NUMBERS AND DISTRIBUTION OF CHROMOSOME KNOBS IN UNITED STATES MAIZE

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THE chromosomes of maize possess a number of distinguishing features used by cytologists to identify members of the complement. Among the more important of these are the dark staining enlargements known as knobs, which have been shown to occur at certain points and only at certain points on the chromosomes. Although chromosome knobs are distinguishable in mitotic prophases they are best studied at the pachytene stage of meiosis at which time they are highly pycnotic when stained with ordinary chromatin dyes. Knob number is constant for any individual plant and in United States maize may vary from 0 in some varieties to 14 in others. It can therefore be used as one criterion in determining the relationships of various kinds of maize, a problem which is becoming increasingly important in modern maize breeding. Although this paper deals only with differences in total knob numbers there is some evidence to indicate that knob size and position might be equally useful as a tool in studying relationships in maize.

LONGLEY (1938) studied knob number and position in a collection of maize from 33 Indian tribes of the United States. He found very few knobs on the chromosomes of most strains from the northern Indian tribes. A slightly higher number of knobs were found in the southeastern varieties and many knobs were observed on the chromosomes of most varieties from New Mexico and Arizona. On the basis of these findings, LONGLEY suggests that "the number of knobs on the chromosomes of a strain of Indian corn may give a clue to the geographical origin of the strain."

MANGELSDORF and REEVES (1939) have suggested that the presence of chromosome knobs in maize is a result of admixture with Tripsacum, a related genus in which high knob number has been established for several species. They suggested further that the hybridization of Tripsacum and Zea with repeated natural backcrossing to Zea resulted in the formation of a new genus, Euchlaena. These investigators point out that so-called "Andean" or uncontaminated maize of the South American highlands has few or no knobs while most types of maize which show morphological evidence of Tripsacum introgression (either directly or through teosinte) have knob numbers roughly in proportion to the amount of putative Tripsacum germ plasm present. Further evidence supporting this hypothesis was offered by REEVES (1944) who, in a study of knob numbers in maize from North, Central and South America, demonstrated a statistically significant relationship between numbers of knobs and proximity to Central America, a region in which in certain areas both Tripsacum and teosinte occur in abundance. However, GRANER and ADDISON

(1944) found that *Tripsacum australe*, a South American species, unlike its Central and North American relatives, has no terminal knobs and few internal ones. These results suggest at least that knob numbers cannot always be taken as a reliable measure of the amount of Tripsacum germ plasm in Zea.

Disregarding the origin of chromosome knobs in Zea and their relation to the Tripsacum hypothesis they do nevertheless represent a stable, easily measured character. As will be shown later, differences in knob numbers and their association with morphological characters, seem to be significant, even in the highly selected maize of the United States corn belt.

MATERIALS AND METHODS

At the time this work was initiated the material used was limited to a series of inbred lines representative of corn belt dent corn. Later, it was felt that the true significance of the differences in knob numbers found in corn belt inbreds could not be fully appreciated without first having available some basic information on the parental types of maize that were combined to produce corn belt dents. For this reason, the field was expanded to include (1) Northeastern Flints, (2) Flints and Flours of the Northern Great Plains and the Midwest, and (3) Southern Dent Corn. A total of 171 strains have been studied representing a reasonably comprehensive collection of the major races of United States maize, exclusive of the southwestern United States and the coastal area of southeastern United States. The material has been studied over a period of three years, from 1945 through 1947. All varieties were grown in the field, the Southern Dents at Gray Summit, Missouri, and the Flints, Flours and Corn Belt Dents at Johnston, Iowa.

Knob numbers were determined from temporary smears of pollen mother cells at the pachytene stage of meiosis. For those inbreds included, most of which were relatively homozygous, sporocytes were collected from only one or two plants of each line. Among the open-pollinated varieties of Northern Flint and Southern Dent Corn, which, of course, were much more variable than the inbred lines, sporocytes were collected from two to four plants.

