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Chapter 8

Origin of Corn Belt Maize and Its Genetic Significance

Several ends were in view when a general survey of the races and varieties of *Zea mays* was initiated somewhat over a decade ago (Anderson and Cutler, 1942). Maize, along with Drosophila, had been one of the chief tools of modern genetics. If one were to use the results of maize genetics most efficiently in building up general evolutionary theories, he needed to understand what was general and what was peculiar in the make-up of *Zea mays*. Secondly, since maize is one of the world's oldest and most important crops, it seemed that a detailed understanding of *Zea mays* throughout its entire range might be useful in interpreting the histories of the peoples who have and are using it. Finally, since maize is one of our greatest national resources, a survey of its kinds might well produce results of economic importance, either directly or indirectly.

Early in the survey it became apparent that one of the most significant sub-problems was the origin and relationships of the common yellow dent corns of the United States Corn Belt. Nothing exactly like them was known elsewhere in the world. Their history, though embracing scarcely more than a century, was imperfectly recorded and exasperatingly scattered. For some time it seemed as if we might be able to treat the problem only inferentially, from data derived from the inbred descendants of these same golden dent corns. Finally, however, we have been able to put together an encouragingly complete history of this important group of maize varieties, and to confirm our historical research with genetical and cytological evidence.

An even approximate survey of *Zea mays*-as-a-whole remains a goal for the distant future, but our understanding of Corn Belt dent corns is already more complete than we had originally hoped. Since our evidence is detailed and of various kinds, it may make the presentation somewhat easier to follow if we give a brief description of the pre-hybrid commercial yellow dents of the United States Corn Belt, review their history in broad outline, and then proceed to an examination of the various kinds of evidence on which these generalizations have been built.

Corn Belt dents, the commercial varieties which dominated the chief centers of corn production in the United States for over half a century preceding the advent of hybrid corn, were variable open-pollinated varieties. They varied from plant to plant, from field to field of the same variety, and from variety to variety. Figure 8.1, based upon an examination of a field of Golden Queen, one of the lesser known of these varieties, will indicate the kind of variation which characterized the fields of that day.

In spite of this variation, or one might almost say, impressed on top of it, was a remarkably persistent combination of generally prevalent characters. Considered from plant to plant or from field to field, *as individuals*, these varieties seemed ephemeral and unimportant. *Seen as populations*, as collections of inter-breeding individuals, the Corn Belt dents as a whole were a well-marked and definite entity, particularly when contrasted with maize in other parts of the world. They tended to have one well-developed ear, frequently accompanied by a small ear at the node below this primary one. The ears had large, nearly cylindrical cobs with red or reddish glumes. The usually golden yellow kernels, pronouncedly dented at the tip, had a pericarp frequently roughened by tiny wrinkles. They were set in from 14 to 22 straight rows with little external indication of the fact that the rows were in pairs. The mathematical perfection of the ear was frequently lessened by a slight tendency for the whole ear to taper toward the apex, and for the rowing of the kernels and the diameter of the cob to be somewhat differentiated in its lowermost quarter.

Characteristically, the plant on which this ear was borne had a single, upright stem, leaves with tight sheaths and strong, arching blades, and a heavy, many-branched tassel. Kernel color was remarkably standardized, a faint flush of coppery red in the pericarp and a yellow endosperm, combining to give varying shades of deep, golden color. Epidermal color was apparent on the culm and leaves at the base of the plant, but seldom or never were there to be found the brilliant reds, dark purples, and other foliage colors which are so characteristic of maize in various parts of Latin America. While there was some variation in anther color and silk color, pinks and dull reds were commonest though greens and bright reds were not unknown.

As we have shown elsewhere (Anderson and Brown, 1950) there cannot be the slightest doubt that these widespread and standardized Corn Belt varieties were the creation of the nineteenth century. They came in large part

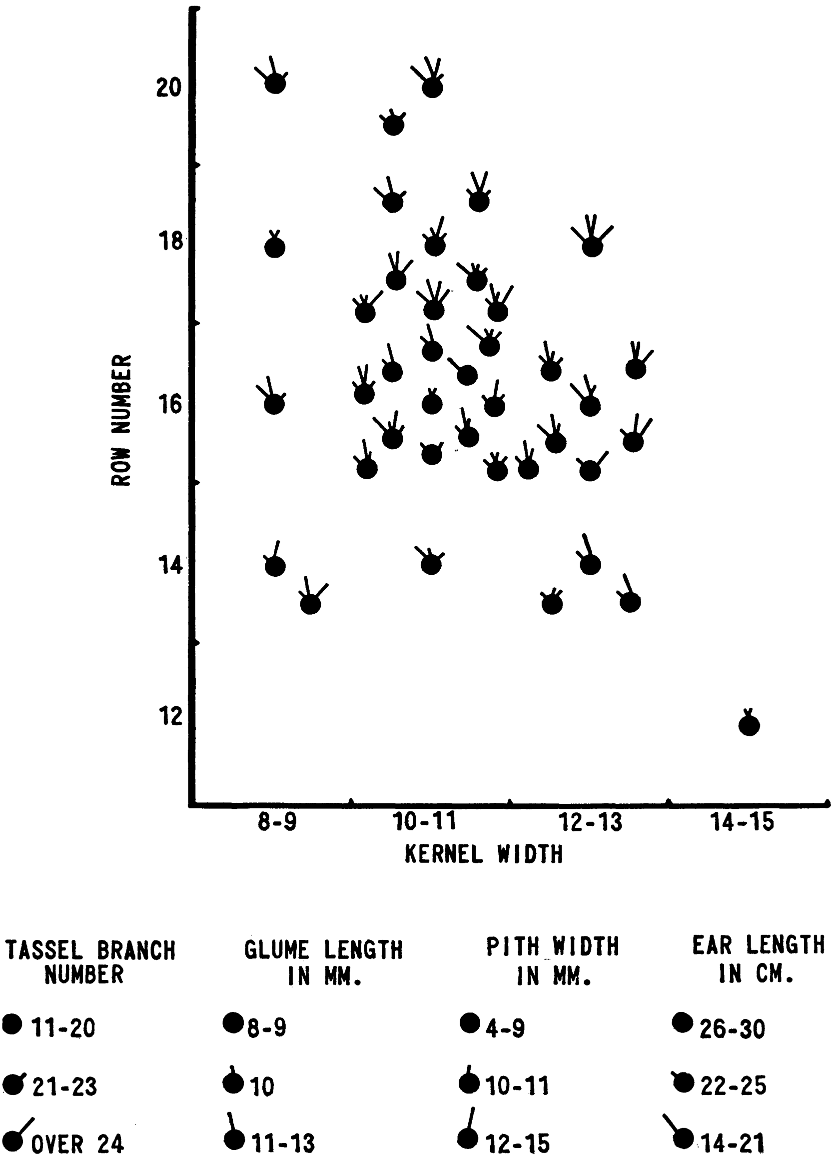

FIG. 8.1—Pictorialized diagram showing relationship between numbers of rows of kernels, kernel width, tassel branch number, glume length, pith diameter, and ear length in an open-pollinated sample of Golden Queen dent corn.

from crosses between White Southern Dents, mostly of Mexican origin, and the long, slender Northern Flints which had dominated the eastern United States for at least some hundreds of years preceding the discovery of America. While these two complexes were of primary importance in the creation of Corn Belt corn, it should be pointed out that germ plasm of other types of maize has undoubtedly filtered into Corn Belt mixtures. Compared to Southern Dents and Northern Flints, these certainly are of minor importance. There are, nevertheless, to be found among dent inbreds of the Corn Belt certain strains which exhibit Caribbean influence and others which seem to contain germ plasm of southwestern United States or western Mexican varieties.

