THE INHERITANCE OF WHITE SHEATH IN MAIZE

THESIS FOR DEGREE OF M. S.

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Maize

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THE INHERITANCE OF WHITE SHEATH IN MAIZE.

I. Statement of the Problem.

The material in this article is the result of an attempt to contribute some more facts concerning the behavior of white sheath in maize. The different phases of the problem which were worked on are as follows:

1. Genetic constitution of the white sheath material.
2. Genetic relationship of this white sheath to Kempton's white sheath.
3. Genetic relationship of white sheath to other genetic factors of maize.

II. Previous Investigations.

White sheath is one of the many chlorophyll defects which have appeared in corn from time to time. The only literature on white sheath up until now is a short article by Kempton of the United States Department of Agriculture in which he briefly describes white sheath and its genetical behavior. He showed that white sheath is recessive to normal green and seems to behave as a simple Mendelian recessive although he was not able to obtain consistent Mendelian ratios in the F_2 generation. He also mentioned the fact that there are different intensities of white sheath, and that these differences are inherited. In the F_2 of a cross made by Kempton involving white sheath and lineate leaf there was an indication of relationship between these two characters, but the population was too small to prove linkage. Kempton in recent correspondence

intimates that white sheath is due to more than one genetical factor.

III. Source of Material.

The white sheath material used in this study originated from the Early Duncan Variety of corn. In 1921, twelve, fourteen, sixteen, and eighteen rowed types of selfed ears were selected from a field of Early Duncan corn at Michigan State College. The following year, many of these selected ears were planted in the ear-to- row series, remnants being saved. In 1923, remnants from three ears of the sixteen row type were combined and used as the pollen strain (36400) in one of the inter-row crossing blocks. White sheath plants were noticed in the pollen strain but nothing was done with them. The ears harvested from plat 36400 were used as check in the corn variety series of 1924. White sheath plants appeared again that summer, and it was these which were turned over to the writer to determine their inheritance.

IV. Description of Material.

White sheath in corn shows up in the early seedling stage and lasts during the entire life of the plant. In a population segregating for white sheath, a few white sheath plants can be distinguished two weeks after planting, but by far the most of them cannot be distinguished with certainty until a week later, although the length of day, amount of sunlight, and other growing conditions affect the time. Table 1 will give some idea of the length of time required for white sheath to express itself.

Table 1---- The number of white sheath seedlings in three plantings are indicated to-gether with the date of planting, the various dates of appearance, the number of days after planting, and the dates harvested.

	No. of days after planting	Date	No. Staked	Date	No. Staked	Date	No. Staked
Planted		Dec.7		Feb8		Apr.1	
Staked	15			Feb23	2		
	18			Feb26	12		
	19	Dec 26	10			Apr.20	12
	20					" 21	5
	21	" 28	20			" 22	6
	22			Mar.2	8	" 23	2
	23	"30	2	" 3	1	" 24	2
	24			" 4	4		
	26			" 6	10		1
	27	Jan.3	2	" 7	1		
	28	" 4	3				
	29	"5	1				
Harvested		Jan.9		Mar.8		Apr27	

It will be noticed that the majority of the white sheath plants in the planting of December 7 were staked on December 26 and 28. Later it was found that a few of the plants staked on these dates did not possess a white sheath. Because of the difficulty of positively identifying white sheath at the end of two weeks, in subsequent progenies only those plants were staked on a given date which were certainly known to have white sheaths.

A glance at the table will show that the progeny planted on April 1 required a somewhat shorter period of growth than the other two progenies. The reason for this difference is that the plants had more sunlight because of the longer spring days. This table indicates that the

final classification of a progeny segregating for white sheath should not be made in most cases until four weeks after planting.

A typical white sheath plant has the following characteristics:- The leaf sheaths are light green to vivid white, the whiteness in the seedling stage often extending into and including the basal half of the leaves. Later in development, the leaves become normal green except in some strains where the whiteness extends into the basal portion of the leaf in the form of irregular white stripes. This striping of the leaves may appear as vividly on a plant with light green white sheath as on one having white sheath of the greatest intensity, but is usually found associated with the latter type. This whiteness of the sheath extends from the very basal portion of the stalk to the tassel node and includes the outer husk covering the ear.