DESCRIPTION OF RACES

The 8 and 10-rowed flints of the northeastern United States, which were at one time the commonest type of corn in eastern North America, are essentially uniform morphologically (BROWN and ANDERSON 1947). These corns are characterized by long slender ears (fig. 1), wide crescent-shaped seeds, long and lax but usually few tassel branches, narrow leaves, many tillers and extensively developed husk leaves. The related varieties of the Northern Great Plains and the Midwest are in many instances very similar to those of the Northeast. In general, however, the flint varieties of the North Central United States are more variable than those of New York and New England. Among these corns one encounters higher numbers of rows of kernels, (fig. 1), more obvious mixture with flour and dent endosperm types, and a closer approach to Corn Belt Dents in plant type. In addition, many of these corns exhibit a series of characteristics which suggest a rather close relationship to certain Indian varieties of the Southwest.

The Southern Dents herein reported upon are quite variable and apparently have undergone a complicated history. Notwithstanding this fact, it is possible, on the basis of comparative morphology and known history, to separate them into two fairly distinct categories. These have been arbitrarily designated as (1) Old Southern Dents, and (2) Derived Southern Dents (BROWN and ANDERSON 1948). The former group is composed of varieties which are either very similar to some present-day Mexican corns or whose culture in the South dates back to Colonial times. Some of the varieties included in this category such as Mexican June and Tuxpan, for example, may actually be recent introductions from Mexico. With the exception of Hickory King, the ears of each of these varieties are typified by a very strong taper from base to tip. The strains which exhibit a high degree of denting tend to have high row numbers and considerable pointing. In practically all varieties of this category there is a strong tendency for the tip of the cob to extend well beyond the rows of kernels (fig. 2). The tassels although variable, usually have many secondary branches which are often highly condensed, particularly in the case of those varieties with high numbers of rows of kernels. Plants of Mexican June and similar varieties frequently have rather short, stiff, upright secondary tassel branches giving a pronounced "whisk broom" appearance to the tassel. The plants are tall, with as many as 24 nodes in some varieties. Ears are usually set high on the culms and internode length frequently becomes increasingly shorter above the ears.

The Derived Southern Dents differ from the former group primarily by exhibiting a more pronounced similarity to corn belt maize. The ears are usually more cylindrical; row numbers tend to be lower and there is a less pronounced tendency for exposed cob tips. Although plant types in the two groups show few consistent differences, it may be significant that the only variety encountered with highly pubescent leaf sheaths was among the Old Southern Dents. As a group the Derived Southern Dents are of somewhat shorter plant height than the Old Southern Dents. There are, however, among the derived sorts, certain varieties as tall as the tallest of the Old Southern Dents. Most varieties included in this category are apparently of more recent origin and are of more heterogeneous genetic background than the Old Southern Dents.

Since dent corn inbreds of the corn belt are widely grown and since they, as a group, are well known by most corn breeders and corn geneticists, it seems unnecessary to describe them in detail. The majority of the present day inbreds are the products of inbreeding open pollinated dent corn varieties of the cornbelt, or of inbreeding single or double crosses of corn belt inbreds. Since corn belt dent corn is itself a heterogeneous mixture resulting from the blending of Northern Flints and Southern Dents it is not surprising to find that corn belt inbreds range in type from strains resembling Northern Flints (fig. 3), to others approaching Southern Dent types, (fig. 4).

DISTRIBUTION OF KNOBS

It will be noted in tables 1, 2 and 3 that knob numbers in this material range from 0 to 12, and that numbers of knobs are closely associated with morpho-