Although the following discussion does not go into detail regarding the influence of these secondary sources of germ plasm on Corn Belt corn, the effects of such influences are important and we have already made small beginnings at studying them. The Northern Flints are in some ways strikingly similar to the common yellow flints of the Guatemalan highlands, strikingly unlike most Mexican maize. They are one of several cultural traits which apparently spread from the Mayan area to the eastern United States without leaving any clear record of the route by which they came. In their general appearance, as well as in technical botanical details, the Northern Flints were very different from the Southern Dents. The hybrid vigor which resulted from mixing these diverse types was soon noted by alert agriculturists. While some of the blending of flints and dents may have been haphazard and accidental, much of it was directed and purposeful. The benefits to be gained were listed in public, and the exact effects of continued mixing and of backcrossing were discussed in detail as early as 1825 (Lorain, 1825). This intelligent, controlled hybridizing proceeded for at least a half century until the new yellow dents were so ubiquitous and everyday that their very origin was forgotten.

For theoretical reasons this neglect of historical tradition was unfortunate. Maize breeders have not understood that the heterosis they now capitalize is largely the dispersed heterosis of the open-pollinated flint-dent mongrels. Maize geneticists are for the most part unaware that the germ plasm they use for fundamental generalizations is grossly atypical of germ plasms in general. We shall return to a detailed discussion of these two points after referring briefly to the evidence concerning the origin of Corn Belt maize.

Though there is abundant evidence that our Corn Belt dents came from mixtures of Northern Flints and Southern White Dents, the evidence concerning these two regional types is very one-sided. The Northern Flints (Brown and Anderson, 1947) were remarkably uniform from place to place and from century to century. The archaeological record is rich going back to early pre-Columbian times and there are numerous naïve but accurate descriptions of these varieties in colonial accounts.

The Southern Dents (Brown and Anderson, 1948) are much more variable. For over a century their variability has been stressed by all those who have discussed them. The samples which we obtained from the South differed from field to field, and from variety to variety. For an accurate understanding of them and their history, we would like many more archaeological specimens than we have for the flints, and many more colonial descriptions. Instead, we have as yet no archaeological record, merely two accounts in early colonial times—one from Louisiana and the other from Virginia. There is one passing mention in a pre-revolutionary diary, and then a truly remarkable discussion by Lorain in 1825. Finally, the United States Patent Office report for 1850 gives us, for region after region, a detailed picture of the extent to which this purposeful mixing had proceeded by that time.

To summarize the historical evidence, the Northern Flints were once the prevailing type of maize throughout the eastern United States (Brown and Anderson, 1947) with an archaeological record going back at least to A.D. 1000. There is as yet no archaeological evidence for their having been preceded in most of that area by any other type of maize, or of Mexican-like dents having been used there in pre-Columbian times. The Northern Flints belong to a type of maize rare or unknown over most of Mexico, but common in the highlands of Guatemala. The Southern Dents, on the contrary, obviously are largely derived from Mexican sources, and by 1700 were being grown as far north as Louisiana and Virginia (Brown and Anderson, 1948). As to how and when they spread north from Mexico, we have no evidence other than the negative fact that they are not known archaeologically from the eastern United States, and are not represented in the collections of early Indian varieties from that region.

As early as 1800, the benefits of crossbreeding these two different types of maize were appreciated by at least a few experts. By 1850 the process was actively under way from Pennsylvania to Iowa, and south to the Gulf states. By the '70's and '80's, a new type of corn had emerged from this blending, although crossing and re-crossing of various strains continued up to the advent of hybrid corn. During the latter half of the process, the origin of Corn Belt dents from 50 to 100 generations of selective breeding of crosses of Northern Flints and Southern Dents was almost completely forgotten. Having at length resurrected the evidence (Anderson and Brown, 1950) for this mingling of two fundamentally different types of maize, we shall now turn to the genetical and cytological evidence which first called the phenomenon to our attention and led us to search for historical proof.

CYTOLOGY

The most important cytological contribution on the origin of Corn Belt maize is found in a comparison of the numbers and distribution of chromosome knobs in the Northeastern Flints, open-pollinated varieties of Southern

Dents, and inbred strains of Corn Belt dents. As has been shown previously (Longley, 1938) and (Reeves, 1944), chromosome knobs may be an important tool in studying relationships in maize. Our work with North American corn not only supports this contention, but suggests that knob data may be even more important than has previously been supposed.

The 8–10 rowed flint and flour varieties of New York, Pennsylvania, and New England are nearly knobless. In the material we have examined, they have 0 to 2 knobs. These observations are in agreement with Longley's earlier conclusions that maize varieties of the northern Indians were characterized by having few knobs. Longley's material, however, included no strains from northeastern United States—the area in which the flint ancestors of Corn Belt corn were highly concentrated. It is interesting, moreover, to note that varieties from this segment of North America have even fewer knobs than do the strains from most Northern Plains Indian tribes.

In contrast, many more knobs were to be found in the open pollinated varieties of Southern Dent corn. In these strains we have found numbers ranging from 5 to 12, for those varieties representing the least contaminated segment of present-day Southern Dent corn. These cytological data are in complete agreement with the known facts regarding the history of Northern Flints and Southern Dents.

There seems little doubt that the Gourdseed-like Dents[1] of the southeastern United States have stemmed directly from Mexico where morphologically and cytologically similar corns can be found even today. Likewise, we have found in highland Guatemala varieties of maize with ear characteristics strikingly similar to Northern Flints and with as few as three knobs. Insofar as cytology is concerned, therefore, it is not at all difficult to visualize a Guatemalan origin for Northeastern Flint corn. The Corn Belt inbreds with which we have worked (Brown, 1949) have knob numbers of 1 to 8. The distribution of numbers in these strains is almost exactly intermediate between that of Northern Flints and Southern Dents (Fig. 8.2). This evidence, based on a character which certainly has not been intentionally altered by selection, strongly fortifies the archaeological and historical facts pointing to a hybrid origin of Corn Belt dent corns.

GENETIC EVIDENCE

The genetical evidence for the origin of Corn Belt maize from mixtures of Northern Flints and Southern Dents is of various kinds. In its totality, it is so strong that, had we not been able to find the actual historical evidence, we could have determined what had happened from genetic data alone. In the first place we have demonstrated, by repeating the cross, that it is possible to synthesize Corn Belt dents from hybrids between Southern Dents

[1] The name "Gourdseed" has been used since colonial times to describe the extremely long seeded, white Southern Dents, whose kernels are indeed not so different in appearance from the seeds of gourds of the genus Lagenaria.

and Northern Flints. Our experiments in crossing a typical white gourdseed from Texas and a typical yellow flint from New York State are now only in the third generation and are being continued. However, it is already evident that some of the segregates from this cross are within the range of variation of Corn Belt dents (Fig. 8.3).

In spite of the 50 to 100 generations of mixing which has taken place, the characters of Northern Flints and Southern Dents still tend to be associated in Corn Belt dents. Anderson (1939) has shown that in crosses between species

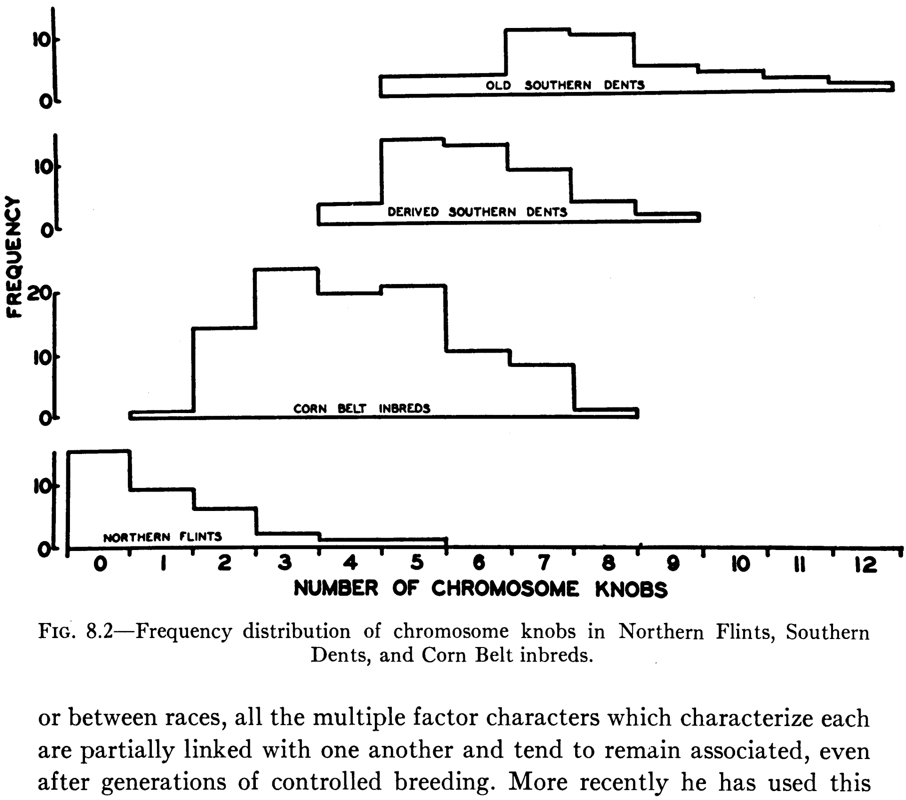

FIG. 8.2—Frequency distribution of chromosome knobs in Northern Flints, Southern Dents, and Corn Belt inbreds.

or between races, all the multiple factor characters which characterize each are partially linked with one another and tend to remain associated, even after generations of controlled breeding. More recently he has used this principle in the development of *the method of extrapolated correlates* (Anderson, 1949) by which the original characteristics can be deduced from the mixtures even when previously unknown.

