PRODUCTION OF HIGH-PROTEIN MAIZE BY MENDELIAN METHODS¹

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INTRODUCTION

Some plant breeders have preferred to attack crop-improvement problems by empirical methods while others have thought it first necessary to learn the genetics of important crop characters. Thus we have such studies as the Illinois continuous-selection experiments for the purpose of producing maize races which differ in the greatest possible degree in certain chemical constituents such as high and low oil and high and low protein. Experiments of this nature show very clearly the possibilities of plant breeding. They have been widely quoted as illustrations of the creative power of selection. While they show the possibilities of selection they do not materially increase our knowledge of the genetics of maize.

An appreciation of the necessity of a knowledge of the genetics of maize led Dr. E. M. EAST to start an investigation on the physiology of maize inheritance at the CONNECTICUT EXPERIMENT STATION. The present writer had a part in these investigations during the five-year period from

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1910 to 1914, inclusive. During this period the work was carried on in coöperation with Dr. EAST. From 1915 until the present time studies in maize breeding have been carried on by the writer at the MINNESOTA EXPERIMENT STATION.

The view of learning the genetics of important economic characters and the building of improved maize varieties through the application of these principles has been the main aim at Minnesota. One phase, therefore, of the Minnesota work has been the isolation of self-fertilized lines and their recrossing.

Protein content is of much interest in the light of the Illinois studies and the writer's experience at Connecticut showed that the genetics of protein content was a complex subject. It was therefore decided to continue this investigation with Minnesota varieties. This plan was followed, not because of the belief that high-protein races were necessarily of great economic importance, but because it was thought that a knowledge of the correct genetic methods of obtaining good-yielding, high-protein races would have a direct bearing on the breeding of maize varieties which excel in other important economic characters.

REVIEW OF PREVIOUS STUDIES

A preliminary report which indicated that high-protein maize could be produced by the isolation through self-fertilization of high-protein races and their subsequent crossing was made by HAYES and GARBER (1919). The main purpose of this paper was to show that the isolation of self-fertilized lines and their subsequent crossing was a logical method for the production of improved economic varieties. Since the publication of this preliminary note, JONES (1920) has discussed the self-fertilization method of corn improvement in some detail. The views of the writer do not materially differ from those of JONES with one exception. JONES states that the recrossing of selfed lines and subsequent field selection will probably lead to the production of a variety which does not materially differ from the normal variety from which the self-fertilized lines were obtained. As all corn varieties contain many abnormalities, the elimination of these and the subsequent crossing of lines which seem of most promise seems a promising method of producing an improved variety.

EAST and JONES (1921) have recently presented an interesting paper on the genetics of protein content and have reviewed much of the literature in this field. The reader is referred to this paper and to those of JONES (1920) and HAYES and GARBER (1919) for reviews of literature in relation to the problem.

The paper by EAST and JONES (1921) will be discussed later in relation to the facts presented in this paper. The present study helps in a measure to clear up some further points in relation to EAST and JONES's discussion. Much of the data collected at Minnesota will be presented only briefly in summarized form for the purpose of showing results with a different series of varieties.

MATERIALS AND METHODS

Standard Minnesota varieties have been used in this problem. Methods of controlling pedigrees and the production of crossed and selfed seed have been carried on in much the same way as at Connecticut. For this reason it does not seem necessary to further discuss these phases.

One of the difficulties of maize breeding by artificial-pollination methods is the possibility of heavy showers which wet the tassel bags and make pollination difficult. A plan used with advantage under Minnesota conditions is to immediately replace all partially damaged bags after each rain.

Two men work together at pollination, one caring for the bag which covers the silk and the other removing the tassel bag and carefully dusting the pollen over the silk. Various men have assisted in this work: P. J. OLSON and M. N. POPE during 1915 and 1916, R. J. GARBER 1917 to 1920, and FRED GRIFFEE in 1920. The analyses have been made by the Division of Agricultural Biochemistry, the percentage figures for protein content being on a dry basis. All analyses were made in duplicate and officially recognized analytical methods were followed.

