. Dwarf Yellow milo x Club	0	all
13	do.	0	all
14	do.	0	all
15	do.	0	all
16	Dwarf Yellow milo x Res. Dwarf Yellow milo	40	12
17	do.	37	23
24	Res. Dwarf Yellow milo x Dwarf Yellow milo	58	17
25	do.	66	23
26	do.	63	16
27	Dwarf Yellow milo	all	0
28	do.	all	0
29	do.	all	0
30	Res. Dwarf Yellow milo x Dwarf Yellow milo	44	22
31	do.	64	26
32	do.	70	22
33	do.	50	14
34	do.	50	19

Name	Observed number of plants: Susc.	Res.	Observed ratio	Calculated (3:1) number of plants: Susc.	Res.	Deviation from calculated number of plants	PE	Dev./PE
Club x Dwarf Yellow milo	107	42	2.5:1	111.75	37.25	4.75	± 3.56	0.75
Res. Dwarf Yellow milo x Dwarf Yellow milo	542	194	2.8:1	552.00	184.00	10.00	± 8.02	1.24

The largest F_2 population grown in the milo disease nursery at Garden City was of the cross between the resistant and susceptible selections of Dwarf Yellow milo. The observed numbers in this cross were 542:194, closely approaching the calculated numbers, 552:184 $\pm$ 8.02. The observed ratio is 2.8:1 and the goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, 1.24. The observed ratio in the cross, Club x Dwarf Yellow milo, is 2.5:1, and the goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, is 0.75. These results agree with those obtained in the greenhouse and approach the expected ratio of 3 susceptible to 1 resistant.

Studies of F_3 Populations, 1934-1935

Seed from 27 F_1 heads studied in the greenhouse in 1933-1934 was grown in the sorghum breeding nursery at the agronomy farm in 1934. A relatively small number of plants survived the drought and severe chinch bug attacks, which were especially destructive in the cross, resistant Dwarf Yellow milo x Dwarf Yellow milo.

Eighty-two heads, including both selfed and open pollinated heads, of which less than 50 percent yielded viable seed, were selected on November 8 for studies of the F_3 generation in the greenhouse. This plot was surrounded by other sorghums, and it is possible that a small amount of natural crossing occurred which would modify the observed ratios and account for the presence of susceptible plants in an otherwise resistant population and for resistant plants in a population otherwise susceptible.

The exact number of F_3 lines tested is not known, as in some cases more than one head was taken from a single plant without recording this fact. Seedlings from 38 heads were tested, and it is estimated that about 20 F_3 lines are represented. F_3 lines classed as homozygous susceptible contained no resistant plants. The F_3 lines classed as homozygous resistant contained 1 susceptible and 10 intermediate plants. Seven of these intermediate plants were so classified solely because of reddish spots on the roots. At the time notes were taken, it was thought that these spots might be the first symptoms of disease that would develop later. Such spots, however, were later found on roots of resistant Dwarf Yellow milo plants, and it is possible that they were merely the result of an injury, or of localized infection. These plants classed as susceptible may be the result of natural crossing, seed mixtures, or damping off. At the time the notes were taken, the disease had not advanced far enough to affect the appearance of the subcrown internode or aerial parts of the plants.

The last series of plants grown in the greenhouse in 1934-1935 were much more vigorous and did not show signs of the disease so early as the other plantings. This may have been due to the effects of nitrogenous fertilizer mixed with the soil when the flats were filled. It seems likely that the late appearance of the disease symptoms can also be attributed to the effect of the nitrogen as Myers (1934) has reported that the life of susceptible plants is lengthened when they are grown on soil of high nitrogen content.

In order to include the data from these plantings in this thesis, it was necessary to take the notes before the disease had advanced as far as usual. This probably explains the large number of intermediate plants recorded. These plants showed typical disease symptoms and were easily distinguished from the resistant plants. These plants possessed a well-developed set of roots originating above the original set and above the discolored portion of the crown. These roots probably enabled them to remain alive. This development of secondary roots seemed to be more pronounced than in any of the previous plantings. There were indications that many of these new roots had been infected and that the plants would have died in a relatively short time.