Using this method in a relatively crude form, we were able (in advance of our historical evidence) to demonstrate (Brown, 1949) in Corn Belt inbreds, the association of low knob numbers, flag leaves, cylindrical ears, few tassel branches, and flinty kernels—all characteristics which typify the Northern Flints. Similarly, it was possible to show the association among these 98 Corn Belt inbreds of high knob numbers, no flag leaves, tapering ears, dented kernels, and many tassel branches—a combination of characters which is typical of the Southern Dents. As a matter of fact, by this technique Brown predicted the knob numbers of the Northern Flints, even when that fact was unknown to us.

The association of characters in actual open-pollinated fields of Corn Belt dents is so complex that one might suppose any study of it would be hopeless. However, from a study of character association in an open-pollinated field

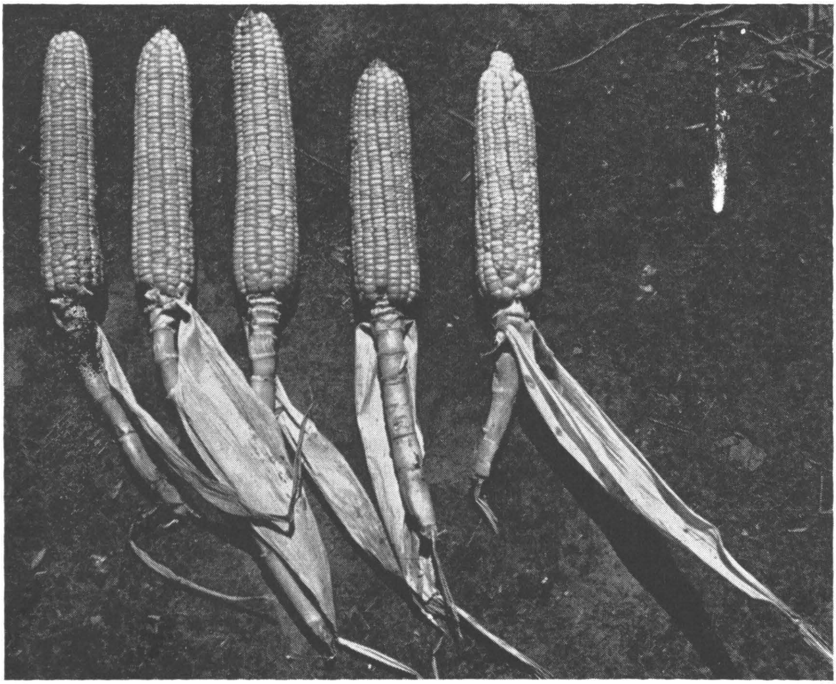

FIG. 8.3—Corn Belt Dent-like segregates from an F_2 generation of cross of Longfellow Flint × Gourdseed Dent.

of Golden Queen Dent (Fig. 8.1) we were able to demonstrate the association of: (1) wide kernels, (2) low row numbers, (3) short glumes, (4) few tassel branches, (5) long ears, and (6) narrow central pith in the ear—all of these characterizing Northern Flints. The opposing combination: (1) narrow kernels, (2) high row numbers, (3) long glumes, (4) many tassel branches, (5) short ears, and (6) wide central pith also tended to be associated and is characteristic of Southern Dents. In other words, some of the characters which went in together from flints and dents were still in this open-pollinated variety tending to stay together on the average. The existence of such character complexes has been appreciated by experienced corn breeders, though apparently it has never been commented on in print. Of course, corn breeders and corn geneticists differ in their endowments for apprehending such phenomena in advance of the published facts, and the existence of these strong linkages has been more apparent to some than to others.

WIDTH OF CROSS

The demonstration that Corn Belt dents largely are derived from hybridization between Southern Dents and Northern Flints is of particular importance because this is such a wide cross. Our evidence for this assertion is largely morphological, though there is supporting evidence from cytology and genetics.

In nearly all species of cultivated plants there are conspicuous differences in color and shape. These differences give the various cultivated varieties of a species a false aspect of difference from one another, and from their wild progenitors. False, because these differences are usually due to a few genes, if not being actually monofactorial. The striking differences between such varieties are therefore no true indication of the distinctness of their germ plasms.

On the other hand, there are subtle differences in form, proportion, and indument which, though difficult for a novice to apprehend, are more like the differences which distinguish distinct species of the same genus. These taxonomically important differences have proven valid criteria for indicating the diversity of germ plasms. So it has been proven that the subtle taxonomic differences between the Old World and New World cottons are much more representative of the genetic diversity and relationships of these two groups of varieties than are the conspicuous differences in color and leaf-shape which are found within each group. In the Cucurbits the striking differences in color and form of fruit, which differentiate the varieties of *Cucurbita Pepo* and of *C. moschata*, are superficial compared to the taxonomically significant features which separate these two groups. The latter, moreover, have been proved to be a significant index of genetic diversity, either between these two groups of Cucurbits or in assaying the variation within *C. Pepo* itself (Shifriss, 1947) (Whitaker and Bohn, 1950).

The difficulty in relying upon such taxonomic criteria is that the method is highly subjective. Taxonomy is of necessity still more of an art than a science. This means that one must personally examine the evidence if his opinion is to be worth anything. It also means that the worker's opinion is worth no more than his understanding of the taxonomic entities included in his judgment. However, until more objective criteria are evolved for this field, we shall have to use fairly traditional taxonomic methods for want of anything better. Accordingly, the senior author has for two years spent one day a week in a technical, agrostological, herbarium survey of all the grasses conceivably related to *Zea mays*—all the genera in the tribes Andropogoneae and Maydeae. With that background, his judgments may well be mistaken but they are certainly informed.

From this point of view, the variation within *Zea mays* is without parallel, not only in the cultivated cereals but in any other domesticated plant or animal. There are such superficial characters as aleurone color, pericarp color, plant color, carbohydrate composition, and such amazing single factor differences as tunicate and teopod. In addition, there are a whole battery of characters which are difficult to work with genetically, but which are the kinds of differences that agrostologists find significant in the deployment of species and genera: spikelet shape and venation, spikelet arrangement, rachis morphology, pubescence, leaf-shape, internode proportions, etc. Using such criteria, the hybridization of the Southern Dents and the Northern Flints represents the mingling of two basically different germ plasms.

For evidences of relationship, the male inflorescence of maize (the tassel) is of particular importance. Inflorescence differences generally have proved to be of primary taxonomic importance in the Gramineae. Variation in the male inflorescence of Zea would likely be less obscured by domestication than the female inflorescence (the ear) which has been deliberately selected for various peculiarities. The entire male inflorescence of the Southern Dents has been extensively modified by condensation (Anderson, 1944), a sort of fasciation which telescopes adjacent nodes, and in the ear produces increases in row number. It is an abnormality conditioned by at least two pairs of recessive genes and its expression is certainly modified by still other genes.

