White Hulless Popcorn:
FIFTEEN GENERATIONS OF SELECTION FOR IMPROVED POPPING EXPANSION

By B. L. Weaver
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FIFTEEN GENERATIONS OF SELECTION FOR IMPROVED POPPING EXPANSION IN WHITE HULLESS POPCORN

By B. L. Weaver and A. E. Thompson[1]

POPPING EXPANSION — the increase in volume of the popcorn kernel after popping — is an economically important quality factor. Greater expansion not only is a factor in improving eating quality; it also contributes to higher yields of the popped product. Each volume increase in expansion means an increased return to the commercial popper of about $4.50 from a 100-pound bag, according to Eldredge's calculations (10)*.

Exploratory tests with commercial varieties of popcorn at the Illinois Agricultural Experiment Station were begun in 1937. Popping tests showed wide variation in both quality and popping expansion. In 1938 a two-ear sample of a white hulless type was obtained from a farmer in central Illinois who claimed to have grown this strain for 25 years.[2] A portion of the seed was planted in 1938 and, when compared with other hulless varieties, it was found to be later in maturity, far more vigorous, and higher yielding. The quality and ability to pop were considered only fair. It was thought that a recurring type of selection for increased popping expansion over a period of years would result in a general improvement in the performance of the strain. The new accession was grown in larger quantity in 1939 and the initial selection for improved popping expansion was made. Fifteen generations of selection were completed in 1953. From this material was developed the high-quality, open-pollinated variety, Illinois Hulless. Numerous inbred lines have also been developed and experimental hybrids produced.

The objective of this publication is to present the significant findings of this study, and to point out certain implications suggested by the breeding method that was employed.

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* This and similar numbers refer to the literature citations on page 18.

Review of Literature

Brunson (2) demonstrated that continuous selection of seed ears on the basis of individual popping tests over a seven-year period could improve the popping expansion of a strain. The variety Sunburst, which was subsequently named Supergold, was developed by this method from the unselected variety Queen Golden. The average popping expansion was raised from 19.3 volumes for Queen Golden to 26.1 volumes for Sunburst. Brunson stated that the ears of Sunburst were less variable in popping expansion than Queen Golden, and the occasional very poor ear frequently found in unselected sorts had been virtually eliminated.

Factors affecting popping expansion are adequately discussed and summarized by Huelsen and Bemis (17). Additional information is available on popping expansion and the derivation of varieties and hybrids of popcorn (3, 11, 25).

Willier and Brunson (28) conducted rather extensive experiments on the relationship of kernel characteristics to popping expansion of White Rice and Yellow Pearl varieties. The kernel characters studied include: percentage of soft starch; weight of 100 kernels; number of kernels in 25 cc.; and length, breadth, and thickness of kernel. The correlations involving expansion indicate that in general those ears with smaller kernels and those with kernels containing the least proportion of soft starch gave the greatest increase in volume on popping. They further concluded that large kernels were more likely to have a large proportion of soft starch than small kernels. Length, breadth, and thickness of kernel were all negatively correlated with expansion. Length and thickness were more highly correlated with starchiness than with weight, and breadth was correlated about equally with starchiness and with weight. The multiple correlation coefficient between expansion and the kernel characters was calculated. Only approximately one-third of the variability of expansion is accounted for by variations in the size and starchiness of the kernel. Lyerly (23) concluded from correlation studies that smaller, shorter, and narrower kernels tended to give the highest popping expansion. These data agree with those of Willier and Brunson (28) for weight, length, and width of kernels. Lyerly found, however, that thickness of kernel was positively correlated with popping expansion. Density of kernel and the ratio of thickness to width were also positively associated with popping expansion.

Crumbaker *et al.* (7) investigated the inheritance of popping expansion by studying segregating progenies of dent-popcorn crosses. They concluded that low popping expansion was partially dominant over high. They observed that two backcrosses to the recurrent parent were sufficient to recover popping expansion equal to that of the popcorn parent inbreds. Johnson and Eldredge (21) studied the performance of recovered popcorn lines derived from outcrosses to dent corn. The recovered popcorn lines were agronomically superior to the original popcorn parents. Among 74 recovered lines tested in crosses, 31 percent were significantly lower, 7 percent significantly higher, and 62 percent not significantly different in popping expansion from the performance of the original parents. Johnson and Eldredge (21) suggest that since recovery of popping expansion was not difficult, the character must be rather simply inherited.