F_3 lines were grown from seed of 19 F_2 heads. Additional F_3 lines were grown, but germination was so poor that only small numbers were obtained. Of the 19 F_3 lines tested, 7 were homozygous resistant, 7 were homozygous susceptible, and 5 showed clear-cut segregation. The segregating F_3 lines gave ratios approximating 3:1, even though the number of plants in each line was rather small. These results are presented in table 5.

Table 5.--Reaction of F_3 lines to milo disease as tested in the greenhouse, Manhattan, Kansas, 1934-1935.

Name	Number of plants: Total	Susc.	Inter-mediate	Total Susc.	Total Res.	Reaction of F_3 lines
Club x Res. Dwarf Yellow milo	41	0	0	0	41	Resistant
do.	17	0	0	0	17	do.
do.	44	0	0	0	44	do.
do.	21	3	0	3	18	do.
do.	42	0	0	0	42	do.
Res. Dwarf Yellow milo x Club	39	0	0	0	39	do.
do.	41	0	0	0	41	do.
do.	36	0	1	1	35	do.
do.	35	0	0	0	35	do.
do.	42	2	0	2	40	do.
Club x Dwarf Yellow milo	28	14	6	20	8	Segregating
do.	41	38	3	41	0	Susceptible
do.	89	21	51	72	17	Segregating
do.	4	1	3	4	0	(a)
do.	192	74	118	192	0	Susceptible
do.	200	80	120	200	0	do.
do.	252	108	144	252	0	do.
do.	1	1	0	1	0	(a)
do.	204	1	3(b)	4	200	Resistant
do.	264	0	1(b)	1	263	do.
do.	192	0	2,3(b)	5	187	do.
Dwarf Yellow milo x Res. Dwarf Yellow milo	28	8	14	22	6	Segregating
do.	1	0	0	0	1	(a)
Res. Dwarf Yellow milo x Dwarf Yellow milo	7	3	4	7	0	(a)
do.	49	7	35	42	7	Segregating
do.	68	15	35	50	18	do.
do.	78	0	0	0	78	Resistant
do.	38	0	0	0	38	do.
do.	31	0	0	0	31	do.
do.	4	0	0	0	4	(a)
do.	6	0	0	0	6	(a)
do.	36	20	16	36	0	Susceptible

Table 5. (cont.)

Res. Dwarf Yellow milo x Dwarf Yellow milo	1	0	1	1	0	(a)
do.	53	0	0	0	53	Resistant
do.	1	1	0	1	0	(a)
do.	41	37	4	41	0	Susceptible
do.	32	14	18	32	0	do.
do.	7	0	1	1	6	(a)

(a) Total number of plants is too small to warrant any statement as to reaction of that particular line.

(b) Small red areas on a few of the roots.

Two segregating F_3 lines of the cross, Club x Dwarf Yellow milo, gave observed ratios of 2.5:1 and 4.2:1. The observed numbers of plants differed from the calculated numbers by 1 and 5.25, respectively, and the goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, was 0.65 and 1.91, respectively. A segregating F_3 line of the cross, Dwarf Yellow milo x resistant Dwarf Yellow milo, gave a 3.6:1 ratio. The deviation from the expected number of plants was only 1. The goodness of fit, $\frac{\text{Dev.}}{\text{PE}}$, was 0.65. Two segregating F_3 lines of the cross, resistant Dwarf Yellow milo x Dwarf Yellow milo, gave ratios of 3.4:1 and 2.77:1 and deviated from the calculated number of plants by 1.25 and 1, respectively. The goodness of fit was 0.61 and 0.41, respectively. A summary of the reaction of the segregating F_3 lines is presented in table 6.

Table 6.--Summary of reaction of segregating F_3 lines to the milo disease, as tested in the greenhouse, Manhattan, Kansas, 1934-1935.