On the sheath of a normal green plant, anthocyanin pigment shows as a dull dark red color, but on a white sheath individual it is bright red. Often the contrast between the bright red color on the base of the stalk and the intense white color above is very striking.

V. Field Methods.

All of the white sheath plants which appeared in the check rows in 1924 were staked with long white poles, and were classified into three types, A, B. and C,-- A being the most intensely white type, while C was only slightly

Fig. 1.- A normal plant on the left and an A type white sheath plant on the right. The true contrast between these two types can be appreciated only by seeing them grow side by side in the field.

Fig. 2-- A normal plant (left), and a B type white sheath plant (right). As can be seen, white sheath effects all the sheaths of the stalks, including those of the ear.

Fig. 3 a- From left to right, a normal plant and a C type white sheath. The contrast between these types, although slight, is plainly evident in the field.

white, and B was intermediate. As can be readily imagined, difficulty was experienced in classifying some plants. In general, the method used was to classify the extreme types as A and C types and to put the remainder in the B class. A tag was tied to each plant, on which was written the plot number, plant number, and type of plant. The plants were staked and classified the second week in July, but owing to the fact that the season was very backward, the plants were only in the middle of the seedling stage. A reclassification of the plants was made at a later date, and it was found that they had retained their original degree of whiteness.

Out of a population of approximately 10,000 plants there were 165 white sheath plants consisting of 22 A type, 113 B type, and 30 C type. Many of these plants were self-pollinated and selfed ears from the different types were obtained as follows:-- 2 of A type, 55 of B type, and 21 of C type. The small number of ears obtained from the A type plants was due partly to the fact that these plants were used exclusively for all crossing work with the exception of half a dozen intercrosses which were made between white sheath types. Seven A type plants were selfed but owing to the weakness of this type, only two ears were obtained.

Seed from these crosses and self-pollinations was planted in the field in 1935. The plots from self-pollinated B types showed segregation in almost every case, but difficulties of classifying the grades of white sheath are so great that no definite ratios were obtained.

Fig. 4-- The contrast between these plants is very great. The plant marked with a cross is a typical A type white sheath and to the right of it is the F_1 of a C X C cross with greenish-white sheaths.

The plots from selfed C type showed much greater uniformity than those of B type, and two or three plots were evidently homozygous or nearly so. There were only two plots of selfed A plants, and these gave predominantly A type.

In the summer of 1925, many self-pollinations were made in the different plots and of the various types within the plot. Self pollinations were also made in the F_1 plots resulting from crosses involving the other factors of maize. Many intercrosses were made between white sheath plants of the same plot and different plots, the type of plant being carefully noted.

Some F_1 seed from crosses with the chromosome testers was planted in the new greenhouse during the fall and winter of 1924-25 for the purpose of obtaining F_2 grain. In spite of the fact that the temperature often hovered around freezing, due to only temporary steam connections, these plants finally matured to the degree of producing seed. It was necessary to harvest this seed before it was mature, but it grew fairly well in the field in the summer of 1925. Owing to the limited amount of seed the plots were small and very little data were obtained from them. They did show, however, that the expression of white sheath is not determined by a single factor. The scarcity of white sheath plants in these small plots made them of little value for determining linkage.

By far the greater part of the linkage tests of this problem were made in the greenhouse during the fall and winter of 1925-26. It was necessary to obtain most of the linkage data from F_2 progenies because no double recessives had been available for backcrosses. A few backcrosses had been made however involving dominant factors. F_2 segregating progenies were grown on a bench in the greenhouse. Two weeks after planting some white sheath plants could be distinguished, and these were staked. White sheath plants were staked as soon as they were detected. After three and one half weeks no more appeared, and the plants were pulled out at the end of four weeks, and another progeny planted. These progenies served both for a factorial study of white sheath and for linkage determinations.

