POPCORN BREEDING

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POPCORN is a peculiarly American crop. Not only was it unknown to white men before the discovery of North America, as was all maize, but its cultivation and use for popping is almost entirely restricted to the New World. European visitors frequently express surprise at this unique form in which corn is available for human consumption.

It seems practically certain that popcorn was grown and popped by the Indians before the coming of Columbus. The records, although fragmentary, indicate that popped corn either whole or pulverized was used in native food dishes by various tribes in both North America and South America. Popcorn kernels and specially shaped earthenware dishes thought to be corn poppers have been discovered among prehistoric Indian remains in South America. In early Spanish writings, reference is made to the rituals of the Aztecs in which one hour before dawn there sallied forth all these maidens... crowned with garlands of maize, toasted and popped, the grains of which resembled orange blossoms, and on their necks thick festoons of the same which passed under the left arm.

BASIS OF POPPING BEHAVIOR

The phenomenon of popping in corn is not limited to popcorn, but is exhibited to the greatest degree in this subspecies (Zea mays var. everta Bailey). Many flint corns under proper conditions will pop passably well, and some of the horny dents will occasionally pop a little. Even among the true popcorns there is a wide variation in the degree of popping. The ability to pop seems to be conditioned by the relative proportion of horny endosperm where the starch grains are embedded in a tough, elastic colloidal material, which confines and resists the steam pressure generated within the granule until it reaches explosive force. Some varieties of sorghum with seed of a dense flinty structure, such as Pink kafir, pop very well. Manufacturers of breakfast cereals have perfected mechanical methods of confining steam pressure within grains until it is suddenly released, when they puff or pop to several times their original volume.

DISTRIBUTION, VARIETIES, AND DESIRABLE QUALITIES

Compared with dent corn, popcorn is a relatively minor crop. Only about 0.1 percent of the total corn acreage of the United States ordinarily is occupied by popcorn. It is grown almost solely for human consumption as freshly popped corn or as a basis of popcorn.

confections. It has approximately the same chemical analysis and the same feeding value as dent corn. Thus, popcorn may be substituted for dent corn as feed for livestock if occasion demands, although the lower acre yield and the hardness of the endosperm, which necessitates grinding, make it uneconomical to do so under ordinary circumstances.

It is probable that popcorn is grown as a family garden crop for home consumption in every State in the Union. A very considerable proportion of the total popcorn production is represented by these small growers whose crop is used in the home or is sold only locally. A multitude of varieties, colors, and types of popcorn are used for this purpose.

Commercial production to supply vendors, manufacturers of popcorn confections, and the general retail grocery trade has been highly specialized and localized until the last 2 or 3 years. Sac and Ida Counties in western Iowa have been the principal center of commercial popcorn production. Valley County in central Nebraska and four or five counties in northeastern Kansas have also been important in commercial production.

Very recently Iowa, Nebraska, and Kansas seem to have been somewhat less important as centers of commercial production. This has been due in part to a changing demand, which in recent years has favored varieties too late to mature satisfactorily in northern regions, but more largely to the unprecedented series of disastrous droughts during the last few seasons that have centered around the traditional commercial popcorn region. As a consequence of crop failures, popcorn prices have been abnormally high, and therefore scattered growers in many localities outside the worst of the drought area have found popcorn growing very profitable during the years when the total production of the country was at a low ebb. Whether the present distribution will continue during years of normal production is a question for the future which only the complex interaction of economic and agricultural factors can decide.

Although there are in existence innumerable types and varieties of popcorn, only five or six are of commercial importance. Until comparatively recently, White Rice, Jap Hullless (Japanese Hullless), and Queen Golden were the chief varieties used. The variety of popcorn called South American, which was introduced some 15 years ago, increased rapidly in favor in the popcorn trade and soon became a serious competitor of the other varieties. The large size of the kernel, its yellow color, and its peculiar "mushrooming" characteristic in popping seemed to catch the public fancy enough so that its toughness and mediocre quality were largely overlooked. An old variety renamed Spanish popcorn was in vogue for a few years, because the large size of its kernels and its ability to withstand processing fitted it admirably for the manufacture of caramel confections. A small-kerneled, smooth, yellow variety of high popping expansion, known variously as Supergold, Sunburst, or Yellow Pearl, also has become of commercial importance. The old Queen Golden corn has now been almost entirely displaced by South American and Supergold, its yellow competitors.