Name	Observed number of plants: Total	Dead (susc.)	Intermediate (susc.)	Total: Susc.	Res.	Observed ratio	Calculated (3:1) number of plants: Susc.	Res.	Deviation from calc. number	PE	$\frac{Dev.}{PE}$
Club x Dwarf Yellow milo	28	14	6	20	8	2.5:1	21	7	1	±1.54	0.65
Club x Dwarf Yellow milo	89	21	51	72	17	4.2:1	66.75	22.25	5.25	±2.75	1.91
Dwarf Yellow milo x Res. Dwarf Yellow milo	28	8	14	22	6	3.6:1	21	7	1	±1.54	0.65
Res. Dwarf Yellow milo x Dwarf Yellow milo	49	7	31	38	11	3.4:1	36.75	12.25	1.25	±2.04	0.61
Res. Dwarf Yellow milo x Dwarf Yellow milo	68	15	35	50	18	2.77:1	51	17	1	±2.41	0.41

A cross showing a monohybrid ratio in F_2 should segregate 1:2:1, as to F_3 lines. The number of F_3 lines which it was possible to study, however, was too small to show a good fit. The results obtained fit a 3:1 ratio better than a 9:7 or 13:3 ratio.

The F_3 lines, with a total of 358 plants from 10 F_2 heads of the cross, resistant Dwarf Yellow milo x Club, were all resistant, with the exception of 6 plants. It is possible that these susceptible plants are the result of natural crossing. It is possible that they were killed by the damping-off fungus, but this is unlikely. These results seem to justify the conclusion that no complimentary factors for disease susceptibility, other than the single recessive factor indicated above, are carried by either one of the varieties, resistant Dwarf Yellow milo or Club. The factor for disease susceptibility is brought into the cross by susceptible Dwarf Yellow milo.

Notes on Coleoptile Color

In connection with the studies on the inheritance of resistance to the milo disease, some observations were made on (1) coleoptile color, (2) effect of temperature on the development of the disease, and (3) hybrid vigor. It was noticed in the young plants grown in the greenhouse, that crosses between Club and the milo selections were segregating for red and colorless coleoptiles as found in Dwarf Yellow milo and Club, respectively. Some of the coleoptiles of the F_2 plants were neither red nor colorless, but an intermediate pink, suggesting that the factor for red color was not completely dominant to colorless. A preliminary record of the segregation for coleoptile color was made in one of the earlier plantings, but owing to the difficulty in securing counts, because of the early death of susceptible plants, no further records were made. Limited observations indicate that coleoptile color and resistance are not linked in this cross. In the F_3 plantings, some lines evidently pure for coleoptile color were observed.

Effect of Temperature on the Development of Milo Disease

When the studies of milo disease in the greenhouse were commenced, it was thought advisable to make a preliminary study to determine the most favorable air temperature for the expression of this disease. The plantings were arranged for the purpose of observing any effects of differences in temperature.

Two flats of diseased soil were divided into 3 parts and one part of each flat planted with seed of resistant Dwarf Yellow milo, Dwarf Yellow milo, and Club. Seed of Beaver, White Kaoliang, and Sharon kafir were planted in the other flat. Two flats were kept in the cold section of the agronomy greenhouse which had a temperature range of 65° to 70° F. Two other flats planted to the same varieties were kept in the warm section of the greenhouse with a temperature range of 75° to 80° F.

Beaver and Dwarf Yellow milo were susceptible and the other varieties resistant in both environments. The plants in the warm greenhouse grew much faster than those in the cold section and consequently showed symptoms of the disease earlier, although both had produced approximately the same amount of growth when the susceptible varieties were killed by the causal organism.

A second planting was made which included resistant Beaver C.I. 871 G.C. Sel. 31-2-1, susceptible Beaver C.I. 871, resistant Wheatland C.I. 918 G.C. Sel. 302-8-6(S)-b(S), susceptible Wheatland C.I. 918 G.C. Sel. 302-6-2(S)-b(S), resistant Dwarf Yellow milo, and Dwarf Yellow milo. The reaction of Beaver, susceptible, White Kaoliang, and Sharon to the milo disease is shown in Plate V.