F_2 progenies of crosses involving kernel characters, or plant characters which show up in the early seedling stage, were obviously the only material from which linkage data could be obtained in such a short time.

Some seed of Kempton's white sheath was obtained and grown in the greenhouse and crossed with this white sheath to determine whether or not the two types are genetically the same.

F_1 plants of intercrosses between the A, B, and C types of the writer's white sheath were grown nearly to maturity to determine if possible what causes the different gradations of white sheath. As far as possible, F_1 material resulting from the crossing of individuals of homozygous plots was used.

Fig. 5 -- A general view of corn growing in the greenhouse during the winter of 1936. In the immediate foreground on the left is a young seedling progeny spaced 4" X 4". On the right, is an F_2 progeny segregating for golden and white sheath.

The rest of the green-house space was devoted to F_2 progenies segregating for white sheath and some character such as golden which requires more than four weeks to fully express itself. In 1926 all seed planted in the greenhouse was planted directly in the soil and not first grown in pots as was done the year before. The methods of planting and spacing used in this study proved very satisfactory in dealing with white sheath.

During the winter of 1925, plants used for crossing were spaced 15" X 15", but in 1926 a distance of 12" X 12" proved satisfactory. Progenies segregating for white sheath and other characters which show up in the seedling stage, such as liguless leaf, were spaced 4" X 4". When plants of such progenies are grown closer together, they become spindling, and it is difficult to determine whether or not they have white sheaths. Plants grown as close together as this would of course become crowded if left much longer than four weeks.

In all crossing work, both in the field and greenhouse, the method in vogue at Michigan State College was used. Transparent glassine sacks 3" by 6" were used to cover the ear buds before the silks appeared. Twelve pound size, pinch-bottom paper sacks were used to cover the tassels, and were clipped onto the tassel about twenty-four hours before pollinating. When performed correctly, this method of pollination offers little chance for outside contamination.

VII. Factorial Composition of White Sheath.

Table 2. F_2 Progenies segregating for White Sheath.

Pedigree No.	F_1	Observed Nor.	Observed ws	Calculated* Nor.	Calculated* ws	D	P.E.	D / P.E
370-384	normal	528	27	518	37	10	3.84	2.60
531602	normal	255	19	257	17	2	2.7	.74
531604	normal	68	4	68.56	4.5	.5	1.38	.36
531605	normal	261	19	263	17	2	2.73	.74
	Total	1112	69	1107	74			

Total Difference = 5 ± 5.6

* Calculated on basis of 15:1

Results obtained from F_2 and backcross data show that white sheath depends for its expression upon the presence of two complimentary recessive factors. The composition of a white sheath plant may then be indicated as follows:- $ws_1\ ws_1\ ws_2\ ws_2$. There would be 8 different types of green plants:-

1 $Ws_1\ Ws_1\ Ws_2\ Ws_2$
2 $Ws_1\ Ws_1\ Ws_2\ ws_2$
1 $Ws_1\ Ws_1\ ws_2\ ws_2$
2 $Ws_1\ ws_1\ Ws_2\ Ws_2$
4 $Ws_1\ ws_1\ Ws_2\ ws_2$ — 15 Green Sheath
2 $Ws_1\ ws_1\ ws_2\ ws_2$ — to
1 $ws_1\ ws_1\ Ws_2\ Ws_2$ — 1 white sheath.
2 $ws_1\ ws_1\ Ws_2\ ws_2$
1 $ws_1\ ws_1\ ws_2\ ws_2$

The validity of the above theory is readily seen by referring to Tables 2 and 3. The F_2 progenies ~~in~~ (Table 2)

in each case segregated in the ratio of 15 green sheath to 1 white sheath, and backcrosses (Table 3) gave 3 green sheath to 1 white sheath.