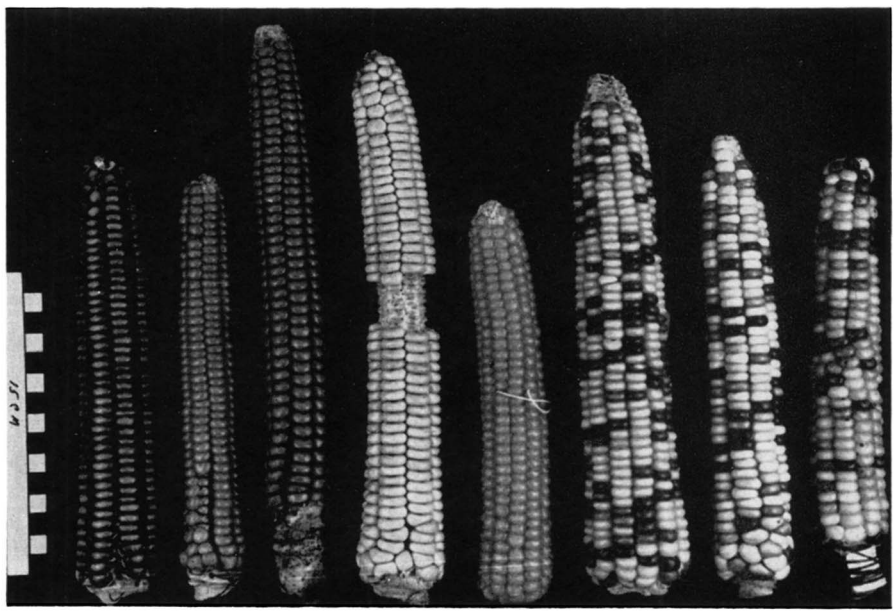

FIGURE 1.—Representative ears of flint and flour corns of the Northeast, Northern Great Plains, and the Midwest. Left to right. Stevens Flint—0 knobs; 8-row Flint (New York)—0 knobs; 8-row New England Flint—1 knob; New York Flour Corn—1 knob; Gehu Flint—0–2 knobs; 12 row Dakota Flint—3 knobs; Sax and Fox Flint—3 knobs; Bear Island Flint—2 knobs.

FIGURE 2.—Representative ears of "Old" and "Derived" southern dent corns. Left to right. Gourdseed—6, 7, 8 knobs; Shoepeg—6, 7, 8 knobs; Mexican June—7, 8, 9, 10, 11 knobs; Mosby's Prolific—5, 6, 7, 8 knobs; Clark's Yellow Dent—5, 6 knobs; Huffman—5 knobs.

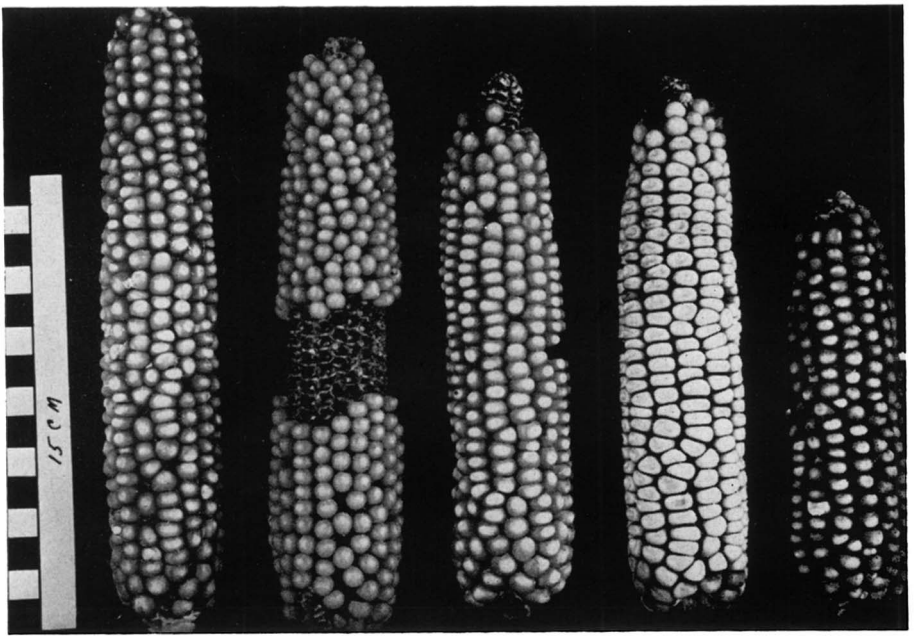

FIGURE 3.—Ears of inbred strains possessing low numbers of chromosome knobs. Left to right. L317—3 knobs; Ind. 38-11—3 knobs; I13—3 knobs; G1P1—1, 2 knobs; LDG—2 knobs.