The expected reactions were secured with the exception of Beaver, a susceptible variety, which contained a number of resistant plants. These may have been seed mixtures or natural crosses. The difference in the time necessary for the susceptible plants in both greenhouses to succumb to the milo disease was similar to that which occurred in the first planting. The data from both plantings are presented in table 7.

Table 7.--Reaction of sorghum varieties and selections to the milo disease under different temperature ranges in the agronomy greenhouse, 1933-1934.

Variety or selection	Warm section of greenhouse 75°-80° F. Number of plants Total	Susc.	Res.	Cool section of greenhouse 65°-70° F. Number of plants Total	Susc.	Res.
Resistant Dwarf Yellow milo	5	0	5	16	0	16
Dwarf Yellow milo	23	23	0	31	31	0
Club	36	0	36	38	0	38
Beaver	21	21	0	17	17	0
White Kaoliang	52	0	52	38	0	38
Sharon kafir	49	0	49	50	0	50
Resistant Wheatland Sel.	59	0	59	53	0	53
Wheatland	40	40	0	31	31	0
Resistant Beaver Sel.	52	0	52	50	3	47
Beaver	46	38	8	47	41	6
Resistant Dwarf Yellow milo	52	0	52	38	0	38
Dwarf Yellow milo	46	46	0	51	51	0

It is evident from these results that a temperature range of 10 degrees has no observable effect upon the ultimate results, although a longer time is necessary for the manifestation of the disease at lower temperatures. This agrees with unpublished data by Melchers and Lefebvre from experiments in which resistant and susceptible milo selections have been grown over a wide range of controlled soil and air temperatures.

Heterosis of F_1 Sorghum Hybrids

Marked heterosis was exhibited by the F_1 generation of all the crosses grown in 1934 and by the Club x Dwarf Yellow milo crosses grown in 1933. The cross between Dwarf Yellow milo and the disease resistant selection of this variety did not show any hybrid vigor. This would be expected, since it is well known that, in general, crosses between closely related types exhibit little or no hybrid vigor.

The F_1 plants of the cross, resistant Dwarf Yellow milo x Dwarf Yellow milo could not be distinguished from the parents by observation, as they exhibited neither of the two characteristics commonly observed in F_1 sorghum hybrids; namely, heterosis and late maturity. It seems likely that the resistant selection of Dwarf Yellow milo differs from the parent variety only in regard to the gene governing the reaction to milo disease.

Heterosis was still evident in the F_2 generation of the crosses between Club and the two milo selections but was not nearly so marked as in the F_1 generation. F_3 lines of these crosses varied in height of young plants, showing that they were segregating for size factors, as would be expected in normal Mendelian inheritance.

Data on height of F_1 plants and the parental varieties are presented in table 8. Five of the measurements were secured in 1933, and in comparing them with the measurements made in 1934, consideration must be given to the different seasons and their influence upon plant growth.

Table 8.--A comparison of the height of F_1 plants and parental varieties, Manhattan, Kansas, 1933-1934.

Cross	Plant height in inches	Parent	Plant height in inches	Parent	Plant height in inches	Increased height of F_1 over taller parent, in inches
Res. Dwarf Yellow milo x Dwarf Yellow milo	54(a)	Dwarf Yellow milo	52(a)	Res. Dwarf Yellow milo	40	2
Resistant Dwarf Yellow milo x Club	96(a)	Club	64(a)	Res. Dwarf Yellow milo	40	32
Dwarf Yellow milo x Club	96(a)	Club	64(a)	Dwarf Yellow milo	52(a)	32
Res. Dwarf Yellow milo x Beaver	54	Beaver	27	Res. Dwarf Yellow milo	40	14
Res. Dwarf Yellow milo x Early kalo	68	Early Kalo	33	Res. Dwarf Yellow milo	40	28
Res. Dwarf Yellow milo x Wheatland	50	Wheatland	24	Res. Dwarf Yellow milo	40	10
Res. Dwarf Yellow milo x Custer	59	Custer	33	Res. Dwarf Yellow milo	40	19
Res. Dwarf Yellow milo x (kafir x milo)	49	(kafir x milo)	29	Res. Dwarf Yellow milo	40	9
Res. Dwarf Yellow milo x (Kan. Orange x milo)	56	(Kan. Orange x milo)	31	Res. Dwarf Yellow milo	40	16

(a) Plants grown in 1933.