The first pedigree number in Table 2 (370-384) represents fourteen very small F_2 plots segregating for white sheath. These plots when taken separately did not give a definite Mendelian ratio because of their very small size, but when taken en masse, a deviation of 10 ± 3.84 was obtained on the basis of a 15:1 ratio. Such a deviation could be expected to occur due to chance about once in thirteen times. This deviation although fairly large is well within the limits of probable error. The other three pedigree numbers in Table 2 represent the progenies of single ears. The deviations of the progenies of these ears from a 15:1 ratio are respectively 2 ± 2.7, .5 ± 1.38, and 2 ± 2.73. The total population of these F_2 progenies was 1182 and the deviation of the total from a 15:1 ratio was 5 ± 5.6. Such a deviation would occur due to chance once in two trials. The above data from F_2 progenies indicate therefore that white sheath depends for its appearance upon two complimentary recessive factors.

Table 3. Backcrosses Involving White Sheath.

Pedigree No.	F_1	Observed Nor.	Observed ws	Calculated* Nor.	Calculated* ws	D	P. E.	D/P.E.
534201 x 531400	normal	201	64	199	66	2	4.85	.41
534202 x 531400	normal	46	14	45	15	1	2.26	.44

*Calculated on basis of 3:1

The backcross data in Table 3 strengthen the above supposition for in backcrosses involving white sheath, we would expect to obtain a ratio of 3 green sheath to 1 white sheath. The backcross and resulting genotypes expected may be represented as follows:-

Backcross $Ws_1\ ws_1\ Ws_2\ ws_2 \times ws_1\ ws_1\ ws_2\ ws_2$

Resulting types.

$Ws_1\ ws_1\ Ws_2\ ws_2$	
$Ws_1\ ws_1\ ws_2\ ws_2$	3 green sheath
$ws_1\ ws_1\ Ws_2\ ws_2$	to
$ws_1\ ws_1\ ws_2\ ws_2$	1 white sheath

A glance at Table 3 will show that this expectation was realized. A very close fit to a 3:1 ratio was obtained as the deviations were only 2 ± 4.85 and 1 ± 2.26. These deviations could be expected to be due to chance more often than to some other factor.

Although only A type white sheath plants were involved in these crosses, the fact that intercrosses between the A, B, and C types of white sheath gave only white sheath would indicate that differences between these three types are due to additional modifying factors, and not due to differences in the elemental factorial composition. Further work will be necessary to establish this point. We can say however with reasonable certainty, that two complimentary factors in the recessive condition must be present in the case of A type white sheath.

VIII. Genetic Relationship of this White Sheath to Kempton's White Sheath.

During the winter of 1925-26, some of the writer's

Fig. 6 -- Kempton's white sheath on the left and the writer's A type on the right.