Although recognizing that the individual seed is the genetic unit and not the plant, nevertheless it was apparent that the protein content of the seeds of an ear are not greatly modified by the immediate effect of cross-pollination. The analysis of an ear represents therefore the development of protein which is possible in the light of the genetic factors carried by the mother plant and under the environmental conditions under which the plant develops.

The effect of environment and the conditions under which an artificially pollinated ear develops in relation to protein content will be first discussed.

PROTEIN CONTENT IN RELATION TO CULTURAL CONDITIONS

EAST and JONES (1921) present analyses compiled by JENKINS and WINTON showing the percentage protein content of the five subspecific maize groups. These results show that the groups do not differ very widely

in average protein content. On the other hand, the range of variation for different analyses showed a content as low as 7.7 percent in one analysis of flint corn while one analysis of sweet corn showed a content as high as 17 percent. EAST and JONES compared analyses of self-fertilized upper and lower ears for six different plants. In general there was a close agreement between the protein content of the upper and lower ear of the same plant. This shows that position on the plant does not widely modify the percentage protein content.

In 1919 three normal corn varieties and one twelve-year self-fertilized strain of Red Flint were grown under different cultural conditions. In the Plant Pathology plot the environmental conditions were favorable and a heavy application of manure was made. The Plant Breeding plot appeared to lack a normal supply of food nutrients and likewise suffered from lack of moisture. Therefore the plants did not develop very vigorously and many of the leaves showed a light green color about tasseling time. Self-fertilized ears under the favorable and unfavorable conditions were analysed for protein content (see table 1).

TABLE 1

Percentage protein content under favorable and unfavorable cultural conditions.

VARIETY	PLACE GROWN	NUMBER EARS	RANGE	AVERAGE NUMBER SEEDS PER EAR	AVERAGE PROTEIN PERCENTAGE	PROTEIN P. PATHOLOGY MINUS PROTEIN P. BREEDING
King Phillip	Plant Pathology	10	12.03-14.78	228	13.64	
	Plant Breeding	15	7.83-14.09	224	11.28	+2.36
Rustler	Plant Pathology	9	9.16-14.82	296	12.35	
	Plant Breeding	4	8.97-12.81	308	10.94	+1.41
Red Flint selfed 12 years	Plant Pathology	39	12.73-14.70	112	13.67	
	Plant Breeding	7	12.69-13.86	91	13.36	+0.31
Minnesota No. 13	Plant Pathology	10	10.91-14.38	471	13.08	
	Plant Breeding	5	8.75-13.75	400	11.51	+1.47

Results in 1920 again show that protein content is very markedly influenced by cultural conditions. Ten ear samples obtained from normally pollinated Minnesota No. 13 were taken from each of two rows of Minnesota No. 13. Border rows of Minnesota No. 13 were grown which surrounded each row from which ten ear samples were taken. The ten ears for each sample were from consecutive plants in the row, the plants being spaced eighteen inches apart in the row. Results were as follows:

It is apparent that the samples from row 108 are uniformly higher in protein content than the samples from row 96. Thus, as with most economic characters, it is impossible to determine the genetic characters of a plant without growing and examining its progeny.

Correlation between percentage protein content of self-fertilized ears grown in 1919 and average percent protein in the progeny, 1920.

1919 protein content selfed ears	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5
8.5	1														
9.0		1													
9.5			1												
10.0				1											
10.5					1										
11.0						1									
11.5							1								
12.0								1							
12.5									1						
13.0										1					
13.5											1				
14.0												1			
14.5													1		
15.0														1	
15.5															1

$r = +.190 \pm .085$

TABLE 4

Correlation between number of seeds per ear and protein content in first-year selfed ears of Mercer Flint.

		Number of seeds per ear										
		75	125	175	225	275	325	375	425	475		
Percentage protein content	11.5					1	1				2	
	12.0		1		1	1					3	
	12.5		1		2				1	1	5	
	13.0	1			3	2					6	
	13.5		1		2		1				4	
	14.0		1		1						2	
	14.5					2					2	
	15.0			1		1					2	
	15.5										0	
	16.0		1								1	
		1	5	1	9	7	2	0	1	1	27	

$r = -.254 \pm .121$

TABLE 5

Correlation between number of seeds per ear and protein content in first-year self-fertilized ears of Minnesota No. 13.