The heterosis exhibited by these crosses is clearly illustrated in Plate VI which shows a typical F_1 plant and the parents of Club x Dwarf Yellow milo. The relative size of the F_1 and parental heads of this cross are shown in Plate VII. This cross is wider than any of the other crosses studied but will serve to illustrate the marked heterosis exhibited by all crosses studied, except the one between Dwarf Yellow milo and the resistant selection of Dwarf Yellow milo, which showed no vigor. The F_1 plant and the parents of the latter cross are shown in Plate VIII.

CONCLUSIONS

Greenhouse and field studies made in the years 1933 to 1935 of F_2 populations and F_3 lines of the crosses, Club x Dwarf Yellow milo, Club x resistant Dwarf Yellow milo, and Dwarf Yellow milo x resistant Dwarf Yellow milo, and F_2 studies of resistant Dwarf Yellow milo x Beaver and resistant Dwarf Yellow milo x Custer, indicate that resistance to the milo disease is inherited in a simple 3:1 ratio.

These results suggest that resistance is based on a single recessive factor. The allele of this gene, when present as a homozygous dominant, allows the plant to die at an early stage in its development when the causal organism is present in the soil. The heterozygous individuals are probably examples of incomplete dominance. If this hypothesis is correct, it will, perhaps, account for that group of intermediate individuals which show some of the symptoms of milo disease, but which do not die until later than the plants which are homozygous for susceptibility. Such plants are classed as intermediate but are included with the susceptible plants in making the 3 class of the 3:1 ratio. The diseased condition in some of these plants is probably due to the late infection by the organism, which causes little damage because of the advanced development of the plant.

The heterozygous individuals would have the factorial formula Ss, S representing the gene for susceptibility and s the gene for resistance. The F_1, Ss x Ss, when self-pollinated, produces one homozygous susceptible, SS, two heterozygotes, Ss, and one homozygous recessive, ss, which is resistant.

The gene for susceptibility to milo disease seems to be inherited independently of other observed characters in these crosses. It should not be extremely difficult to secure resistant selections of economic value from crosses between resistant and susceptible sorghum varieties.

Resistant selections have recently been made by F. A. Wagner, of Garden City, from susceptible varieties which appear equal to the original varieties in all respects. This suggests that the gene for susceptibility is not stable but occasionally mutates or is lost during synapsis through some chromosomal aberration.

F_1 plants were compared with the parents in regard to vigor. The F_1 plants of the cross, Dwarf Yellow milo x resistant Dwarf Yellow milo, could not be distinguished from the parents except by their reaction to the milo disease, when grown on infested soil. This observation is in agreement with the theory that, in general, the wider the cross the greater the hybrid vigor, and that crosses between closely related types exhibit little or no hybrid vigor.

Results from duplicate plantings of susceptible and resistant sorghum selections made in two sections of the agronomy greenhouse show that a difference in air temperature of approximately 10° F. has no observable effect upon the ultimate expression of the milo disease. A longer period of growth, however, is necessary for the development of the disease at lower temperatures, although the total plant growth attained at the time the susceptible plants succumb to the disease is nearly the same at both temperatures.

It was observed that F_2 populations from the crosses, Club x Dwarf Yellow milo and Club x resistant Dwarf Yellow milo, were segregating for coleoptile color. The coleoptiles of some seedlings were a light pink color suggesting a condition of incomplete dominance, for the factor for red color of Dwarf Yellow milo and the factor for colorless coleoptile of Club. More than one factor might also be responsible for coleoptile color. The presence of susceptible plants in the crosses made it very difficult to secure accurate plant counts of coleoptile color; hence, no definite conclusions can be drawn. Some F_3 lines appeared homozygous for colored coleoptiles, some for colorless, and others segregated.