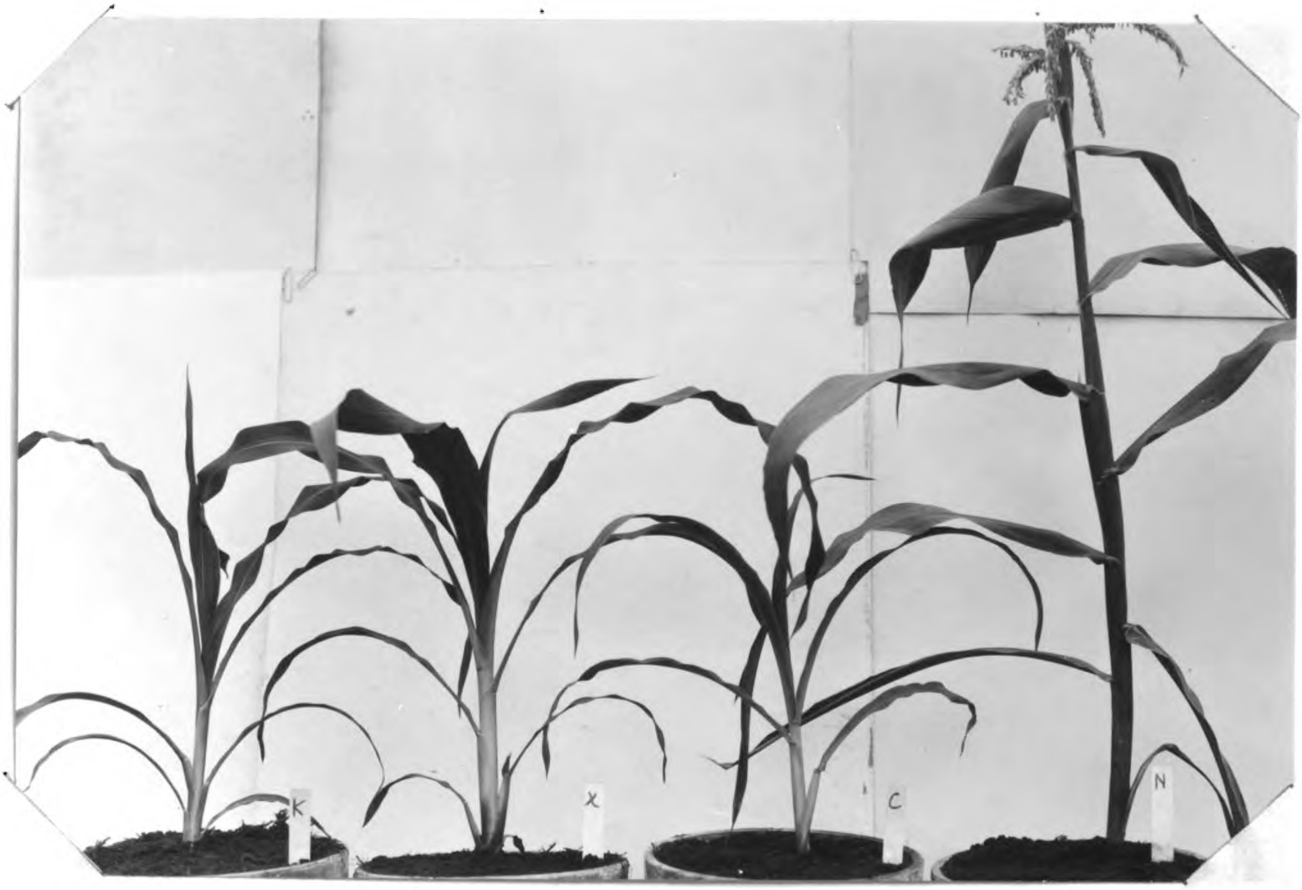

Fig. 7 -- Kempton's white sheath on the left, the writer's white sheath on the ~~extreme~~ right, and the F_1 of a cross between these two types in the center. A normal plant on the extreme right.

A type white sheath plants were crossed with Kempton's white sheath. The seed from these crosses was planted in the green-house and the resulting plants all had white sheaths. This proves that Kempton's white sheath plants carry the same two recessive factors which cause the white sheath studied in this problem. There is the possibility, of course, that Kempton's material may contain other factors for white sheath in addition to those demonstrated by these crosses.

IX. The Leaves of White Sheath Plants.

It has already been mentioned that in some strains of white sheath, the whiteness of the sheath extends into the leaves. This condition usually manifests itself in the form of white stripes which may be fine or broad, regular or irregular, and which are confined mostly to the lower leaves. The expression of this striping differs so much in different plants that it is difficult to describe it. On some white sheath plants grown in the greenhouse, the entire basal third of the lower leaves was vivid white in appearance, but this condition has not as yet been noted in the field. The striping of the leaves is generally strongest on A type plants, and is usually lacking on C type. However, an A type plant may lack the striping while a C type plant may possess it.

A chlorophyll analysis was made of the leaves of plots resulting from self-pollinated A, B, and C types and from intercrosses between these types. The sheaths of plants even within a single plot differed somewhat in degree of whiteness, and the only value of these results is that they demonstrate

Fig. 8-- A normal plant on the left and an A type with striped leaves on the right.

Fig. 9 -- A normal plant (left) and a B type with striped leaves (right). The leaf striping shows up very plainly in this picture and is characteristic of the A and B types of white sheath.