		Number of seeds per ear										
		75	125	175	225	275	325	375	425	475		
Percentage protein content	10.0				1						1	
	10.5										0	
	11.0										0	
	11.5		1								1	
	12.0			1		1		1			3	
	12.5			1		1					2	
	13.0			1	1	2	1				5	
	13.5			1	2	1	1			1	6	
	14.0		1	1	1		1				4	
	14.5		2	1	1						4	
Percentage protein content	15.0	2	1	1							4	
	15.5		1		1						2	
		2	6	7	7	5	3	1	0	1	32	

$r = -.357 \pm .104$

TABLE 6

Correlation between number of seeds per ear and protein content in first-year selfed ears of Rustler Dent.

		Number of seeds per ear							
		125	175	225	275	325	375		
Percentage protein content	10.0						2	2	
	11.5				1			1	
	12.0		1					1	
	12.5			3	4	2		9	
	13.0		3			1		4	
	13.5		2	1				3	
	14.0	1	1		1			3	
	14.5		1					1	
	15.0							0	
	15.5			1				1	
		1	8	5	6	3	2	25	

$r = -.643 \pm .104$

TABLE 7

Correlation between number of seeds per ear and protein content in Minnesota No. 13 strain, 13-46-227-1-6, which has been self-fertilized for five years.

		Number of seeds per ear					
		75	125	175	225		
Percentage protein content	14.5				1	1	
	15.0			1		1	
	15.5			1	1	2	
	16.0	1	1			2	
	16.5		1	1		2	
	17.0		1	3		4	
	17.5	1				1	
	18.0		1			1	
		2	4	6	2	14	

$r = -.536 \pm .128$

TABLE 8

Correlation between number of seeds per ear and protein content in self-fertilized ears of related strains, 13-30-211-10-6, -10-7, -10-18, and -10-3, which have been self-fertilized for five years.

Percentage protein content	Number of seeds per ear								
	125	175	225	275	325	375	425	475	525
11.0						1			1
12.0		1							1
12.5									0
13.0				2	1	1			4
13.5				1					1
14.0		1		1	1				3
14.5		2		2		3		1	8
15.0		1	2	1	2	2		1	10
15.5		2		1	1	2		1	7
16.0		2	1			1	2	1	7
16.5	2	4	1	1		1	3		12
17.0		2	2			1			5
17.5		2	2	2		1			7
18.0									0
18.5		1		1					2
	2	18	8	12	5	13	5	4	1
	$r = -.198 \pm .079$								68

TABLE 9

Correlation between number of seeds per ear and protein content in selfed ears of F_1 crosses, 13-30-211-13 $\times$ 13-46-226-1 and 13-30-211-7 $\times$ 13-46-226-2.

Percentage protein content	Number of seeds per ear								
	25	75	125	175	225	275	325	375	425
10.5							1		1
11.5								1	1
12.0				1					1
12.5							2		3
13.0								1	2
13.5						3			3
14.0						1			1
14.5				2	2	2	1		7
15.0	1		1	1	2	2		2	9
15.5	1	1		8	1	3	1		15
16.0	1	1	2	3	2	1			10
16.5		1	1						2
	3	3	4	15	7	13	5	2	3
	$r = -.553 \pm .063$								55

of the ears of the Red Flint strain which had been self-fertilized for twelve years were about the same for plants growing under unfavorable as under favorable conditions.