Tassels of the Northern Flints are without any condensation. Though condensation modifies the general aspect of the tassel, it is relatively superficial. The presence of so much condensation renders difficult the demonstration of a much more fundamental difference. The central spike of the Northern Flints is decussately arranged. That is, the pairs of spikelets are in alternate whorls of two; whereas the spike of the Southern Dents (allowing for the modifications produced by extreme condensation) is fundamentally in whorls of 3, or mixtures of whorls of 3 and whorls of 2. The rachis of the Northern Flints is slender with long internodes, that of the Southern Dents is short and flattened (Fig. 8.5). Pedicels of the upper spikelets always are long in the Northern Flints. In the Southern Dents they may be so short that one cannot distinguish the normally pedicellate spikelet from its sessile partner.

Correlated differences are seen in the ear. That of the Northern Flints has a narrow central pith and is long and slender, characteristically with 8–10 rows. The ear of the Southern Dents is short and thick with a wide central pith, and with from 16 to 30 or more rows. Pairing of the rows is markedly evident in the Northern Flints, even when they are pushed closer together in those occasional ears with 10 or 12 rows (Fig. 8.4). There is little or no row pairing in the Southern Dents. The kernel of the Southern Dents is long, flat, and narrow. Its largest diameter is near the base. By contrast, the kernel of the Northern Flints is wider than it is high, and is considerably thicker at the apex than it is at the base.

The ear of *Zea mays* is terminal on a secondary branch, which is hidden by

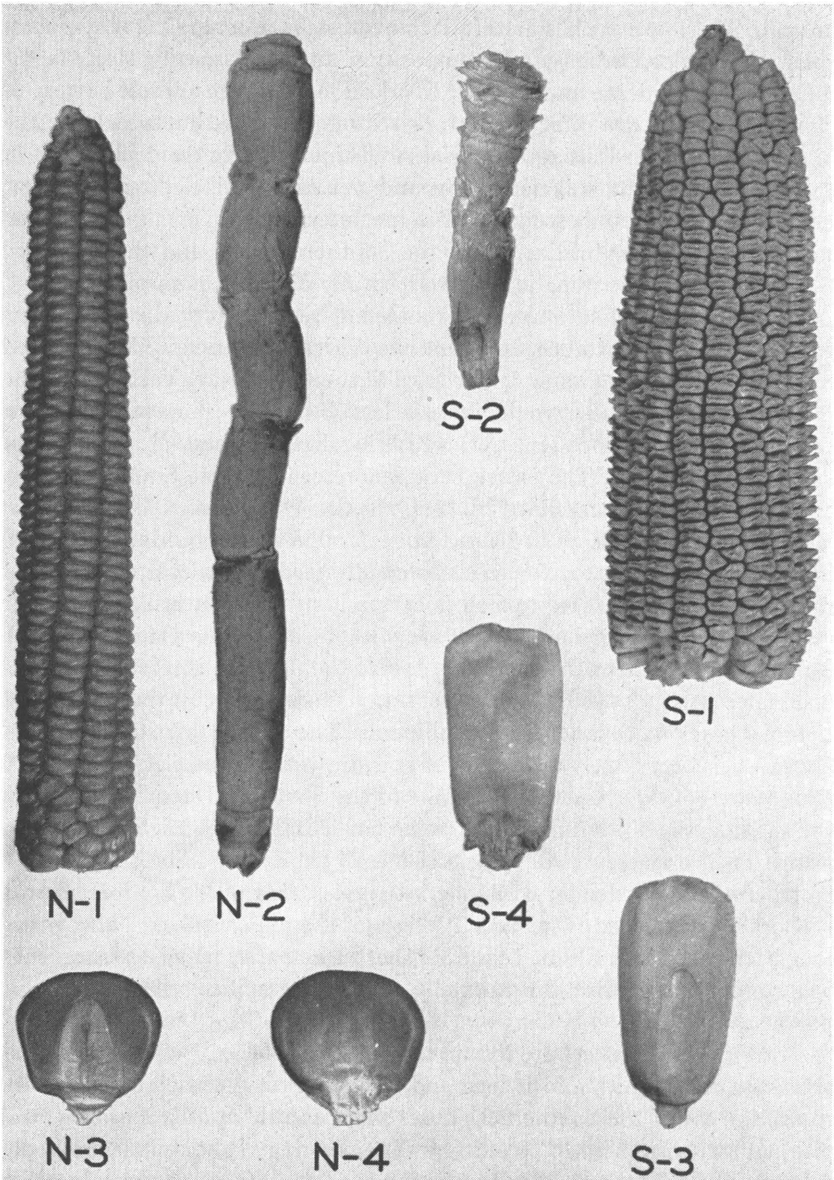

FIG. 8.4—Typical ears (*1*), shanks (*2*), and seeds (*3* and *4*) of Northern Flint (*N*), and Southern Dent (*S*).

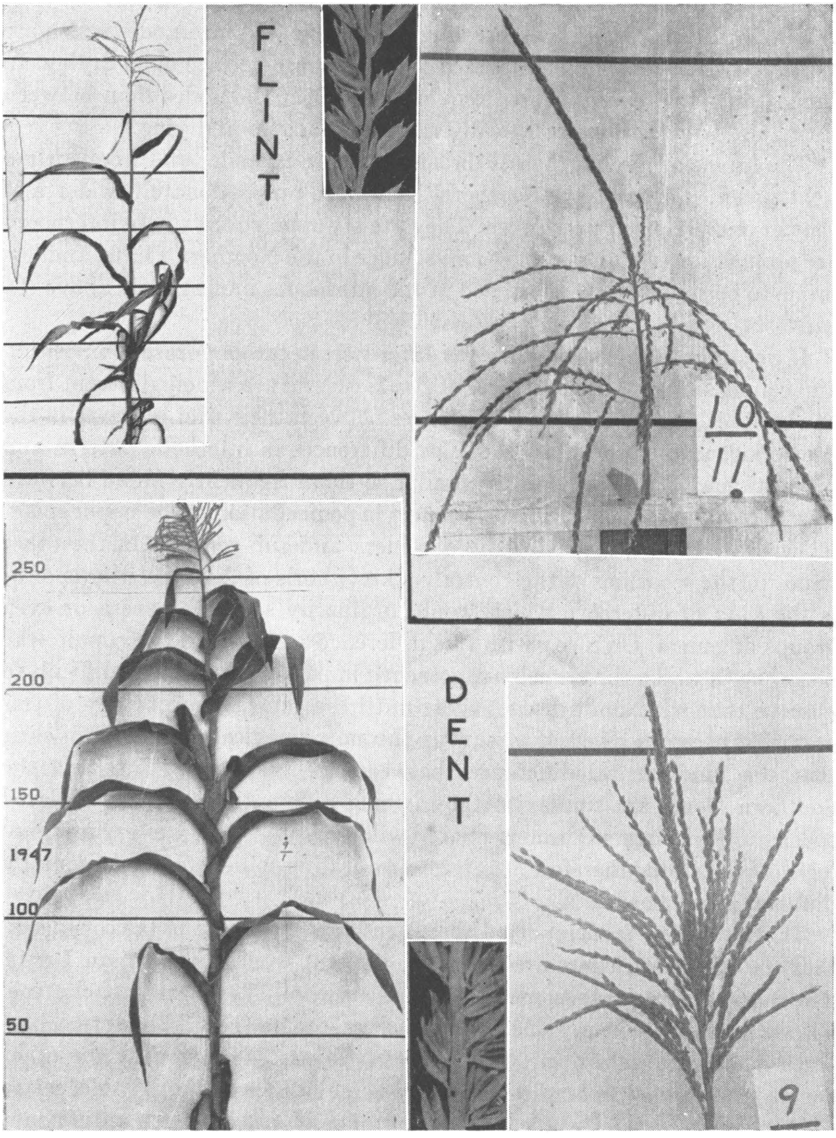

FIG. 8.5—Typical plants, tassels, and staminate spikelets of Northern Flint and Southern Dent.

its specialized leaves or husks. When dissected out, these ear shoots (or shanks) are diagnostically different in Northern Flints and Southern Dents (Fig. 8.4). In the former they are long, with elongated internodes which are *widest* between the nodes, and which have a smooth surface upon drying. In the latter they are very short, frequently *wider* at the nodes than between them, and have a characteristically ribbed surface upon drying.