SUMMARY

A study of the inheritance to resistance to the root, crown, and shoot rot disease of milo was made in F_2 and F_3 generations of sorghum crosses grown on infested soil in the greenhouse at Manhattan, Kansas, 1933 to 1935, and in the milo disease nursery at the Garden City Experiment Station in 1934.

Data collected in this study warrant the conclusion that resistance to the milo disease is dependent upon the expression of a single recessive factor, s, carried by Club and the resistant selection of Dwarf Yellow milo.

Apparently no complimentary factors for disease susceptibility other than the single factor indicated above are carried by either Club or resistant Dwarf Yellow milo. The factor for the expression of susceptibility is partially dominant. Resistant, segregating, and susceptible F_3 lines were secured.

Heterosis was very pronounced in the F_1 plants of all the crosses studied except Dwarf Yellow milo x resistant Dwarf Yellow milo, which exhibited no hybrid vigor.

The reaction of seedling plants to the milo disease was apparently not affected by air temperature differences, in the greenhouse, of approximately 10° F.

Segregation for coleoptile color was noted in F_2 populations of crosses involving Club and selections of Dwarf Yellow milo. Some F_3 lines were homozygous for colored coleoptiles, some for colorless, others segregating.

The results obtained show that the mode of inheritance of resistance to milo disease may be determined in the greenhouse. The greenhouse results were supplemented by observations on F_2 populations of three crosses grown in the milo disease nursery at the Garden City station in 1934. The results of these field tests are in agreement with the conclusions drawn from the greenhouse data.

ACKNOWLEDGMENT

The writer wishes to express his sincere appreciation to his major instructor, Professor L. E. Melchers, for suggesting the thesis problem, for the many helpful suggestions and criticisms which he has given throughout the investigations, and for making it possible to conduct this study. He is also indebted to Dr. John H. Parker for his aid in securing parental and hybrid material and for his constant interest and helpful criticisms during the progress of this research.

The writer also wishes to express his gratitude to Professor H. H. Laude for his help and suggestions in regard to statistical methods and to Dr. C. L. Lefebvre and Mr. C. O. Johnston for their helpful suggestions from time to time, and to all others who have aided in this study.

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Plate I. Reaction to the milo disease of 3 varieties of sorghum used as parents, resistant Dwarf Yellow milo, Dwarf Yellow milo (susceptible), and Club (resistant). Plants grown in infested soil in the greenhouse.