COMPARISON OF PROTEIN CONTENT OF SELF-POLLINATED AND WIND-POLLINATED MAIZE

Results obtained in the early years of study showed that self-pollinated ears were markedly higher in percentage protein content than normally pollinated ears. This was thought at first to be due largely to some change in light or temperature conditions which resulted from covering the self-fertilized ears with a paper bag. A later explanation advanced was given by EAST and JONES (1921), who believe a part of the difference in percentage protein content between self-pollinated and normally pollinated seeds is due to the immediate heterotic effect of cross-pollination. The best sort of evidence to show the immediate effect of cross-pollination is a comparison of selfed and cross-pollinated seeds of the same ear. Results of this nature are discussed in some detail by EAST and JONES who present a total of 52 analyses in which comparisons are made of self- and cross-pollinated seeds from the same ears. Averaging the results presented by EAST and JONES gives a protein content of 11.61 percent for cross-pollinated seeds and 11.76 percent for self-pollinated seeds. This is a reduction of 1.3 percent in protein content as an immediate effect of cross-pollination. Nine ears from similar pollinations, in which low and medium protein strains were used, were studied at Minnesota. The percentage protein content of the self-fertilized seeds was 15.42 and of the cross-pollinated seeds on the same ears 15.48. These differences are very small in relation to the large differences shown by EAST and JONES between open-pollinated and self-pollinated ears.

A fact of some interest not brought out by EAST and JONES would seem to show that the covering of the ear with a bag does not in itself affect the percentage protein content of the seeds produced by such a covered ear. To illustrate this point open-pollinated (O.P.) and selfed ears (S.) of the 1919 crop season are compared for protein content (see table 14).

Very marked differences in protein content for open-pollinated and self-pollinated seeds are shown for ears of F_1 crosses between high- and low-protein races, a difference of over 50 percent being obtained in one case. Of four normal varieties, three gave markedly lower protein content in open-pollinated than in self-pollinated ears. Without discussing the other results in detail we may briefly note the strains which have been selfed for several years. Of five strains of Minnesota No. 13 self-fertilized for

TABLE 14

Comparison of protein content of open-pollinated and self-fertilized ears in relation to number of years that the strain has been selfed. Grown in 1919.

VARIETY AND STRAIN NUMBER	SELFED OR OPEN-POL- LINATED	NUMBER OF YEARS SELFED	NUMBER SELFED EARS	PROTEIN CONTENT	DIFFERENCE S.—O.P.	INCREASE PRO- TEIN CONTENT S. OVER O. P. PERCENT
High Protein × Low Protein, F ₁	S.	1	6	13.62		
	O.P.	0		8.68	4.94	58.3
High Protein × Low Protein, F ₁	S.	1	4	10.99		
	O. P.	0		8.49	2.50	29.4
High Protein × Low Protein, F ₁	S.	1	3	12.28		
	O. P.	0		8.49	3.79	44.6
Longfellow	S.	1	10	13.67		
	O. P.	0		14.11	— .44	—3.1
King Phillip	S.	1	15	12.38		
	O. P.	0		9.14	3.24	35.4
Minnesota No. 13	S.	1	6	11.51		
	O. P.	0		8.72	2.79	32.0
Rustler 31	S.	1	4	10.74		
	O. P.	0		8.95	1.79	20.0
Mercer 33—18	S.	2	12	12.68		
	O. P.	1		9.45	3.23	34.2
Mercer 33—27	S.	2	7	12.20		
	O. P.	1		10.77	1.43	13.3
King Phillip 30—26	S.	2	5	13.83		
	O. P.	1		12.50	1.33	10.6
King Phillip 30—4	S.	2	7	13.00		
	O. P.	1		11.37	1.63	14.3
Rustler 30—23	S.	2	6	13.38		
	O. P.	1		10.30	3.08	29.9
Minnesota No. 13 13—26	S.	2	7	11.67		
	O. P.	1		9.27	2.40	25.5
Minnesota No. 13 13-3	S.	2	3	13.01		
	O. P.	1		10.55	2.46	23.3

TABLE 14 (continued)