The leaves of the Northern Flints are long and slender and frequently a light green. Those of the Southern Dents are proportionately wider and shorter and are often dark green. They are set upon culms whose internodes are proportionately longer and more slender in the Northern Flints, and less prone to become greatly shortened at the internodes immediately above the ear.

If we ignore such abnormalities as differences in carbohydrate composition and condensation, these two races of *Zea mays* still are widely different from one another—as compared to differences between their wild relatives in the Andropogoneae or the Maydeae. The differences in internode pattern and proportion and in leaf shape are similar to those frequently found between species of the same genus. The differences in pedicellation of the upper spikelet would be more characteristic of genera and sub-genera. On the other hand, in the whorling of the central spike (whorls of 2 versus whorls of 3) is the kind of difference which would ordinarily separate genera or even groups of genera. On a par with this difference are those in the cupule (the bony cup in which the kernels are attached in pairs). They are so difficult to observe that we cannot discuss these until the general morphology of this organ has been described. If we sum up the morphological evidence, it is clear that the fundamental differences between the Northern Flints and the Southern Dents are similar to those which differentiate distantly related species (or even genera) among related wild grasses. There is every morphological indication, therefore, that we are dealing with two fundamentally different germ plasms.

The cytological facts reported above lend further weight to the conclusion that the Northern Flints are basically different from the Southern Dents. The former have chromosomes which are essentially knobless at pachytene. The latter average nearly one knob per chromosome (Fig. 8.2). Heterochromatic knobs are known in other grasses besides *Zea mays*. In these other genera, their presence or absence, from such evidence as is available, seems to be characteristic of whole species or groups of species. Such a difference between the Flints and Dents indicates that we are dealing with two fundamentally different germ plasms. It has been shown in Guatemala (Mangelsdorf and Cameron, 1942) and in Mexico (Anderson, 1946) that the varieties with many knobs are morphologically and ecologically different from those with low numbers of knobs.

A further indication that these two germ plasms are physiologically different is given by their pachytene behavior. The pachytene chromosomes of the Northern Flints are easy to smear and give sharp fixation images. Southern Dents are more difficult to smear. The chromosomes do not spread out well and do not stain sharply. This is not a result of differences in knob number, since some of the Mexican Dents with few knobs are equally difficult to smear. Whatever the physiological significance of this reaction, it is direct evidence for a difference in the chemistry of the germ cells. Again such differences in stainability are more often met with, between genera, than they are in different strains of the same species.

There is genetic evidence for the difference between Southern Dents and Northern Flints, in the behavior of crosses between them. The F_1's are fully

TABLE 8.1

PERCENTAGE OF STERILE OR BARREN PLANTS IN GOURDSEED, LONGFELLOW, AND F_2 GENERATION OF CROSS GOURDSEED × LONGFELLOW

	Sterile or Barren	Normal Ear	Total Number of Plants
Gourdseed	37	63	46
Longfellow	2	98	58
F_2 Gourdseed×Longfellow	52	48	101

fertile and exhibit extreme hybrid vigor. The F_2's show a high percentage of completely barren plants—plants which formed ears but set little or no seeds, either because of sterility or because they were too weak to mature successfully—and plants which managed to set seeds, though their growth habit indicates fundamental disharmonies of development.

Table 8.1 shows the percentages of good ears and plants which were either without ears or on which the ears had failed to set any seed, for Gourdseed-Dent, Longfellow Flint, and their F_2, when grown in Iowa. Like Southern Dents generally, the Gourdseed is less adapted to central Iowa than is Longfellow Flint. An F_2 between these two varieties, however, has a much greater percentage than either parent of plants which are so ill-adapted that they either produce no visible ear, or set no seed if an ear is produced. Similar results were obtained in other crosses between Northern Flints and Southern Dents, both in Missouri and in Iowa. From this we conclude that they are so genetically different from one another that a high percentage of their F_2 recombinations are not able to produce seed, even when the plants are carefully grown and given individual attention.

SUMMARY

The common dent corns of the United States Corn Belt were created *de novo* by American farmers and plant breeders during the nineteenth cen-

tury. They resulted in a large measure from deliberate crossing and recrossing of two races of maize (the Northern Flints and the Southern Dents) so different that, were they wild grasses, they would be considered as totally different species and might well be placed in different genera. The origin of two so-different races within cultivated maize is an even larger problem and one outside the scope of this discussion. It may be pointed out parenthetically that the Tripsacum hypothesis (Mangelsdorf and Reeves, 1945) would not only account for variation of this magnitude, it would even explain the actual direction of the difference between these two races of maize. However, the relation between maize and Tripsacum on any hypothesis is certainly a most complicated one (Anderson, 1949). It would be more effective to postpone detailed discussions of this relationship until the comparative morphology of the inflorescences of maize and of Tripsacum is far better understood than it is at present.

SIGNIFICANCE TO MAIZE BREEDING

Derivation of the commercial field corns of the United States by the deliberate mingling of Northern Flints and Southern Dents is a fact. Unfortunately, it is a fact which had passed out of common knowledge before the present generation of maize breeders was educated. From the point of view of practical maize breeding, either hybrid or open-pollinated, it is of central importance. Briefly, it means that the maize germ plasms now being worked with by plant breeders are not varying at random. They are strongly centered about two main centers or complexes. Such practical problems as the development and maintenance of inbreds, the detection of combining ability, and the most effective utilization of hybrid vigor need to be rethought from this point of view. Detailed experiments to provide information for such practical questions already are well under way. While these experiments are not yet far enough along to give definite answers, they have progressed far enough to allow us to speak with some authority on these matters.

HETEROSIS

The heterosis of American Corn Belt dents acquires a new significance in the light of these results, and practical suggestions as to its most efficient utilization take on a new direction. We are immediately led to the hypothesis that the heterosis we are working with is, in part at least, the heterosis acquired by mingling the germ plasms of the Northern Flints and the Southern Dents.

Insofar as hybrid vigor is concerned, the hybrid corn program largely has served to gather *some* of the dispersed vigor of the open-pollinated dents. Preliminary results indicate that this has not been done efficiently in terms of what might be accomplished with somewhat more orientation.

The early days of the hybrid corn program were dominated by the hypothesis that one could inbreed this vigorous crop, identify the inferior strains in it, and then set up an elite cross-pollinated germ plasm. This hypothesis was clearly and definitely stated by East and Jones (*Inbreeding and Outbreeding*, 1919, pp. 216–17).

> Experiments with maize show that undesirable qualities are brought to light by self-fertilization which either eliminate themselves or can be rejected by selection. The final result is a number of distinct types which are constant and uniform and able to persist indefinitely. They have gone through a process of purification such that only those individuals which possess much of the best that was in the variety at the beginning can survive. The characters which they (pure lines) have, can now be estimated more nearly at their true worth. By crossing, the best qualities which have been distributed to the several inbred strains can be gathered together again and a new variety recreated. After the most desirable combinations are isolated, their recombination into a new and better variety, which could be maintained by seed propagation, would be a comparatively easy undertaking.

Though other corn breeders and corn geneticists may not have committed themselves so definitely in print, such a notion was once almost universal among hybrid corn experts. Modified versions of it still influence breeding programs and are even incorporated in elementary courses in maize breeding.

The facts reported above would lead us to believe that heterosis, having resulted from the mingling of two widely different germ plasms, will probably have many genes associated with characters which in their relatively homozygous state are far from the Corn Belt ideal of what a corn plant should look like. It is highly probable that much of the so-called "junk" revealed by inbreeding was extreme segregants from this wide cross, and that it was closely associated with the genes which gave open-pollinated dents their dispersed vigor. It is significant that some very valuable inbreds (L317 is a typical example) have many undesirable features. For this reason, many such inbreds are automatically eliminated even before reaching the testing stage.

If one accepts the fact that Corn Belt dents resulted from the comparatively recent mingling of two extremely different races of maize, then on the simplest and most orthodox genetic hypotheses, the greatest heterosis could be expected to result from crosses between inbreds resembling the Southern Dents and inbreds resembling the Northern Flints. If heterosis (as its name implies) is due to heterozygous genes or segments, then with Corn Belt corn on the whole we would expect to find the greatest number of differing genes when we reassembled two inbreds—one resembling the Northern Flint, the other resembling the original Southern Dent.