Some inbred lines of popcorn have been found to be superior to others in transmitting popping expansion and popcorn-type ears to the progeny, thus indicating differences in combining ability among the lines tested (7). Data presented by Grissom (13) and Clary (4) also demonstrate the existence of different genetic systems for the inheritance of popping expansion among the popcorn lines they studied. A heritability value of 70 percent for popping expansion was calculated by Grissom (13). Calculations made from two sets of single-cross data presented by Clary (4) give heritability values of over 90 percent. The minimal estimate of the number of genes controlling popping expansion in Grissom's (13) study was three to four. Clary's (4) estimates of minimum numbers of effective factors among several inbred lines ranged from one to five. Clary concluded that the estimates were too low, but the maximum number might be less than 20.

Materials and Methods

The initial selection of 201 ears was made in 1939. These ears and those selected in subsequent years were tested for popping expansion. Only those ears that gave high values for popping expansion were saved for seed to be planted ear-to-row the next year. From 1939 to 1945 the number of ears sampled yearly varied from 200 to 320.

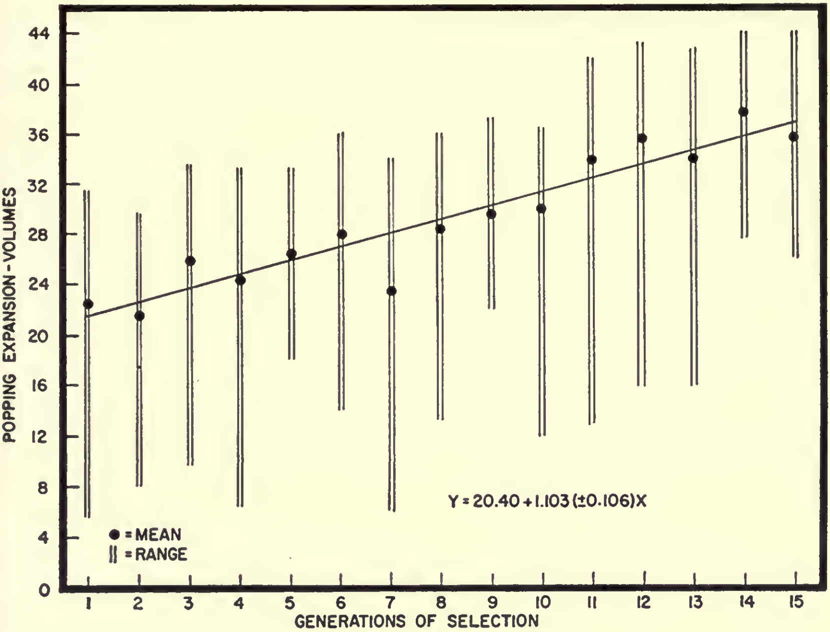
In 1946 the procedure was changed slightly to what might be termed a modified mass selection or "truncation selection," in which seeds for the next year's plantings are taken only from ears having the highest expansion within each of five populations. The large number of individual ear selections was reduced to those from the top five lines, which were given numbers from 1 to 5. From 1946 to 1953 the experimental procedure remained constant. Each of the five lines was grown in plots containing 14 rows of 16 hills each. The spacing was 3′ x 3′ with three seeds planted per hill. The five plots were isolated from other corn plots. However, the five individual plots were contiguous and linearly deployed in a north-south direction. The positions of the individual plots were not randomized, but were maintained in the same systematic arrangement throughout the course of the experiment. Sixty ears from each of the five plots were selected for testing each year and seed from the top-ranking ears from each of the five plots was planted the following year. Usually seed from the top three or four ears within a line was sufficient to make the next year's planting.

The selected ears were all tested for popping expansion. A 25-cc. sample of shelled corn was conditioned to the optimum moisture content by a method adapted from that developed by Dexter (8). The samples were then dry-popped in an ordinary flat-shaker popper. The popper was fitted with ball-bearing rollers that ran on a small track mounted over a gas burner. The popper was agitated at a constant speed by means of a connecting rod, eccentrically driven by a small electric motor. To reduce variability, check samples from a uniform lot of Illinois Hulless were popped. Every fifth sample was a check, and if any significant variation occurred in the performance of the check, necessary adjustments in popping procedure were made. The volumetric increase of the corn after popping was measured in a graduated glass cylinder.

Additional data were collected on each of the selected ears: ear length, ear width, ear weight, weight of shelled corn, and shelling percentage. Correlation analyses were made to determine the possible association of popping expansion and these supplementary measurements. Notes were also taken on whether the kernels were pointed or rounded.