VARIETY AND STRAIN NUMBER	SELFED OR OPEN-POLLINATED	NUMBER OF YEARS SELFED	NUMBER SELFED EARS	PROTEIN CONTENT	DIFFERENCE S. — O.P.	INCREASE PROTEIN CONTENT S. OVER O. P. PERCENT
Minnesota No. 13 13-22	S.	2	10	13.29		
	O. P.	1		11.99	1.30	10.8
Minnesota No. 13 13-23	S.	2	2	12.19		
	O. P.	1		12.18	.01	0.0
Minnesota No. 13 13-24	S.	2	3	13.01		
	O. P.	1		10.13	2.88	28.4
Minnesota No. 13 13-46-227-1-6	S.	5	14	16.39		
	O. P.	4		14.94	1.45	9.7
Minnesota No. 13 13-30-211-10-3	S.	5	14	15.45		
	O. P.	4		15.87	-.43	-2.6
Minnesota No. 13 13-30-211-10-18	S.	5	18	15.52		
	O. P.	4		15.15	.37	0.0
Minnesota No. 13 13-30-211-10-6	S.	5	20	15.45		
	O. P.	4		16.74	-1.29	-7.7
Red Flint	S.	12	7	13.36		
	O. P.	11		13.68	-.32	-2.3

five years, three gave a higher protein content in open-pollinated than in self-pollinated ears. Likewise the twelve-year self-fertilized strain of Red Flint gave a higher protein content in the open-pollinated ears though the differences were very small. These facts seem to show that covering an ear with a bag does not in itself greatly modify protein content.

The facts presented here and the data of EAST and JONES lead to the conclusion that the main cause of the difference in protein content of self-fertilized and normally pollinated ears is the marked correlation between the percentage protein content of an ear and the number of seeds produced by the ear. This fact deserves careful consideration in an analysis of the effects of continuous selection in self-fertilized lines. On the average there is a gradual decrease in yield in self-fertilized lines of maize which for a considerable number of years or until homozygosis is reached is roughly proportional to the number of years which the strain has been self-fertilized. During the period of this reduction in yield there is a corresponding reduction in the average number of seeds produced by either self-pollinated or

normally pollinated ears. This leads naturally, when one considers the correlations previously noted, to a gradual increase in percentage protein content.

INHERITANCE OF PROTEIN CONTENT

It has been noted previously that the percentage protein content of the seeds of an F_1 ear frequently closely corresponds to the percentage protein content of the lower-protein parent. It was also demonstrated by HAYES and GARBER (1919) that F_1 ears of crosses between self-fertilized high-protein races have considerably lower percentage protein content than the parental self-fertilized lines. These facts and a considerable body of similar evidence presented by EAST and JONES led these investigators to conclude that although "there was a semblance of dominance of low protein" over high protein, this was largely due to the effect of heterosis. This apparent dominance has, however, much value from the breeding standpoint. Whether the apparent recessiveness of high protein is due to genetic factors for protein content or partly due to the effect of other growth factors does not detract from the value of the relation between protein content of a self-fertilized ear and the protein content of its progeny. As high protein apparently behaves in inheritance as a recessive character, all that is necessary in order to isolate high-protein races is to practice self-fertilization and then determine which lines breed true for higher protein content by an analysis of the average of the progeny. Even though continued selection isolates higher-protein races, this may not always be due to the isolation of genetic factors for a greater synthesis of protein but due to the elimination of growth factors and the consequent reduction in size of ear and seed which results in a higher percentage protein content.

Crosses between high- and medium-protein races which had been isolated through self-fertilization were made at Minnesota in 1918. A considerable number of F_2 ears were grown in 1920 and normal pollination was permitted. The percentage protein content of the F_2 -generation ears was compared with the content of ears of Minnesota No. 13 and with self-fertilized ears of the long-time-selfed strain of Red Flint which was grown in 1919 (see table 15).

The F_2 generation was about as variable for percentage protein content as normal ears of Minnesota No. 13. The low coefficient of variability of the Red Flint ears is of considerable interest. Comparatively homozygous lines for protein content may therefore be isolated, since segregation does occur in those generations which are commonly known as the segre-

gating generations. Protein content is therefore inherited in much the same way as other characters which are dependent for their full expression on many different inherited factors of the plant and likewise upon environmental conditions.

TABLE 15

Comparison of variability for percentage protein content of normally pollinated Minnesota No. 13 ears, F₂ open-pollinated ears of a cross of Minnesota No. 13 high-protein strain × Minnesota No. 13 medium-protein strain, and self-fertilized ears of a twelve-year self-fertilized strain of Red Flint (1920).