Theory (Anderson, 1939a), experiment (Anderson, 1939b; Brown, 1949), and the results of practical breeding show that linkage systems as differentiated as these break up very slowly. On the whole, the genes which went in together with the Northern Flints still tend to stay together as we have demonstrated above. This would suggest that in selecting inbreds, far from trying to eliminate all of the supposed "junk," we might well attempt to breed for inbreds which, though they have good agronomic characters like stiffness of the stalk, nevertheless resemble Northern Flints. On the other hand, we should breed also for those which resemble Southern Dents as closely as they can and still be relatively easy to grow and to harvest. It would seem as if the opposite generally has been done. A deliberate attempt has been made to produce inbreds which look as much as possible like good Corn Belt maize in spite of being inbreds.

There are, of course, practical necessities in breeding. In this direction the work of corn breeders is a remarkable achievement. Strong attention to lodging resistance, to desirable kernel shapes and sizes, and to resistance to drought and disease has achieved real progress. The inbred-hybrid method has permitted much stronger selection for these necessary characters than was possible with open-pollinated maize. Most Corn Belt dents now plant well, stand well, and harvest well.

Perhaps partly because of these practical points there has been a conscious and unconscious attempt on the part of many breeders to select for inbreds which are like the Corn Belt ideal in all characters, trivial and practical alike. The corn shows are now out-moded, but corn show ideals still influence corn breeding. For instance, there has been an effort to produce plants with greatly arching leaves, whose margins are uniformly ruffled. Such characters are certainly of a trivial nature and of secondary importance in practical programs. Any potential heterosis closely associated with upright leaves, yellow green leaves, tillering, or blades on the husk leaves has seldom had a chance to get into inbreds where it could be tested on a basis of achievement. It would seem highly probable that, in not basing the selection of inbreds more soundly on performance, we have let much potential heterosis slip through our sieve of selection.

Heterosis Reserves

These considerations lead us to believe that there is probably a good deal of useful heterozygosis still ungathered in high yielding open-pollinated varieties. There is also a distinct possibility that still more could be added by going back to the Northern Flints and Southern Dents with the specific object of bringing in maximum heterozygosity. From our experience it is more likely that superior heterosis is to be found among the best flints than among the best dents. On the whole, the Northern Flints have been farthest from the corn breeders' notion of what a good corn plant should look like. Flint-like characteristics (tillering, for example) have been most strongly selected against, both in the open-pollinated varieties and the inbreds derived from them.

Several of the widely recognized sources of good combining inbreds are open-pollinated varieties with a stronger infusion of Northern Flints than was general in the Corn Belt. This is particularly true of Lancaster Surecrop, the excellence of whose inbreds was early recognized by several breeders in the United States Department of Agriculture. In our opinion, it is probable that the greater proportion of flint germ plasm in Lancaster Surecrop has made it an outstanding source of inbreds of proven highly specific combining ability when used with other Corn Belt inbreds. This is not an isolated example, and even more extreme cases could be cited. We think it is a reasonable working hypothesis that Northern Flint varieties of superior productivity might be efficient sources of improved heterozygosity for the United States Corn Belt.

Morphological Characters as Related to Heterosis

To put this hypothesis in different language, morphological characters, if carefully chosen, may be used as criteria of specific combining ability in Corn Belt inbreds. Before presenting data bearing directly on this hypothesis, two points need to be emphasized and discussed: (1) the effective selection of morphological criteria, and (2) the relativity of all measures of effective combining ability.

Previous studies (Kiesselbach, 1922; Jenkins, 1929; and others) have indicated that the only positive correlations between the morphology of inbreds and their combining ability are those involving characters of the inbreds which are indicative of plant vigor. Reference to these investigations shows that the characters chosen were such superficial measurements as date of silking and tasseling, plant height, number of nodes, number of ears, ear diameter, etc. Unfortunately, the morphology of the maize plant is not a simple matter. It is so complex that one needs technical help on morphology quite as much as he would in biochemistry were he studying the concentrations of amino acids in the developing kernel.

Accordingly, we first familiarized ourselves thoroughly with the technical agrostological facts concerning the detailed gross morphology of grasses in general and Zea in particular. Just as in the case of a biochemical study of the kernel, we found that further original research was necessary if the investigation was to be carried on effectively. We have accordingly undertaken detailed studies of internode patterns and branching of the inflorescence; the venation, size, and shape of the male spikelet, the development of the husk leaf blades, the external anatomy of the cob, and the morphology of the shank. Some of these investigations are still continuing, and must continue if inbred morphology and combining ability are to be effectively correlated.

It is impossible to produce an absolute measure of combining ability. When one speaks of combining ability of two inbreds, he always refers to their behavior with each other compared to their behavior with certain other inbreds or open-pollinated varieties. This is such a relative measure that the scoring of a particular F_1 cross as very low or very high in combining ability might depend solely upon our previous experience with the two inbreds. We may illustrate this point with an extreme example. Let us suppose that we have inbreds 1F and 2F derived directly from Northern Flints, and inbreds 10D and 11D derived from Southern Dents. Were we to cross 1F $\times$ 2F and

10D × 11D we would expect relatively little heterosis within either of the crosses. Accordingly, when we crossed 2F × 11D we would rate this cross as having high specific combining ability. On the other hand, had we originally crossed 2F × 10D and 11D × 1F, then there would probably have been almost equally great heterosis in each of the crosses. Had these been used as a basis for comparing the heterosis of 2F × 11D, then our notion as to the amount of heterosis in these crosses would have been very different than it would have been had comparisons been made with 1F × 2F or 10D × 11D.

If the germ plasms of the two main races of maize involved in Corn Belt dents are still partially intact as a result of linkages, it should be possible to classify inbreds on the basis of morphological differences according to their flint and dent tendencies. If this can be done, and if genetic diversity is important in bringing about a heterotic effect in hybrids, one should be able to predict with some accuracy the relative degree of heterosis to be expected from crossing any two inbred lines. With this hypothesis as a background, a series of experiments was started three years ago to determine whether or not hybrid vigor in maize, as expressed in terms of grain yield, could be predicted on the basis of morphological differences of inbreds making up the F_1 hybrids.

Fifty-six relatively homozygous inbred lines consisting of eighteen U.S.D.A. or experiment station lines, and thirty-eight strains developed by the Pioneer Hi-Bred Corn Company were scored for the following characteristics: row number, kernel length, denting, development of husk leaf blades, number of secondary tassel branches, glume length, and chromosome knob number. For each of these characteristics the two extremes in the eastern United States are to be found in Southern Dents and Northeastern Flints. At least twelve plants of each of the fifty-six inbreds were scored, and these scores were then averaged to give a mean value for the line. The resulting means were translated into numerical index values, in which a low value represents Northern Flint–like tendencies, and a high value Southern Dent–like tendencies. For example, the mean row number values for the inbreds studied ranged from 11.2 to 19.5. These were arranged in the following index classes.

1	2	3	4	5	6	7
11.2–11.7	11.8–12.3	12.4–12.9	13.0–13.5	13.6–14.1	14.2–14.7	14.8–15.3

8	9	10	11	12	13	14
15.4–15.9	16.0–16.5	16.6–17.1	17.2–17.7	17.8–18.3	18.4–18.9	19.0–19.5

Index values for the other characteristics were arranged similarly, and from the individual characteristic inbred indices (each being given equal weight) a total "Inbred Index" was determined as is shown by example in Table 8.2.

After index values had been determined for the inbreds, single cross combinations were made and these tested for yield. In 1948, sixty-six single crosses were grown in yield tests in Iowa and in Illinois. Each F_1 hybrid was replicated six times in each test. At the end of the season, yield of grain was determined on the basis of 15 per cent moisture corn. Actual yields in bushels per acre and morphological differences of the inbreds involved in each of the crosses were then plotted on a scatter diagram as shown in Figure 8.6. It will be noted that although the observations exhibit considerable scatter, there is a tendency for grain yields in single crosses to increase as the morphological differences between the inbreds making up the crosses become greater. Actually the correlation coefficient between yield and index differences in this case was $r = +.39$.