Experimental Results

The method of selection utilized proved to be effective in improving the level of popping expansion within the population. The average popping expansion of the population in 1953 was approximately 57 percent greater than the average of the original population in 1939 (Fig. 1). The means of the populations for the last five generations are actually above the highest variates of the first five generations. The lowest variates of the last two generations are approximately four volumes higher than the population means of the first two generations. It would appear that a maximum level had not been reached at the termination of the experiment, although there is some indication that the maximum was being approached.



Improvement made in popping expansion during 15 generations of selection within open-pollinated, white hulless type popcorn. The graph shows the means and best-fitting, straight-line trend, with the range of highest and lowest variates for each generation. (Fig. 1)

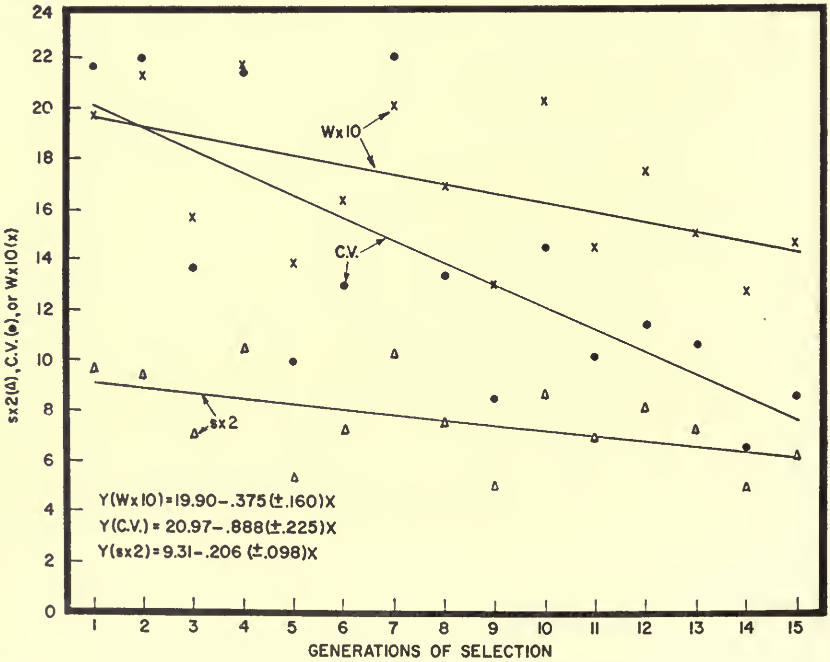
Variability within the 15 selected generations. The variability within the total population tended to decrease (Fig. 2). Variability within the population has been measured by the standard deviation, coefficient of variation, and Weinberg's formula (27). The Weinberg constant (W) was calculated by the formula:

$$W = \frac{s\sqrt{(\text{Highest variate} - \text{lowest variate})}}{\sqrt{(\text{Highest variate} - \text{mean})\ (\text{Mean} - \text{lowest variate})}}$$

where s = the standard deviation of the sample.

The magnitude of the standard deviation and that of the Weinberg constant tend to be parallel. The Weinberg constant is modified by the skewness of the distribution, which is, to a certain extent, taken into account by the denominator of the formula. The extent to which the distributions of the yearly populations are skewed is clearly indicated in Figure 1 and Table 1. Since the Weinberg constant takes the degree of skewness into account, it should present a more accurate picture of the variability than the standard deviation. The slight downward trend for the standard deviation in part accounts for the increased reduction in the magnitude of the coefficient of variation, since the means for each generation tend to increase.

The significance of the regression coefficients for the three measures of variability were tested by means of the *t* test. The *t* values were 2.10, 3.94, and 2.34 with 13 degrees of freedom respectively for the standard deviations, coefficients of variation, and Weinberg constants. The latter two regressions were significantly different from zero at the 0.01 and 0.05 levels of probability respectively. The regression coefficient of the standard deviations was not significantly different from zero at the 0.05 level, but did have a probability value between 0.05 and 0.10. One may conclude from these tests that variability in popping expansion within the population has definitely decreased over the 15 generations in which selection has been practiced.