Fig. 10 -- Leaf striping is rare on a C type white sheath plant. This picture shows a normal plant (left) and a C type with striped leaves (right).

the great variability of the chlorophyll content in different strains of white sheath.

The leaves to be analyzed were placed in manila sacks and dried in an oven at about 60° C. for three days. An electric fan was used to keep the air circulating within the oven. The leaves were then ground up in a power grinder and the resulting powder passed through a 60 mesh screen. The chlorophyll content was determined as follows:- A 5 gram sample of the leaf powder was placed in a flask and shaken up in 100 to 200 c. c. of 85% acetone, and allowed to stand for several minutes. By means of a water pump the chlorophyll solution was sucked through filter paper into a clean flask. This process was repeated with fresh acetone solution until the leaf powder showed by its colorless appearance that it contained practically no chlorophyll. The extracts obtained were diluted to a volume of 500 cc. with 85% acetone, and the percentage of chlorophyll was then determined by the aid of a colorimeter by taking one of the samples as a 100% and comparing the others with it. As soon as homozygous strains can be obtained, a more exact method of analysis can then be used. In the method described above, the different leaf pigments were not separated. Table 4 gives the results of these analyses.

Table 4 -- This table shows the % of chlorophyll found in the leaves of white sheath plots resulting from intercrosses of different types of white sheath plants.

Strains tested	all	upper	lower
C X C check	100		
A x C		74	
A x C			69
B x C		78	
B x C			38
C x B light plants	75		
C x B			51
C x C light plants			46
C x C	47		

In Table 4, it will be noted that the intercross C x C was taken as the standard. The leaves of these plants were normal green in appearance although a few plants in this plot were noticeably lighter and had striped leaves. The leaves from these striped plants were analyzed separately. It can be seen that in all except the standard the analysis of the upper leaves gave nearly the same values while the lower leaves gave widely different results. These figures show that the lower leaves of the white sheath plants are affected much more by the striping than the upper leaves. The results of the above table are not comparable with those of Table 5 because the plants of the former were grown during December and January when there is very little sunlight, and the weather

was also mostly cloudy during this period. The material of the latter table was grown late in the winter and was exposed to much more sunlight.

Table 5 -- This table gives the % of chlorophyll found in the leaves of white sheath plots resulting from self-pollinations and intercrosses of various white sheath plants.

Strain No.	% of Chlorophyll
36400 Check	100
C	86
B x B	75
AV^1	20
BV^1	61
BV^3 x AV^1	61

In Table 5, the check material (green sheath) in which white sheath first appeared was taken for the standard. Because of the smallness of the plots, the upper and lower leaves were analyzed together. This table certainly brings out the fact that strains of white sheath may be isolated which differ greatly in chlorophyll content.

As yet, a genetical analysis of this striping of the leaves has not been made. Segregation of the striping was noted in the field during the summer of 1925, but definite ratios were not obtained. The fact that all gradations from very vivid striping down to no striping at all were noticed in single plots would indicate that the inheritance of this character is very complex. Before much work can be done on this phase of the problem, it will be necessary to obtain material which is known to be homozygous. The only conclusion

that can be advanced at the present time is that white sheath plants differ greatly in the amount of chlorophyll in their leaves.

Relations of White Sheath to other Factors in Maize.

(1) Shrunken Endosperm and White Sheath.

The counts made on F_2 progenies resulting from crosses between white sheath and shrunken endosperm indicate that these two characters are not closely linked.

Table 6.-- F_2 Progeny $ws_1\ ws_1\ ws_2\ ws_2 SH\ SH \times Ws_1\ Ws_1\ Ws_2\ Ws_2\ sh\ sh$

Pedigree	Parental Combinations		New Combinations	
No.	ws SH	ws sh	Ws SH	ws sh
531604	2	29	39	2
531602	14	67	188	5
531 605	16	63	198	3
Actual	32	159	425	10
Calculated 3:15:45:1	29	147	440	10
Difference	3	12	-15	0

$X^2 = 1.79$

$P = .620167$

In Table 6, there is a close fit between the calculated and observed ratios. The odds against this deviation being due to chance are .6 to 1. Such odds are insignificant. It is true that ear 531604 had a very small number of kernels, and the results from this one ear alone would not prove any thing, but the progenies from ears 531602 and 531605 are fairly large and the data from these ears certainly show that the factor for shrunken endosperm is not closely linked with either one of the white sheath factors although it may be

loosely linked with one of them.