The experiment was continued in 1949, in which 100 F_1 hybrids were tested for yield. In this experiment three characters only were used to determine the index of relationship between the inbreds used. These were row number, kernel length, and degree of development of husk leaf blades. Elimination in this experiment of certain morphological characteristics used previously was done largely to facilitate ease and speed of scoring. It had been determined previously that, of the several characteristics used, those having the highest correlation with yield were differences in row number, kernel length, and husk leaf blades. There was likewise known to be a rather strong association between each of these characteristics and tassel branch number, denting, glume length, internode pattern, and chromosome knob number. Therefore the scoring of these three characteristics probably covers indirectly nearly as large a segment of the germ plasm as would scores based on all seven characteristics.

TABLE 8.2

INBRED INDICES BASED ON SEVEN CHARACTERS

Inbreds	Row No.	Kernel Length	Denting	Husk Leaves	Tassel Branches	Spikelet Length	Chromosome Knobs	Inbred Index	Sums of 7 Differences without Signs
Hy.....	9	14	4	14	5	6	12	64	41
Oh40b..	2	8	4	1	4	1	3	23	30
MY1...	14	11	14	14	14	6	9	82	59

The 1949 tests in which each entry was replicated six times in each location were again grown both in Iowa and Illinois. Yields from these tests, plotted against index differences of the inbreds, are shown in Figure 8.7. As in the previous year's data, a pronounced tendency was shown for hybrids made up of inbreds of diverse morphology to produce higher grain yields than hybrids consisting of morphologically similar inbreds. The correlation co-

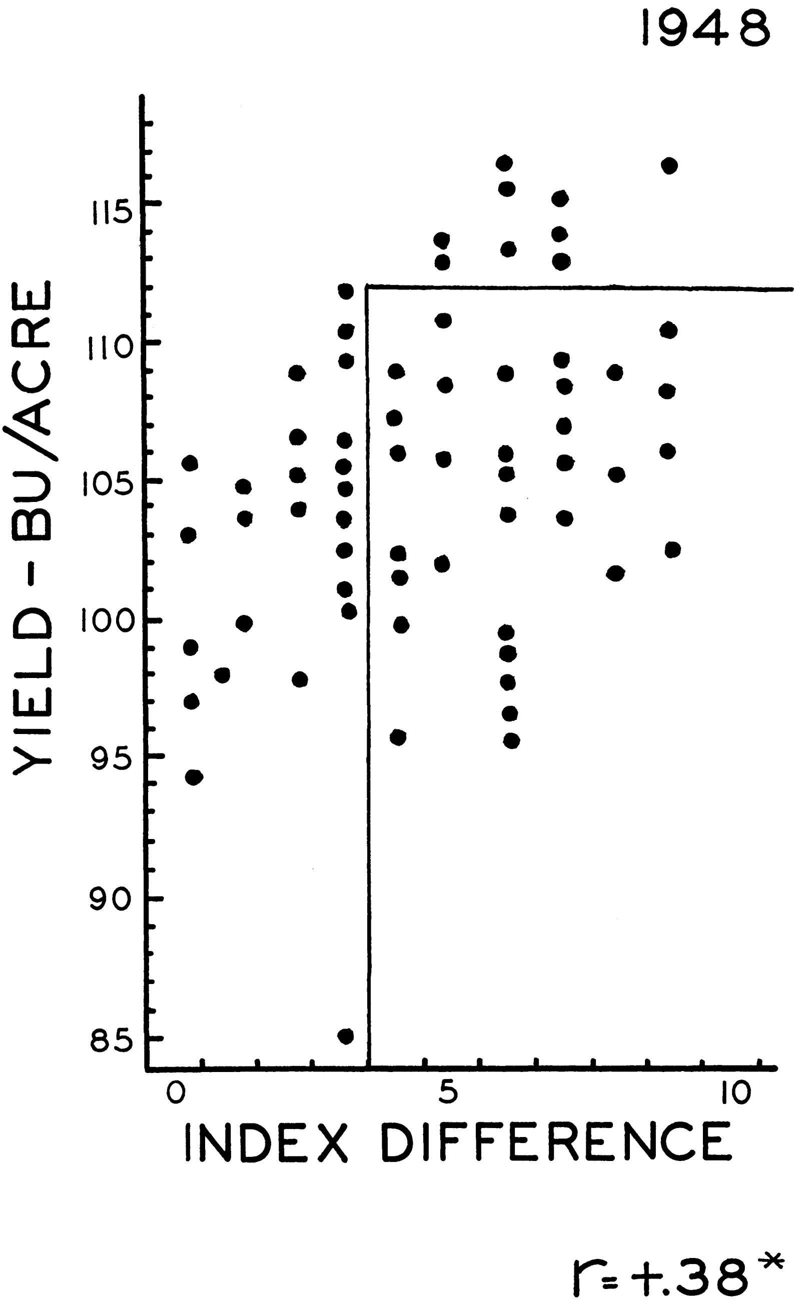

FIG. 8.6—Scatter diagram depicting relationship between grain yields of 66 single cross hybrids and morphological differences of inbred parents of the hybrids. Explanation in text.

efficient between yield and index differences is $r = +.40$, a significant value statistically.

In terms of practical corn breeding, the distribution of single crosses in Figures 8.6 and 8.7 is of particular significance. If these observations are critical (we have produced a repeatable result) it means that one could have eliminated from the testing program the lower one-third of the crosses on the basis of index differences, without losing any of the top 10 per cent of the highest yielding hybrids. In the case of the 100 hybrids in Figure 8.7, one could have eliminated from testing 35 per cent of the crosses, thereby permitting the inclusion of 35 additional hybrids in this particular testing area. If further

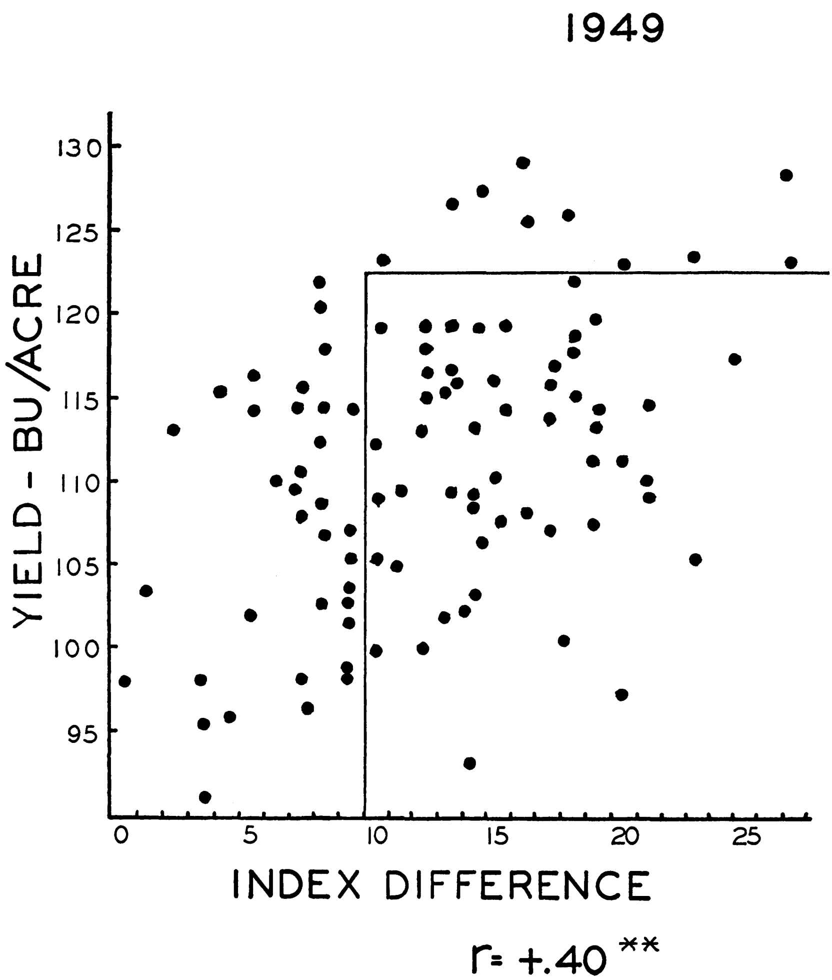

FIG. 8.7—Scatter diagram depicting relationship between grain yields of 100 single cross hybrids and morphological differences of inbred parents of the hybrids. Explanation in text.

experiments show that the method is reliable, such a procedure should expedite most corn breeding programs.