Effect of selection for increased popping expansion on the extent of variability within the 15 generations as measured by the Weinberg constant (W), coefficient of variation (C.V.), and standard deviation (s); actual data and best-fitting, straight-line trends. (Fig. 2)

Table 1. — Change in Composition of Population Effected Through 15 Generations of Selection for Increased Popping Expansion

Year tested	Number of ears	Percentage distribution of popping volumes											Mean popping volume (x̄)
		2.0–5.9	6.0–9.9	10.0–13.9	14.0–17.9	18.0–21.9	22.0–25.9	26.0–29.9	30.0–33.9	34.0–37.9	38.0–41.9	42.0–45.9	
1939	201	0.50	1.00	3.48	12.94	22.39	33.33	23.88	2.49	.....	.....	....	22.25
1940	200	....	1.50	7.00	10.00	26.00	35.50	20.00	.....	.....	.....	....	21.69
1941	310	....	0.32	0.32	2.26	9.03	31.94	45.48	10.65	.....	.....	....	26.01
1942	310	....	0.97	3.55	6.77	14.52	25.16	33.23	15.81	.....	.....	....	24.58
1943	222	....	....	....	....	4.50	25.68	58.56	11.26	.....	.....	....	26.61
1944	310	....	....	....	1.29	5.16	14.84	44.84	30.97	2.90	.....	....	28.06
1945	320	....	1.56	4.69	7.81	16.56	31.25	32.19	5.63	0.31	.....	....	23.43
1946	300	....	....	0.33	1.33	4.67	14.00	37.33	36.33	6.00	.....	....	28.51
1947	300	....	....	....	....	.....	6.67	40.33	48.67	4.33	.....	....	29.68
1948	300	....	....	1.00	1.33	2.67	7.33	18.67	50.67	18.33	.....	....	30.17
1949	300	....	....	0.33	0.33	0.33	1.00	4.33	34.33	46.00	13.00	0.33	34.07
1950	300	....	....	....	0.33	1.33	1.00	4.33	18.00	38.67	34.67	1.67	35.61
1951	300	....	....	....	0.33	0.33	2.00	7.00	27.67	49.33	13.00	0.33	34.04
1952	300	....	....	....	....	.....	.....	1.00	3.67	35.00	58.33	2.00	37.81
1953	300	....	....	....	....	.....	.....	3.67	19.00	48.67	27.33	1.33	35.83
All years	4273	0.02	0.28	1.24	2.67	6.48	14.37	24.67	22.02	17.53	10.27	0.40	29.56

Table 2. — Means of Popping Expansion for Selections and Progenies of Five Open-Pollinated Lines Tested and Selected for Eight Generations

Year tested	Means of lines tested (volumes)										Year means (x̄)	
	No. 1		No. 2		No. 3		No. 4		No. 5			
	Selection	Progeny	Selection	Progeny	Selection	Progeny	Selection	Progeny	Selection	Progeny	Selection	Progeny
1946	29.9	30.5	29.1	29.0	28.8	27.5	29.7	28.1	28.2	27.3	29.1	28.5
1947	35.2	30.8	35.1	29.8	33.7	29.6	33.2	29.6	32.3	28.6	33.9	29.7
1948	35.4	32.1	34.6	29.3	34.4	30.3	33.4	29.3	33.6	29.8	34.3	30.2
1949	36.3	34.2	34.6	33.6	35.0	36.4	35.7	32.5	35.7	33.6	35.5	34.1
1950	38.0	36.4	37.5	34.5	40.0	36.4	38.1	35.5	38.3	35.2	38.4	35.6
1951	41.7	34.5	40.5	33.6	41.9	33.9	41.2	34.6	40.3	33.6	41.1	34.0
1952	40.1	38.6	39.6	38.9	39.0	36.8	40.3	37.7	40.5	37.1	39.9	37.8
1953	42.2	38.1	42.4	34.7	41.2	36.2	40.1	35.6	41.0	34.6	41.4	35.8
Line means (x̄)	37.4	34.4	36.7	32.9	36.8	33.4	36.5	32.9	36.2	32.5	36.7	33.2

The composition of the population was markedly changed over the 15 generations of selection (Table 1). The frequency distributions also indicate the extent of the heterogeneity of the generation variances, which was confirmed by Bartlett's test for homogeneity (1). No actual determination can be made to estimate to what extent the heterogeneity is attributable to seasonal fluctuations of the environment or fluctuations in the frequency of genetic factors conditioning popping expansion. In addition, there may be an interaction of genes and environment, which should not be overlooked as a possible source of variation.