In popcorn the desirable characters to be achieved by the breeder include all of the attributes of a good variety of dent corn, and in addition must include high expansion and tenderness. Fortunately,
high popping expansion and tenderness of the popped kernels seem to be closely correlated, so that in attaining high popability one also is very likely to have a tender product. The absence of a coarse hull and the presence of a good flavor are also desirable characteristics of the final product. Although most people ordinarily do not realize that there are distinctive flavors in various samples of popcorn, these are as characteristic as in different varieties of apples. Some strains have a noticeably sweetish flavor after being popped, some are practically tasteless, while others have a rather strong field-corn flavor.

High expansion in popcorn is dependent upon complete and normal maturity in addition to the inheritance of genes conditioning a dense and elastic endosperm. Since corn diseases usually interfere with normal maturity, it follows that selection for high popping expansion also tends to select for resistance to many of the common corn diseases, such as smut and the stalk and root rots. This is very fortunate for the breeder, since it is, of course, much easier to make improvements in a crop in which desirable characteristics are correlated than in one in which they tend to be mutually exclusive. In the case of popcorn there seems to be a sound basis for placing considerable emphasis on the individual ear-popping test, described later in this article.

**METHODS AND RESULTS IN BREEDING**

**Mass Selection**

Of the various methods of corn breeding that have been tried from time to time, that of mass selection alone has stood the test of time as of general application to improvement within open-pollinated varieties of corn without resorting to inbreeding. This is as true of popcorn as of dent corn. Mass selection lends itself particularly to the improvement of popcorn quality. As in field corn, mass selection in popcorn begins with field selection of a large number of ears from desirable plants when the crop is mature but before the first killing frost occurs. These ears should be dried quickly, but not so thoroughly as they would be for seed. About 14-percent moisture gives nearly maximum popping behavior and insures against loss of viability by freezing under any ordinary storage conditions.

After being numbered for identification purposes, the ears can be popped individually by shelling enough from one side of each to fill a small measure for the popping test. After popping, the volume of the product is measured in a suitable container so that the ratio of the volumes before and after popping may be obtained and recorded as the popping expansion. Unfortunately, a standardized method of testing has never been agreed on, so that comparisons of popping tests made by different people sometimes are misleading. In this laboratory ordinary glass graduates are used, as shown in figure 1.

For individual ear tests a popping charge of 25 cubic centimeters ordinarily is measured out in a small graduate, and the popped corn is later measured in a 1,000 cc graduate. Any convenient modification of this procedure that will give an accurate measure of the popping expansion would do just as well. It is highly important, however, that the tests of the various ears be made under as nearly comparable conditions as possible. The factors particularly to be guarded are:
(1) The moisture content of the ears must remain as nearly constant as possible for the duration of the tests, since moisture content has an important influence on popping expansion. (2) The conditions of popping, such as degree of heat used, absence from drafts, etc., should be the same for all tests. (3) A routine procedure in measuring the samples before and after popping should be followed, in order that the same degree of packing may be obtained for every sample.

When samples from a considerable number of ears from an apparently uniform variety are popped separately, striking differences in the popping expansion of the individual ears will be observed. Usually the best ears will show about twice the popping expansion of the poorest ones. The distribution of popping expansion of 1,152 individual ears taken from a small isolated plot in 1928 is shown in figure 2.

By using only the highest 10 or 15 percent of the selected ears for seed purposes a rather rigid selection on the basis of popping expansion can be made. In order to avoid the injurious effects of close breeding in an open-pollinated variety, care must be exercised not to limit too greatly the number of seed ears utilized to propagate the strain. Although it is difficult to set an arbitrary minimum, a mixture from not less than 50 ears should be used to plant the seed plot each year, and one from 100 or more selected ears would be much safer. In following a system of mass selection, the unpopped remnants of the most desirable ears are simply bulked together to furnish seed for an isolated seed plot the following year.