Our method of scoring does not take into account the variation brought about by the infusion of germ plasm other than that from Northern Flints and Southern Dents. Perhaps this is one reason why we have not obtained higher correlations between differences in inbred morphology and yield. There are a few inbreds in the Corn Belt which appear to be affiliated either with Caribbean flints or the Basketmaker complex. Scoring of such inbreds on a scale designed for Northern Flints and Southern Dents undoubtedly leads to conflicting results. It is hoped that experiments now in progress will aid in clarifying this situation.

SIGNIFICANCE OF FLINT-DENT ANCESTRY IN CORN BREEDING

The Flint-Dent ancestry of Corn Belt maize bears upon many other breeding problems besides those concerned with heterosis. Its widest usefulness is in giving a frame of reference for observing and thinking about the manifold and confusing variation of Corn Belt maize. When one becomes interested in any particular character of the corn plant, he no longer needs to examine large numbers of inbreds to understand its range of variation and its general over-all direction. He merely needs to examine a few inbreds, and a Northern Flint and a Southern Dent. A good part of the variation will then be seen to fall into a relatively simple series from an extreme Northern Flint type to the opposite Southern Dent extreme, with various intermediates and recombinations in between. This is quite as true for physiological or biochemical characters as for glumes, lemmas, or other morphological characters. One is then ready to study further inbreds with a framework in his mind for sorting out and remembering the variation which he finds.

The actual breeding plot efficiency of this understanding will be clearer if we cite a practical example. Now that corn is picked mechanically, the size, shape, texture, and strength of shank are important. When maize was picked by hand, the hand had a brain behind it. Variations in ear height, in the stance of the ear, and in the strength and shape of the shank were of minor significance. Now that machines do the work, it is of the utmost practical importance to have the shank standardized to a type adapted to machine harvesting. When this necessity was brought to our attention a few years ago, there were few published facts relating to variation in the shank. Examination of a few inbreds showed that though this organ varied somewhat within inbreds, it varied more from one line to another than almost any other simple feature of the plant. We accordingly harvested typical shanks from each of 164 inbreds being grown for observation in the breeding plots of the Pioneer Hi-Bred Corn Company. We also examined a number of Northern Flints, and had they been available, we would have studied the shanks on typical Southern Dents. However, simply by using the hypothesis that one extreme would have to come in from the Northern Flints, the other from the Southern Dents, we were able within one working day to tabulate measurable features of these shanks and to incorporate all the facts in a

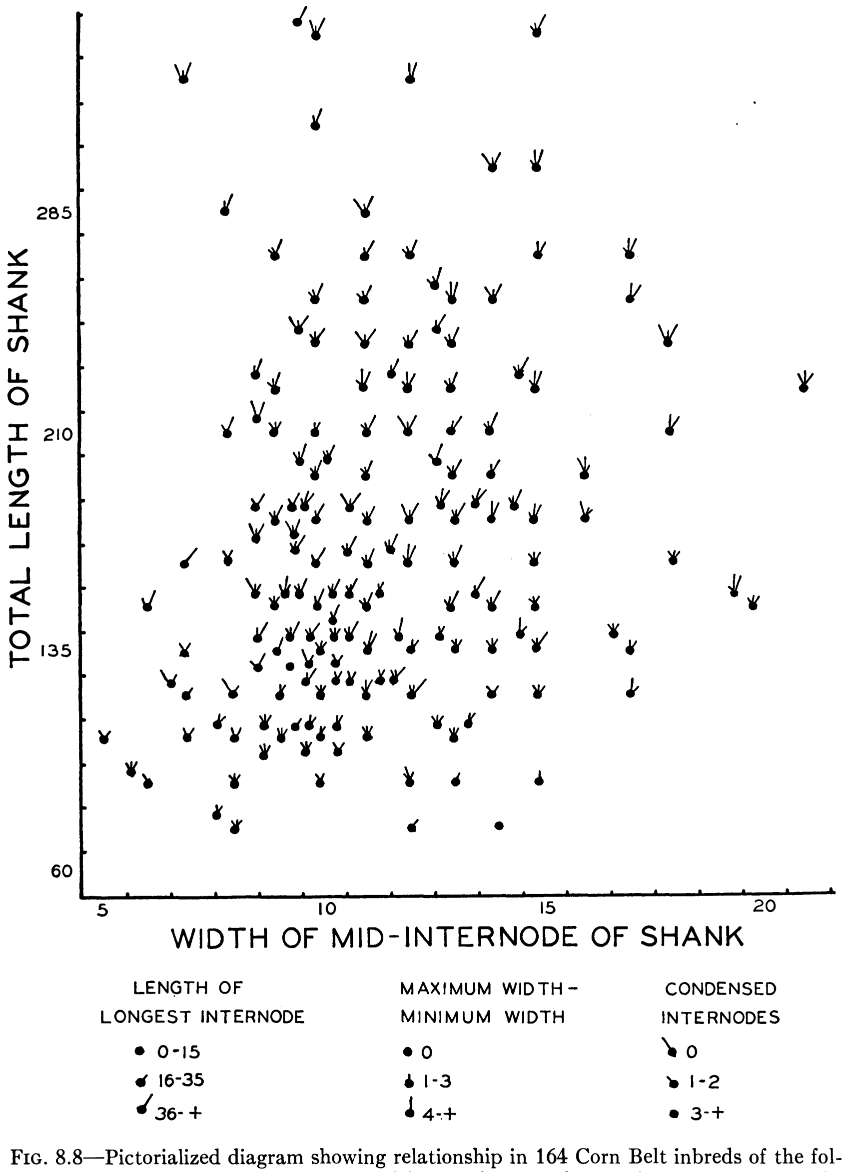

FIG. 8.8—Pictorialized diagram showing relationship in 164 Corn Belt inbreds of the following shank characters: total length, width of mid internode, length of longest internode, maximum width minus minimum width, and number of condensed internodes.

pictorialized scatter diagram (Fig. 8.8). Using the method of Extrapolated Correlates we were able to reconstruct the probable shank type of the Southern Dents. (We later grew and examined them and verified our predictions.) We arranged most of the facts concerning variation in shank type in United States inbreds in a single, easily grasped diagram. All the technical information needed as a background for breeding was available after two days' work by two people. Without the Northern Flint–Southern Dent frame of reference for these miscellaneous facts, we might have worked around the problem for several breeding seasons before comprehending this general, overall picture.

SUMMARY

1. Archaeological and historical evidence shows that the common dent corns of the United States Corn Belt originated mainly from the purposeful mixing of the Northern Flints and the Southern Dents.

2. Cytological and genetic evidence point in the same direction and were used in the earlier stages of our investigations before the complete historical evidence had been located.

3. The Northern Flints and Southern Dents belong to races of maize so different that, were they wild grasses, they would certainly be assigned to different species and perhaps to different genera. Such cytological and genetical evidence as is available is in accord with this conclusion.

4. The significance of these facts to maize breeding problems is outlined. In the light of this information, the heterosis of Corn Belt maize would seem to be largely the heterosis acquired by mingling the germ plasms of the Northern Flints and Southern Dents. It is pointed out that most breeding programs have been so oriented as to be inefficient in assembling the dispersed heterosis of the open-pollinated varieties of the Corn Belt. The possibility of gathering more heterosis from the same sources is discussed and it is suggested that more might be obtained, particularly among the Northern Flints.

5. Morphological characters of dents and flints, if carefully chosen, should be useful criteria for specific combining ability. The problem of selecting such characters is described. Two seasons' results in correlating combining ability and flint-dent differences are reported. They are shown to be statistically significant and of probable practical importance.

6. The practical advantages of understanding the flint-dent ancestry of Corn Belt maize are discussed and illustrated by example. In brief these facts provide a "frame of reference" for detecting, organizing, and understanding much of the manifold variability in Corn Belt maize.