Analysis of the relationship of progeny to parental selections and nature of variation during the last eight generations of selection. A closer analysis of the variation and effectiveness of selection can be obtained by studying the last eight generations of selection. In 1946 the top five lines were selected and continued throughout the remainder of the experiment. The five lines actually trace back to only two original ears tested in 1939 as shown below:

1939	1940	1941	1942	1943	1944	1945	1946
71	3	15	10	6	8	1	Line 1
	5	12	16	9	4	2	Line 2
					5	1	Line 3
95	1	16	22	1	4	1	Line 4
				2	2	2	Line 5

The relationship of progeny to parent is clearly evident if the means for the yearly selections within the five lines and their progenies are studied (Table 2). The correlation coefficient for the association of selection and progeny means was + 0.834, which is highly significant. Approximately 70 percent of the variability in the popping expansion of the progeny can be accounted for by the performance of the parental selections. The regression of the means of the selections on the means of their subsequent progenies was calculated. The regression coefficient, $b = 0.678 \pm 0.073$, was highly significantly different from both 0 and 1 as tested by the *t* test. These data indicate to what extent one might predict the performance of progenies of selections made for improved popping expansion. Over the eight-year period the progenies averaged 3.5 volumes lower than the selections from which they were derived.

An analysis of variance was computed for popping expansion of the tested progenies of selections made within the five open-pollinated lines during the last eight generations (Tables 2 and 3). The analysis is presented with some reservation since the variances from generation to generation were highly heterogeneous, as was previously pointed out. The interaction of generations × lines was highly significant when

Table 3. — Analysis of Variance for Popping Expansion of Five Open-Pollinated Lines Tested and Selected for Eight Generations

Source of variation	Degrees of freedom			Mean square
Generations	7			3,388.01**
Linear component		1		19,714.26**
Deviations from linearity		6		666.97**
Lines	4			255.21**
1+2+3 vs. 4+5		1		456.61**
Among 1, 2 and 3		2		266.61*
1 vs. 2+3			1	481.51**
2 vs. 3			1	51.71
4 vs. 5		1		31.03
Generations × lines (Error)	28			45.10**
Within lines within generations (Sampling error)	2360			11.45
Total	2399			

* Exceeds 0.05 level of significance.
** Exceeds 0.01 level of significance.

tested against the sampling variance — within lines within generations. This interaction was chosen as the appropriate error in testing the main effects and the individual comparisons resulting from their breakdown.

The seven degrees of freedom for the means of eight generations were broken down into a linear component and deviations from linearity. A major portion of the variance can be attributed to the nearly linear increase in the mean popping expansion over the eight generations. However, a highly significant deviation exists that is not accounted for by the linear trend.

The nature of the highly significant differences in performance of the five lines is established by the orthogonal breakdown based on the relationship of the lines (see opposite page). The significance and nonsignificance of the comparisons exactly fit the picture of relationship among the lines.

It would appear that even though the lines were grown in contiguous plots, a certain degree of identity was maintained throughout the eight-year experimental period. There must have been a certain amount of flow or exchange of genetic factors conditioning popping expansion between the five populations. However, the line identity does indicate that some difference in gene frequency must have been maintained as a cryptic population characteristic. This would suggest that breeding methods designed to recombine divergent populations derived from some type of a recurring selection program might result in more rapid gain and even greater increases than the method herein reported.

Table 4. — Means and Standard Errors of Measurements Taken on Ears Selected and Tested for Popping Expansion for 15 Generations

Year tested	Number of ears	Measurements of tested ears					
		Popping expansion (volumes)	Ear length (inches)	Ear width (inches)	Ear weight (grams)	Weight of shelled corn (grams)	Shelling percentage
1939	201	22.25 ± .342	4.99 ± .037	1.62 ± .012	99.5 ± 1.21	82.1 ± 1.07	82.3 ± .21
1940	200	21.69 ± .337	4.56 ± .033	1.63 ± .010	99.2 ± 1.08	80.9 ± 0.91	81.6 ± .23
1941	310	26.01 ± .203	4.39 ± .027	1.57 ± .015	93.9 ± 0.76	75.5 ± 0.64	80.5 ± .17
1942	310	24.58 ± .299	4.15 ± .030	1.65 ± .009	96.1 ± 0.87	77.9 ± 0.74	81.1 ± .19
1943	222	26.61 ± .179	4.10 ± .031	1.16 ± .007	80.4 ± 0.77	63.8 ± 0.63	79.4 ± .26
1944	310	28.06 ± .208	4.72 ± .023	1.62 ± .009	89.4 ± 0.71	72.3 ± 1.12	79.8 ± .18
1945	320	23.43 ± .289	4.66 ± .020	1.77 ± .007	107.3 ± 0.78	85.8 ± 0.66	79.9 ± .20
1946	300	28.51 ± .220	4.63 ± .028	1.15 ± .011	118.6 ± 0.79	94.2 ± 0.60	79.4 ± .20
1947	300	29.68 ± .146	4.57 ± .029	1.67 ± .008	86.9 ± 0.69	67.1 ± 0.60	77.1 ± .22
1948	300	30.17 ± .252	5.27 ± .022	1.63 ± .007	107.2 ± 0.67	86.0 ± 0.60	80.3 ± .19
1949	300	34.07 ± .201	4.96 ± .020	1.66 ± .006	104.6 ± 0.63	86.3 ± 0.56	82.4 ± .21
1950	300	35.61 ± .236	5.11 ± .020	1.68 ± .006	109.7 ± 0.82	90.5 ± 0.65	82.8 ± .22
1951	300	34.04 ± .210	5.21 ± .023	1.65 ± .005	104.2 ± 0.60	82.3 ± 0.56	78.9 ± .22
1952	300	37.81 ± .144	4.90 ± .021	1.64 ± .006	91.7 ± 0.67	71.3 ± 0.53	77.8 ± .23
1953	300	35.83 ± .180	4.80 ± .022	1.53 ± .005	75.5 ± 0.58	56.4 ± 0.49	74.7 ± .31