SOURCE	PROTEIN PERCENTAGE CLASSES												TOTAL	MEAN	C. V.
	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0			
Normal Minnesota No. 13	7	8	12	19	18	10	12	2					88	12.2 ± .07	7.46 ± .38
F ₂ cross.....		2	3	9	12	21	16	11	7	4	2	1	88	13.3 ± .07	7.59 ± .39
12-year self-fertilized Red Flint.....						2	6	17	17	4			46	13.7 ± .05	3.50 ± .25

ISOLATION OF HIGH-PROTEIN RACES THROUGH SELF-FERTILIZATION

EAST and JONES have given considerable evidence to show the ease with which high-protein races may be isolated through self-fertilization. For this reason Minnesota data will be only briefly noted. The facts are presented solely for the purpose of showing that high-protein races may be isolated in standard Minnesota varieties (see table 16).

It hardly seems necessary to emphasize these results by extended discussion. The results corroborate those of EAST and JONES and show the value of the method. Perhaps it may serve a useful purpose to point out that similar methods seem the logical means of isolating self-fertilized families which are resistant to plant diseases such as corn smut and root rot. Chlorophyll degeneracies which are prevalent in nearly all commercial varieties may be eliminated by similar means. The idea deserves wide consideration in the hands of plant breeders interested in maize. If all experimental stations in the corn belt could vigorously attack the problem and if coöperation between investigators could be more fully developed the results would be of undoubted value to the corn-growing industry.

THE USE OF SELF-FERTILIZED LINES IN MAIZE IMPROVEMENT

Several methods of the utilization of self-fertilized lines suggest themselves. JONES'S (1920) suggestion of the double cross seems worthy of extended trial. The practical difficulties of the method, while not so

great as the use of F_1 crossed seed of two self-fertilized lines (a method originally outlined by SHULL), are due to the necessity of producing four

TABLE 16

Isolation of high-protein strains by self-fertilization.

STRAIN NUMBER	NUMBER YEARS SELFED	YEAR GROWN	PROTEIN CON- TENT OF PARENT	PROTEIN CON- TENT BULK ANALYSIS OF PROGENY
Minnesota No. 13 13-30	1	1916	16.52	14.47
Minnesota No. 13 13-46	1	1916	16.66	15.82
Minnesota No. 13 13-12	1	1916	16.99	14.10
Minnesota No. 13 13-30-211	2	1917	16.90	13.06
13-46-226	2	1917	—	12.44
13-46-227	2	1917	17.16	14.03
13-12-181	2	1917	17.40	10.87
Minnesota No. 13 13-30-211-10	3	1918	—	14.88
13-46-227-1	3	1918	15.10	15.31
13-46-227-3	3	1918	12.72	14.88
13-12-181-2	3	1918	15.28	15.81
Minnesota No. 13 13-30-211-10-6	4	1919	17.19	15.88
13-30-211-10-14	4	1919	17.19	15.45
13-30-211-10-18	4	1919	17.69	15.15
13-30-211-10-3	4	1919	16.50	15.87
13-46-227-3-6	4	1919	16.19	14.94
13-46-227-1-8	4	1919	15.31	—
13-12-181-2-1	4	1919	15.69	—
Minnesota No. 13 13-46-227-3-6-26	5	1920	15.59	17.87
13-46-227-3-6-20	5	1920	16.50	17.62
13-30-211-10-6-6	5	1920	16.73	18.12
13-30-211-10-6-10	5	1920	16.57	16.59
13-30-211-10-14-9	5	1920	17.16	17.90
13-30-211-10-14-13	5	1920	18.43	18.22
13-30-211-10-18-22	5	1920	15.20	17.46
13-30-211-10-18-25	5	1920	17.47	16.90
13-12-181-2-1-1	5	1920	14.63	16.44
13-12-181-2-1-9	5	1920	16.72	16.45
13-12-181-2-1-14	5	1920	14.81	18.00
Rustler 31-26-6	2	1920	14.70	17.22
King Phillip 30-4-3	2	1920	13.91	17.50
Mercer 33-27-1	2	1920	15.00	15.03

strains annually and the making of three crosses before obtaining seed for commercial planting.