(2) Aleurone R and White Sheath.

A few of the white sheath crosses involved the factor R. The F_1's ($CCRrAAPrPrWs_1ws_1Ws_2ws_2$) of these were backcrossed with white sheath plants of the composition $CCrrAAPrPrws_1ws_1ws_2ws_2$. The purple and colorless kernels resulting from these backcrosses were planted separately and the results are shown in Tables 7 and 8.

Table 7.--Backcross involving aleurone R and white sheath.

	Colored Aleurone		Colorless Aleurone	
Pedigree No.	Ws	ws	Ws	ws
534201 x 531400	97	26	104	38
Calculated 3:1	92	31	107	35
Deviation	5 ± 3.24		3 ± 3.48	

Table 8.-- Backcross involving aleurone R and white sheath.

Pedigree No.	Colored Aleurone		Colorless Aleurone
	Ws	ws	
534202 x 531400	46	14	
Calculated 3:1	45	15	not planted
	1 ± 2.26		

With both the colored and colorless kernels, in every case a deviation from a 3:1 ratio was obtained which would occur more than once in every two trials by chance. Such small deviations indicate that neither one of the factors for white sheath is closely linked with the aleurone factor R.

Due to lack of time and space, not all of the backcross material involving R and white sheath was planted. Since back-

crosses involving white sheath give a 3:1 ratio of normal to white sheath, the above populations, although small, are sufficiently large to give reliable results.

Data obtained from some F_2 progenies segregating for white sheath and golden plant color (Gg) indirectly suggest loose linkage between white sheath and R. It must be remembered that G and R are on the same chromosome, but some distance apart. The population involved was so small that no definite assertions can be made. Difficulty was encountered in distinguishing golden plants from the double recessive golden-white sheath plants and for this reason no table is given for g. The expected number of non-golden white sheath plants failed to appear. Further work will be carried on in the field to determine whether or not white sheath is linked with G and R.

(3) Liguless Leaf and White Sheath

Table 9 shows the ratios that were obtained from F_2 progenies segregating for white sheath and liguless leaf.

Table 9.-- F_2 progenies segregating for liguless leaf and white sheath.

Progeny No.	Parental Combinations		New Combinations	
	wsLg	Wslg	WsLg	wslg
531200	11	64	181	7
531202	28	99	309	6
532100	10	47	181	3
Actual	49	210	671	16
Calculated 3:15:45:1	44	222	665	15
	-5	+ 12	-6	-1

$X^2 = 1.33$

$P = .723972$

The difference between the actual and calculated ratios is very small, and X^2 is only 1.33. The odds against this deviation being due to chance are only .4 to 1. These figures show that white sheath and liguless leaf are not closely linked.

Summary

1. White sheath, a chlorophyll abnormality of maize, is shown to depend for its expression on the presence of two complimentary recessive factors (ws_1 ws_1 ws_2 ws_2). The great variation in the intensity of this character makes it seem likely that additional modifying factors are involved in its expression.

2. Crosses between the white sheath used in this study and Kempton's white sheath prove that the latter type also carries the two factors ws_1 and ws_2.

3. Chlorophyll analyses show that the leaves of different types of white sheath plants differ greatly in chlorophyll content.

4. Linkage studies show that white sheath is not closely linked with shrunken endosperm (sh), aleurone (R), or liguless leaf (lg).

5. The close fit of the actual to the theoretical ratios in Tables 2 and 3 indicate that the two recessive factors causing white sheath (ws_1 and ws_2) are inherited independently of each other.

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