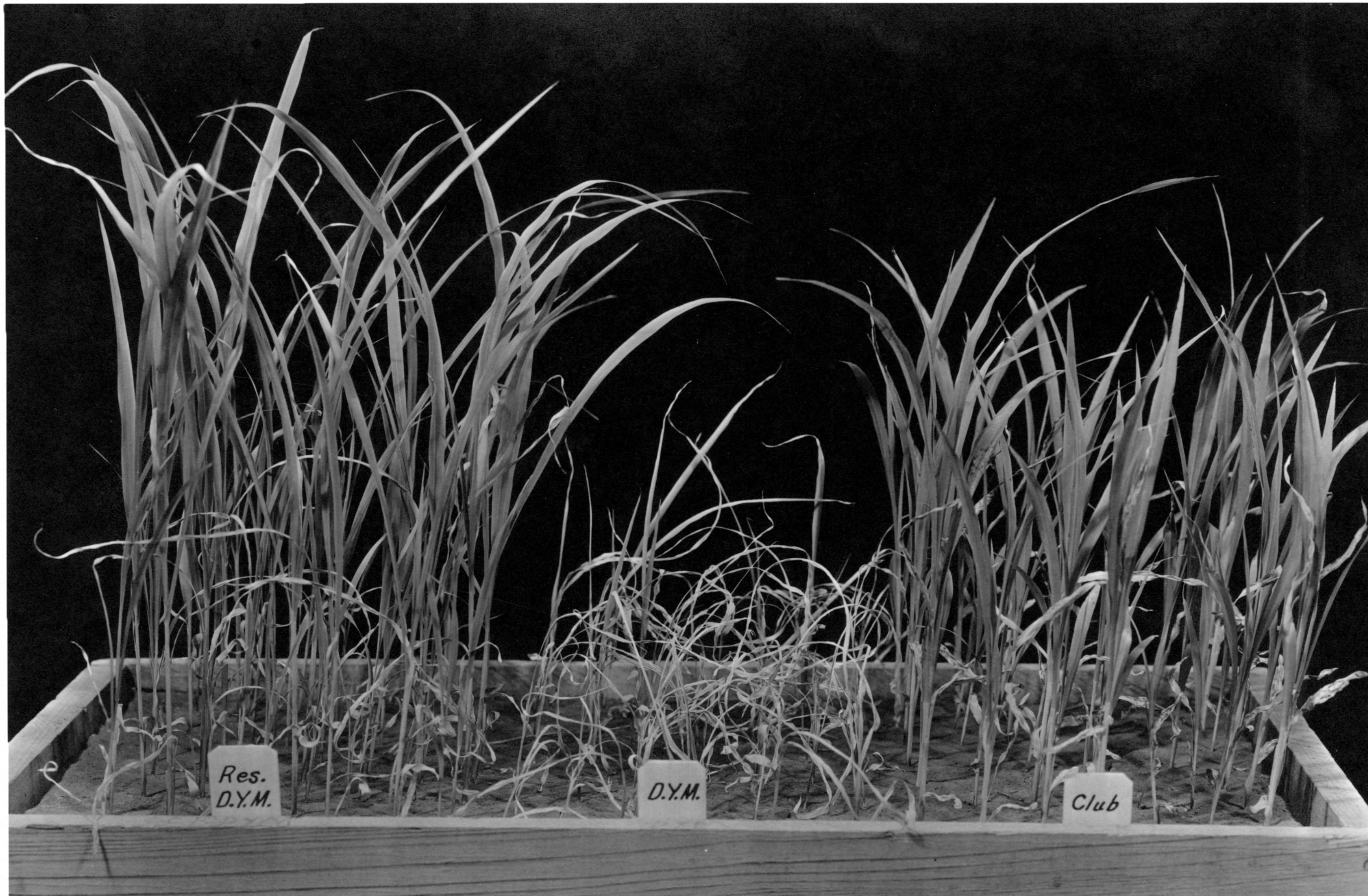
Res.
D.Y.M.
D.Y.M.
Club

Plate II. Reaction of (1) resistant selection of Wheatland and (2) susceptible selection of Wheatland to milo disease, as grown on infested soil in the greenhouse.


1
2

Plate III. Reaction of the F_2 population of resistant Dwarf Yellow milo x Dwarf Yellow milo to the milo disease, as grown on infested soil in the greenhouse. The tall, healthy plants are resistant segregates; the short, dead plants are susceptible.


Res.
D.Y.M.
×
D.Y.M.

Plate IV. Plants of the 3 classes from the F_2 population of the cross, resistant Dwarf Yellow milo x Dwarf Yellow milo. The three classes are (1) resistant, 20 plants, (2) intermediate, 15 plants, and (3) susceptible, 60 plants.


1
2
3
C5054.

Plate V. Reaction of sorghum varieties to the milo disease as grown on infested soil in the greenhouse. Beaver, susceptible; White Kaoliang, resistant; Sharon kafir, resistant.


Beaver
Wh. Kao.
Sharon

Plate VI. Heterosis shown by an F_1 plant of Club x Dwarf Yellow milo. Left, Dwarf Yellow milo parent; center F_1 plant; right, Club parent.


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Plate VII. Heterosis shown by an F_1 head of Club x Dwarf Yellow milo. Left, normal head of Dwarf Yellow milo parent; center, F_1 head; right, normal head of Club parent.