In contrast to the mass-selection method, the pedigree or ear-to-row method may be used, in which each row is planted from a single ear and a preliminary selection is made on the basis of individual rows, followed by selection within the row. It is probable that this method has no advantages over mass selection to counterbalance its disadvantages of more labor and greater likelihood of close breeding.

As in all selection work, there is a constant drag of regression toward the mean of the population in selection for high popping expansion.
Consequently, one may not expect the average popping expansion of the crop produced to be nearly so high as the average of the selected ears that are planted. If the work is carefully and consistently done, however, some progress in raising the mean is accomplished each time, and over a period of years real improvement may be effected, although such improvement may not be expected to continue indefinitely.

In an experiment conducted cooperatively by the Department and the Kansas Agricultural Experiment Station to test the efficacy of mass selection in popcorn breeding, the popping expansion was increased from 19 to 26 volumes in 6 years. Comparatively little increase in popping expansion has been effected since that time, which indicates that the practical limits of improvement have about been reached. This work was initiated by J. G. Willier, formerly assistant agronomist in the Bureau of Plant Industry. The resulting improved strain, originally known as Sunburst, but later changed to Supergold, has been distributed by the Kansas station.

Where some attempt at improvement of quality is desired, but where the labor of popping a large number of individual ears for seed selection is out of the question, a modification of the mass-selection method based on kernel structure may be used. A reasonably good correlation \( r = -0.59 \pm 0.022 \) has been found between the amount of soft white starch in the center of the kernel and the popping expansion of the ear from which it came. Since the correlation is negative, it means that the ears with the least amount of soft starch in the kernels will on the average pop the best. In selecting seed, three or four kernels from each ear may be split with a sharp knife to determine those with the least amount of soft white starch. These ears should be saved for seed. Although selection for high popability from kernel examination is much less desirable than from direct popping tests, it is much better for the maintenance of a good strain than no selection at all. It is particularly valuable as a means by which to cull out the traces of mixture with dent corn which tend continually to creep into popcorn varieties.

Hybridization between inbred lines, the newest and most promising method of corn breeding, is equally as applicable to popcorn as to

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dent corn or to sweet corn. A general discussion of corn breeding appears in the 1936 Yearbook of Agriculture, in which the methods and results of hybrid corn production are fully described. With the exception that popping expansion and eating quality must be given paramount consideration in popcorn, the technique followed is the same as for field corn. The possibilities are fully as promising, but thus far comparatively little work has been done in the production of popcorn hybrids.

The only hybrid popcorn known to the writer that has been released for commercial production is Minhybrid 250, from the Minnesota Agricultural Experiment Station. Inbreeding of 200 to 250 lines of Michigan Pop, a selection of Jap Hulless, was begun in 1925 by H. K. Hayes and H. E. Brewbaker. Since 1930 the breeding work has been done by H. K. Hayes and I. J. Johnson. The original lines were culled severely on the basis of agronomic characteristics, so that when the first crosses were made in 1929 only seven remained. These seven inbreds were combined in all possible combinations of single crosses and tested thoroughly during the 4 years 1930–33. On the basis of these trials, single cross C–1 × C–6 was selected as the best combination and named Minhybrid 250. Representative ears of inbreds 1 and 6 and of the single cross are shown in figure 3. The component inbreds were distributed in 1934, and small commercial acreages have been grown in 1935 and 1936. As an average of 3 years' tests at University Farm, Minhybrid 250 has produced 16 percent higher yield and 29 percent higher popping expansion than the standard open-pollinated Jap Hulless used as a check. The adaptation of this hybrid seems to be limited to central Minnesota. In a trial in the southern part of the State the hybrid was much less satisfactory.

In 1931, the Minnesota station also started inbreeding a group of lines from Burbank Pure Gold, a 10-rowed yellow pearl variety. These inbreds are now just ready for top-cross tests and trials of recombination.