EAST and JONES point out a logical means of improving strains and show that for high protein the method has proven valuable. This is the isolation of high-protein races, the cross of these races and the subsequent selection in the segregating generations of those self-fertilized ears which

FIGURE 1.—Average ears of Minnesota No. 13 grown in comparison with the double cross of four high-protein strains, 1920. (Photo by HORTON.)

FIGURE 2.—Double cross of four high-protein self-fertilized strains. Same focus as above ears of Minnesota No. 13, 1920. (Photo by HORTON.)

excel for protein content. This is the Mendelian plan which has been adopted by several breeding centers as a means of increasing the yield or improving the economic characters of self-fertilized plants such as our small grain crops.

Another method deserves trial by maize breeders. After several strains have been isolated they may be crossed and field selection practiced for desirable stalks and ears. Such a synthetically produced variety should in some cases, depending on the value of the combination obtained from crossing the selfed strains, give a variety of maize which is a great improvement over the normal variety from which the selfed strains were originally obtained.

FIGURE 3.—Comparative vigor of Minnesota No. 13, left, and the double cross of four self-fertilized high-protein strains at the right. 1920. (Photo by HORTON.)

A double cross of four high-protein strains was tested in 1920. One of the original crosses was made by JONES of Connecticut who used a high-protein strain of Leaming and one of Illinois High Protein. The cross between two Minnesota No. 13 high-protein strains was crossed with the F_1 cross made by JONES and the double cross grown in replicated plot tests in 1920 and compared with Minnesota No. 13. The double cross was slightly later than Minnesota No. 13 but it produced ears very freely and looked very promising. Due to dry weather late in the season the Minnesota No. 13 filled somewhat better than the double cross. Compara-

tive yields and protein content of Minnesota No. 13 and of the double cross are given in table 17 (see figures 1 to 3).

TABLE 17
Comparison of protein content, yields and shelling percent of Minnesota No. 13 and reciprocal double crosses.

SOURCE	SHELLED CORN PER STALK GRAMS	SHELLING PERCENT	PERCENTAGE PROTEIN CON- TENT
Double cross.....	128.2	77.0	14.92
Reciprocal.....	141.9	76.0	15.14
Minnesota No. 13.....	144.9	80.6	12.37

An attempt was started in 1916 to produce synthetically a high-protein variety of corn by crossing isolated high-protein races of Minnesota No. 13

FIGURE 4.—Average ears of Minnesota No. 13. Isolated pasture plot, 1920. (Photo by HORTON.)

FIGURE 5.—Average ears of High Protein Minnesota No. 13. Produced by crossing two high protein strains and subsequent selection. Isolated pasture plot, 1920. Same reduction as figure 1. (Photo by HORTON.)

The original cross was made between two apparently high-protein strains. In the F_2 generation, however, lethal white chlorophyll seedlings were obtained. F_3 lines were grown from self-fertilized F_2 ears and reciprocal crosses within a line and between different lines were made. Only those families were used which were homozygous for an absence of the white-seedling degeneracy. Seeds of those F_3 reciprocal crossed ears which showed high protein content in both parents, were mixed together and used to plant an isolated plot. A determination of the yield and protein content of this isolated plot was made and compared with a similar plot of Minnesota No. 13 (see table 18 and figures 4 and 5).

TABLE 18

Comparison of yields and protein content of normal Minnesota No. 13 and a synthetically produced Minnesota No. 13 obtained by crossing high-protein strains.

SOURCE	YIELD EAR-CORN PER STALK, GRAMS	PROTEIN CONTENT PERCENTAGE
Normal Minnesota No. 13.....	122.6	12.01
High Protein No. 13.....	122.6	14.99

The results indicate the value of the method. These studies have led to the attempt to breed maize at Minnesota for economic characters other than protein by an adoption of a Mendelian plan which, except for the details of the work, is not essentially different from the method which is being used for small grains and which has already proved its value through actual test.

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