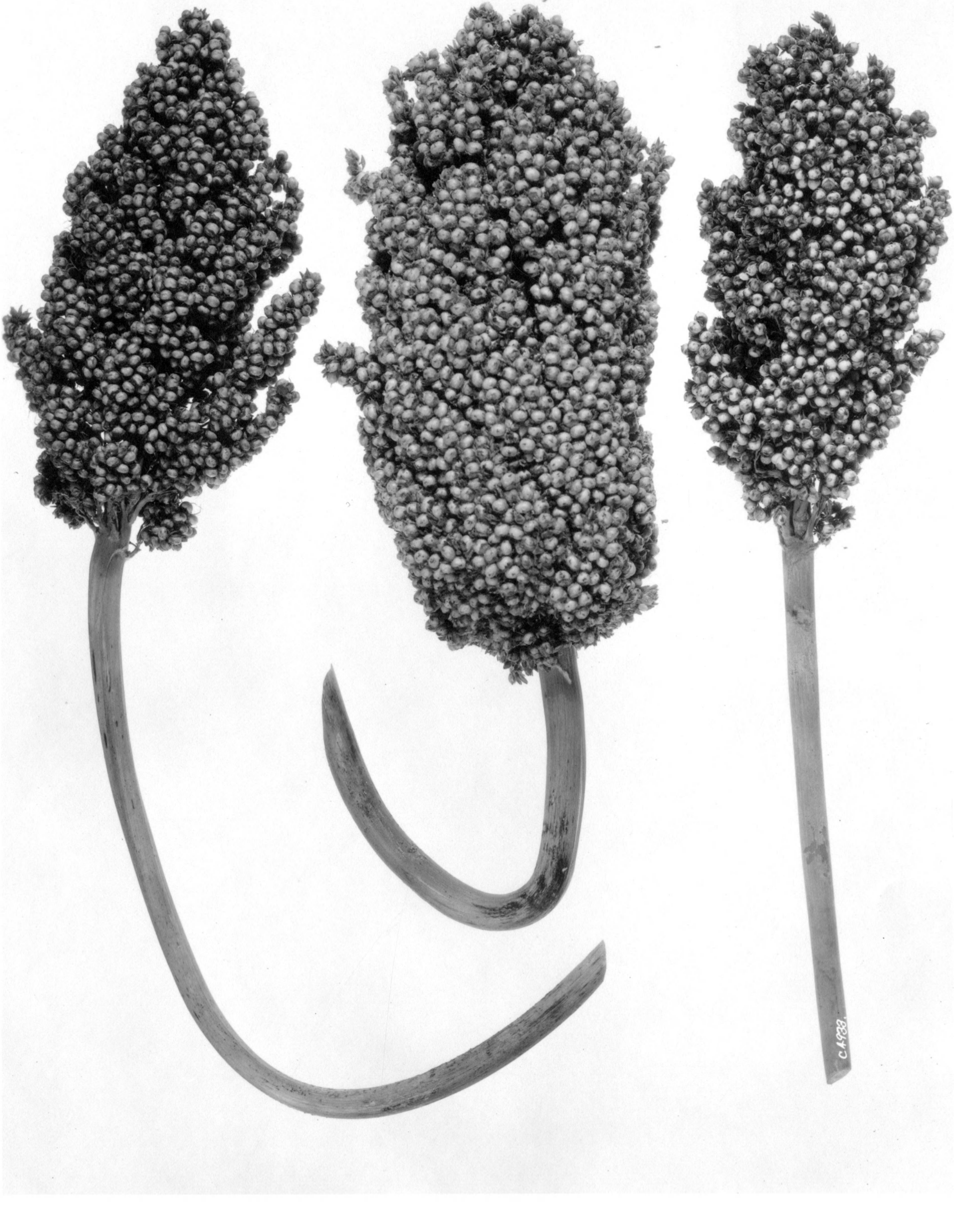
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Plate VIII. A cross between two closely related types of Dwarf Yellow milo x resistant Dwarf Yellow milo, showing no heterosis. Left, Dwarf Yellow milo parent; center, F_1 plant; right, resistant Dwarf Yellow milo parent.


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