At the Iowa Agricultural Experiment Station J. C. Eldredge began inbreeding in 1928 with 50 ears of Jap Hulless, part of which were selected from a mass selection plot of the previous year and part from various commercial growers. These lines have been culled to about 20 inbreds between which combinations have been tested during the period from 1933 to 1936. On the basis of these tests the most promising hybrid seems to be a three-way cross which has averaged about a 20-percent increase in yield and a 20-percent increase in popping expansion over the open-pollinated Jap Hulless used as foundation material. An extensive State-wide test of this hybrid is planned for 1937. No distribution for commercial production has yet been made from Iowa.

In 1933 a new group of inbreds from Jap Hulless, South American, and Supergold were started at the Iowa station, which are still in the developmental stage.

In 1923, J. G. Willier, of the Bureau of Plant Industry, then at Washington, D. C, and later at Manhattan, Kans., in cooperation with the Kansas station, started inbred lines with a yellow pearl popcorn similar to Queen Golden. Later, C. W. Bower, also of this
This investigation was started mainly as an experiment to compare the efficacy of inbreeding compared with mass selection and ear-to-row breeding as a means of popcorn improvement. Careful selection was practiced during the inbreeding period, both within and among the inbred lines, for popping behavior as well as for characters of agronomic importance. At the conclusion of the work in 1931 it was found that hybrids much superior to the foundation material had been produced. During the same period, however, marked improvement in the original variety had been effected by mass selection, as referred to earlier in this article, so that when the mass-selection strain was used as the basis of comparison the hybrids showed no superiority in popping expan-

Figure 3.— Representative ears of the two component inbred lines and of the cross in Minhybrid 250: A, Line C-1; B, line C-6; C, Minhybrid 250.
New and much better inbred lines were beginning to be available from the strain already improved by mass selection, so it was decided to drop the original lines and wait until hybrids distinctly superior to existing open-pollinated varieties in popping expansion as well as in yield were available before commercializing them. Preliminary trials of hybrids from this newer material have been very promising, although the corn failures of 1934, 1935, and 1936 at Manhattan have greatly retarded the recent development of the work. In a cooperative field trial near Colfax, Ill., in 1935, 19 of 81 hybrids produced in Kansas had popping expansions of 25.0 volumes or more in comparison with an average popping expansion of 24.1 volumes for the parent stock, Supergold, grown in the same test. The highest popping expansion for any hybrid was 28.5 volumes. Yield was increased even more than popping expansion, the average yield of 72 of the 81 hybrids having uniform stands being 3,218 pounds per acre in comparison with 2,517 pounds per acre as the average of the Supergold checks. Unfortunately, the highest yielding crosses did not also possess the highest popping expansion, but a few were distinctly superior to the parent open-pollinated strain in both respects.

The difficulty of combining top yields and superior popping expansion in the same strain or hybrid of popcorn seems to be a common experience. Apparently the genetic constitution necessary to produce extremely high yields also produces too much soft starch in the centers of the kernels for best popping results. Why this is so is not definitely known. Perhaps the plant is unable, with the plant food materials at hand, to produce more than a given amount of the colloidal matrix in which the starch granules are embedded in the horny portions of the endosperm, and when greater amounts of endosperm are produced, increasing proportions are left in the form of soft starch. If this be the case, the situation is roughly analogous to the difficulty of obtaining a dairy cow with maximum milk production and maximum butterfat content in the same individual. Whatever the causes, it has been the experience of the writer that some compromise must be made in either yield or popping expansion or both to secure the best all-round popcorn hybrids from the utility standpoint.

Less loss of vigor from inbreeding is experienced normally in popcorn than in dent corn. Because of the ability to find comparatively productive inbreds, and because of the small amount of seed required per acre, it probably will be possible to utilize single crosses largely in commercial production. The shape of popcorn kernels from inbreds is about the same as that from their parent varieties, and the size is usually but little smaller, so that no mechanical difficulties with corn planters are encountered in using seed grown on inbred lines in the production of single crosses. The commercial use of single crosses simplifies hybrid seed-production problems and makes possible a most uniform market product.