Relationship of popping expansion to supplementary ear characteristics. The length, width, and weight of ear; weight of shelled corn; and the shelling percentage were measured on each ear tested for popping expansion (Table 4). The individual values for popping expansion were statistically correlated with the supplementary measurements to determine the extent of association existing between these variables (Table 5). No consistent relationship exists between popping expansion and ear length. Ear width, ear weight, weight of shelled

Table 5. — Summary of Correlation Coefficients for Popping Expansion and Supplementary Characteristics of Tested Ears Selected for Popping Expansion for 15 Generations

Year tested	Number of ears	Supplementary measurements of tested ears				
		Ear length	Ear width	Ear weight	Weight of shelled corn	Shelling percentage
1939	201	− .177*	− .220**	− .333**	− .388**	− .383**
1940	200	+ .011	− .236**	− .318**	− .424**	− .466**
1941	310	+ .075	+ .018	− .126*	− .232**	− .432**
1942	310	+ .097	− .071	− .132*	− .246**	− .464**
1943	222	+ .013	− .081	− .133	− .207**	− .166*
1944	310	+ .030	− .145*	− .062	− .008	− .282**
1945	320	− .209**	− .128*	− .315**	− .384**	− .263**
1946	300	+ .184**	− .204**	− .173**	− .239**	− .142*
1947	300	+ .033	+ .116*	+ .141*	+ .149**	+ .084
1948	300	+ .096	− .099	− .332**	− .405**	− .382**
1949	300	− .035	− .034	− .193**	− .277**	− .249**
1950	300	− .009	− .134*	− .209**	− .302**	− .191**
1951	300	+ .141*	− .186**	− .289**	− .423**	− .425**
1952	300	+ .197**	− .063	− .022	− .061	− .058
1953	300	+ .073	− .145*	− .074	− .111	− .087
Average	4273	+ .040	− .102**	− .167**	− .240**	− .263**

* Exceeds 0.05 level of significance.
** Exceeds 0.01 level of significance.

corn, and shelling percentage are all negatively correlated with popping expansion. Although the relationships are quite consistent over the 15 generations and the over-all averages are statistically significant, the correlations are not large enough to be of much value in selection or prediction.

Data were also taken on shape of kernels on the individual tested ears. The ears were classified as having either pointed or rounded kernels. The number of ears and mean popping expansion within the two classes were summarized for the years in which comparisons could be made (Table 6). It is clearly evident that ears with pointed kernels gave expansions consistently superior to those for ears with rounded kernels. The significance of this difference is confirmed by the highly significant *t* value for the comparison (Table 6).

Table 6. — Comparison of the Mean Popping Expansion of Ears Classified as to Shape of Kernel — Pointed or Rounded

Year tested	Pointed kernels		Rounded kernels		Difference in mean popping expansion (volumes)
	Number of ears	Mean expansion (volumes)	Number of ears	Mean expansion (volumes)	
1940	138	22.25	62	20.58	1.67
1941	292	26.05	18	24.76	1.29
1942	195	25.75	115	22.57	3.18
1943	171	26.83	51	25.73	1.10
1944	210	28.62	100	26.90	1.72
1945	266	23.88	54	21.20	2.68
1946	290	28.63	10	26.61	2.02
1947	295	29.69	5	29.12	0.57
1949	217	34.46	83	33.06	1.40
1951	209	34.65	91	32.63	2.02
1952	283	37.87	17	36.92	0.95
Means and totals	2566	28.97	606	27.28	1.69

$t = \frac{1.69}{.230} = 7.35^{**}$ with 10 degrees of freedom

** Exceeds 0.01 level of significance.

Discussion and Conclusions

The aim of breeding work is the formation of types of plants adapted to specific conditions. Generally speaking, little is actually known about the extent of variability of plant material. Data are accumulating that indicate the existence of greater variability of plant material than had previously been thought possible. Mather (24) divided variability into two components: (1) free variability which manifests itself phenotypically and (2) potential variability which is released slowly only by recombination of gene complexes governing quantitative characters.