In the limited trials thus far made, popcorn hybrids between inbreds from different varieties have given the most outstanding increases in yield. This confirms the experience with dent corn hybrids, where crosses between entirely unrelated stocks in the main have been
most successful. Hybrids between inbreds of Supergold and South American have given some extremely high yields, but the tendency toward a negative correlation between yield and popping expansion, referred to above, has seriously limited the usefulness of most individual crosses of this group. A very unusual situation is encountered in crossing South American and Supergold, in that the combination is perfectly fertile when South American is used as the pollen parent, but is almost completely sterile when Supergold is used as the pollen parent. Utilization of hybrids involving this combination must therefore be planned so that Supergold may serve as the seed-producing parent. Demerec reports a similar case of sterility in popcorn, although the varieties involved and the source of material are not clearly stated.

Synthetic Varieties

One variant of the inbreeding method, which has interested corn breeders for some time, is the possibility of recombining a fairly large number of selected inbreds into a synthetic variety that might be better than the original variety and which, because of the number of component lines, could be continued by open pollination without serious reduction of vigor and yield. Starting about 1920 with observational plots and yield tests of all available popcorn varieties, J. R. Duncan, of the Michigan Station, has selected Australian Hullless, Japanese Hullless, Japanese Dwarf Rice, and Queen Golden as the most promising varieties for his conditions and has started inbred lines within these varieties. It is planned to recombine the best inbreds into two synthetic varieties, one within the hull-less group and one within the yellow pearl group. Although in field corn no synthetic variety of outstanding yielding ability has yet been produced, it should be possible, by rigid selection of the inbred lines on the basis of popping expansion, to produce in popcorn a synthetic of high quality. No results of the Michigan experiment are as yet available, but its progress is being watched with interest.

Breeding for Resistance to Diseases and Insects

Resistance to disease is an important consideration in popcorn breeding. Any parasite that saps the vitality of the plant or prevents complete and normal maturity of the grain tends to lower popping expansion. Moreover, the diseases generally grouped as the ear rots are particularly objectionable, since occasional moldy kernels are very undesirable and are practically impossible to separate from corn after it is shelled. The majority of commercial popcorn dealers and processors sort the corn by hand before it is shelled, in an attempt to eliminate diseased ears. Frequently, however, portions of ears with early stages of infection are not easily recognized, and although such corn frequently will pop, it has distinctly undesirable flavors.

No project dealing specifically with breeding for disease resistance in popcorn is known to the writer, although in practically all work, both with open-pollinated varieties and with hybrids, attention is given to freedom from diseases as one of the bases of selection. In the many field-corn hybrids produced experimentally from which the

commercial hybrids now in production represent a small and highly selected portion, there has been marked variation in quality. It is likely that just as wide a range of disease resistance will be found in popcorn hybrids. Some of the experimental popcorn hybrids referred to above are very distinctly superior to open-pollinated varieties in freedom from diseases.

Insect damage also is very objectionable in popcorn and is severely discriminated against by the trade. Corn earworms are the cause both of direct damage to the grain and of indirect damage through secondary infestations by other insects and infections with ear rots. Injury by the corn earworm and by storage insects is particularly severe in the Southern States, where it is a serious problem, especially in popcorn, which is used primarily as human food.

At the Texas Agricultural Experiment Station, P. C. Mangelsdorf is attempting to combine the superior resistance of some southern varieties of field corn with the popping ability of popcorn. Of the varieties tried, Yellow Creole has given the most promise of transmitting insect resistance without interfering with popability. By means of a series of crosses, backcrosses, and recombinations coupled with rigid selection, progress is being made and hopes are entertained that a desirable popcorn may result that will be resistant to grain injury by insects.

GENETICS AND CYTOLOGY

The genetics and cytology of popcorn are the same as for other subspecies of Zea mays. These subjects have been discussed in the article already referred to in the 1936 Yearbook of Agriculture, to which attention is directed for detailed information. As a matter of fact, many of the testers used in unraveling the linkage relations in corn have been popcorns or popcorn derivatives. Popping behavior is unquestionably a heritable character, but it is probable that it represents one of the more complex cases of quantitative inheritance conditioned by many genes.

⁵ Jenkins, M. T. See footnote 3.