The data presented here appear to be a good example of the release of potential variability. A classical example of such a release is the experiment conducted at the Illinois Agricultural Experiment Station on selection for both high and low oil and protein content in corn. The results of selection for popping expansion confirm in all essential respects those reported by Woodworth *et al.* (29) in their summarization of fifty generations of selection for oil and protein content. They concluded that progress in the direction of selection apparently was still being made in the High Oil and Low Protein strains, while little progress had been made in either High Protein or Low Oil in the last 15 to 20 generations of selection. Two generations of reverse selection, begun in 1948, have indicated that High Oil, High Protein, and Low Protein may still possess considerable genetic variability.

Variability in popping expansion, as measured by both the coefficient of variation and the Weinberg formula, has significantly decreased over the 15 generations of selection (Fig. 2). Woodworth *et al.* (29) reported that variability for high oil, low oil, and high protein content had either increased or remained virtually unchanged over the 50 generations of selection. The trend of variation in response to selection for low protein was downward, and thus in agreement with the popcorn results.

To some extent the reduction of variability over the 15 generations of selection can be attributed to the gradual elimination of the types giving low expansions from the effective breeding population (see Table 1). In general, the elimination of undesirable genotypes of the character under selection is similar to that obtained by selfing and selection. The recurring type of selection program would be slower in bringing this about, but complete fixation would be avoided. Since the recurrent type of selection allows for recombination, new raw material for positive selection is constantly being created. It is only through some such breeding system that a selected population can be advanced to a point where it may exceed the range of the original unselected population, as has been herein demonstrated (see Table 1 and Fig. 1).

One may conclude from these data that the number of genes conditioning popping expansion is relatively smaller than that for either protein or oil content in corn. The inheritance of popping expansion must be considerably more complex than Crumbaker *et al.* (7) and Johnson and Eldredge (21) suggest. The level of popping expansion in their studies was relatively low compared with the population means of the last five generations of selection in the current study. The number of genes differentiating popcorn from other types of corn may be relatively few in number. However, the number of genes conditioning quantitative differences in popping expansion must be of a much higher order.

The consistent negative association of popping expansion and ear width, ear weight, weight of shelled corn, and shelling percentage can be interpreted to confirm that reported by Willier and Brunson (28) and Lyerly (23). Even though these negative relationships are relatively small, they should be considered in a popcorn breeding program since ear and kernel measurements are components of yield. In this instance it would appear that expansion of the popped kernels can be increased by selection, but at the expense of other yield components. However, it might be expected that there could be specific combinations of inbreds that would result in hybrids not exhibiting a negative relationship between popping expansion and the other components of grain yield.

The consistent relationship of kernel shape and popping expansion is also of interest from the standpoint of improving popcorn by plant breeding. In this instance those individuals with pointed kernels consistently outyielded the rounded types. This observed difference may possibly be explained by the difference in shape and conformation of the popped kernels of the two types. The pointed kernels very frequently expand into what is commonly termed the "butterfly type," which has wing-like projections from the sides of the popped kernel. Within this material this type of expansion appeared to be much less frequent among the rounded kernels. Rounded kernels usually form the more compact, "mushroom" type of popped kernel. Differences in frequency of the types of popped kernels could readily alter the volumetric readings of the expanded kernels. Whether such a relationship would exist in types of popcorn other than that used in this experiment is not known.

Considerable attention has been given recently to new breeding and selection systems that maximize the frequency of desirable genes. Sprague and Brimhall (26) point out that under a system of inbreeding and selection within inbred lines, a potential ceiling is established at the time of the first selfing, determined by the genotype of the plants selected. It seemed plausible to them that a much higher potential ceiling might be established by a somewhat different approach. They outlined a general approach to the problem and tentatively termed the new system "truncation selection." The essential features are as follows: evaluate a series of individual plants for a given character, truncate the frequency distribution at some desired level, and intercross the individuals comprising the truncated tail. This recombination would then serve as source material for a new cycle of selection.

Considerable similarity exists between truncation selection and the selection method employed in the study under discussion. The selection methods reported by Woodworth *et al.* (29) and Brunson (2) are also very similar to the truncation-selection method. A breeding system similar to that proposed by Sprague and Brimhall (26) had been suggested previously by East and Jones (9) and Hayes and Garber (15). Maternal-line selection proposed by Fryer (12) to improve seed production of alfalfa and the fixation of selected characters in partially isolated populations of side-oats grama as used by Harlan (14) also bear similarity to the above-cited systems of selection. Selection of a type similar to that cited above has proved effective with animals as well as plants. Craig *et al.* (6) report that selection of a recurrent type was effective for high and low weights in Hampshire swine at 154 and 180 days of age.

The above-mentioned systems all embody the basic principles of recurrent selection. Hull (18) in 1945 proposed a procedure which he called recurrent selection for specific combining ability. Jenkins (19), however, published a detailed description of the recurrent-selection method in 1940. The two differ in that Hull's method used a homozygous tester instead of a heterozygous tester proposed by Jenkins. Comstock *et al.* (5) suggested a system whereby recurrent selection could be carried out reciprocally.

Much effort has been expended in the last decade on testing the effectiveness of systems of recurrent selection. Hayes *et al.* (16) and Johnson (20) present a good review of literature and discuss the utilization of recurrent selection in plant breeding. Johnson (20) classified the systems of recurrent selection into three rather distinct categories, based on objectives and the resulting changes in gene frequency for any given character: recurrent selection for specific combining ability, recurrent selection for general combining ability, and recurrent selection for specific phenotypic characters.

The similarity between recurrent selection for a specific phenotypic character and controlled mass selection was pointed out by Johnson and Goforth (22). They stated that for characters with a relatively high heritability, a system of mass selection in which only desired phenotypes are permitted to interpollinate might prove to be an effective yet simple method of plant breeding. That such a breeding program would be successful is substantiated by the currently reported results, since the increased level of popping expansion resulted from a selection method basically similar to controlled mass selection. It is of interest that Clary (4) suggested that a program of mass selection, followed by recurrent selection either in the original open-pollinated varieties of popcorn or in a synthetic variety made from tested inbred lines, should result in isolation of lines superior in popping expansion to those he investigated.

The similarity between controlled mass selection, truncation selection, and recurrent selection for a specific phenotypic character is rather obvious. Actually it is difficult to make a concise differentiation between these methods. They may differ slightly in operational procedures with the various crops for which they may be employed and in the extent of the selection pressure exerted in each instance on the character under selection. The three methods should yield essentially the same end results.

The method herein reported cannot be considered terminal in breeding a crop such as popcorn in which hybrids are the most acceptable form for commercial production. It should be considered a means of maximizing the frequency of desirable genetic factors and integrated subsequently with the regular methods of inbred production and improvement. If the genetic factors involved are largely additive in effect, inbred lines derived from this material should possess a potentially higher level of effective genetic factors than those isolated from the original population.

Summary

Selection for improved popping expansion through 15 generations was initiated in 1939 and completed in 1953. Individual ears were tested for popping expansion and only those with the highest expansions were planted to produce the next generation. The method of selection was a recurrent type similar to those termed modified mass selection or truncation selection.

The selection method employed proved effective in increasing the level of popping expansion within the population. The mean popping expansion was 22.2 volumes for the initial population and increased to 35.8 volumes at the end of the selection period. The mean increase in popping expansion over the last eight generations was shown to be very nearly linear. The magnitude of the lowest and highest variates also showed a corresponding increase throughout the selection period. The lowest variate increased from 5.6 in 1939 to 26.0 volumes in 1953, while the highest variate increased from 31.6 to 44.0 volumes for the same

period. Cryptic differences in popping expansion appeared to be maintained among the five lines established in 1946 and continued to the end of the experimental period, even though opportunity for genetic recombination existed between the five lines. Variability in popping expansion as measured by the coefficient of variation and the Weinberg formula has decreased significantly over the 15 generations as a result of selection.

A consistent negative correlation between popping expansion and the width and weight of ear, weight of shelled corn, and the shelling percentage was demonstrated, but the association was not considered sufficiently large to be of significant value in selection or prediction. No consistent relationship exists between popping expansion and ear length.

Individual selected ears were classified as having either pointed or rounded kernels. Those ears with pointed kernels on the average yielded 1.69 volumes higher expansion than those with rounded kernels.

This selection method is not considered terminal, but rather a means of maximizing the frequency of desirable genetic factors. It is proposed that such a system would be of value for increasing the frequency of genes that are largely additive in effect before employing the usual methods of inbred production and improvement. Fixation by inbreeding should establish a potentially higher level of effective genetic factors from the selected population than would prove possible from the original population.

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