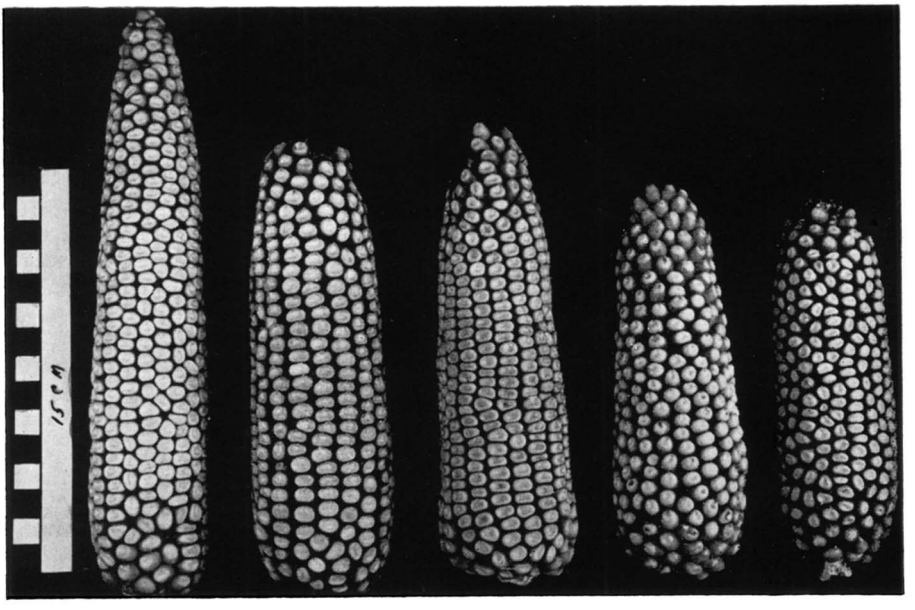

FIGURE 4.—Ears of inbred strains possessing high numbers of chromosome knobs. Left to right. Ill. R4—7 knobs; Os420—7 knobs; SI1—7 knobs; Ill. HY—6 knobs; L21—7 knobs.

logical type. The Northeastern Flints, for example, have few if any knobs. A number of these varieties have no distinct knobs and even the nucleolus organizer is frequently light-staining and indistinct. The maximum number of knobs in any of these varieties is 2, while several have but one knob, frequently

TABLE 1

Numbers of chromosome knobs in Northern flint and flour corn.

VARIETY	SOURCE	NUMBER OF CHROMOSOME KNOBS
Canada Flint	Feeding Hills, Mass.	0
Dutton	Newark Valley, N. Y.	2
Harris Mammoth Yellow	Rochester, N. Y.	0
Longfellow	Ontario, Canada	1
Mammoth Yellow	Ithaca, N. Y.	2
Parker's Flint	Potsdam, N. Y.	0
Quebec Flint	Restigouches, Que., Canada	1
Smut Nose	Bath, N. Y.	2
Stevens	Ithaca, N. Y.	0
Thayer Flint	Searsport, Me.	0
Thompson Flint	East Andover, N. H.	0
12-row Red Flint	Dryden, N. Y.	1
12-row Yellow Flint	Dryden, N. Y.	0
Wilbur's Flint	Hudson Falls, N. Y.	0
Assiniboine	North Dakota	1
Bear Island Flint	Minnesota	2
Dakota Squaw	North Dakota	1
Dakota White	North Dakota	0
14-row Dakota Flint	South Dakota	0
Gehu	North Dakota	0
Gehu	Iowa	2
Harris Mammoth Yellow	Iowa	0
Longfellow	Wisconsin	1
Mandan & Arikara	North Dakota	4
Mercer County Flint	North Dakota	0
Rainbow	North Dakota	1
Russian Extra Early	North Dakota	2
Russian Extra Early	Wisconsin	2
Sac & Fox	Iowa	3
Smut Nose	Wisconsin	1
Spanish Pop	Iowa	0
12-row Dakota Flint	South Dakota	3
Winnebago	North Dakota	1
Zuni Blue	North Dakota	5

at the terminal position on the short arm of chromosome 9. A wider range of knob numbers is encountered in the flint and flour varieties of the Northern Great Plains and the Midwest. Among these corns, numbers range from 0 to 5. Variation in numbers of knobs is here accompanied by considerable variation in morphological type.

The highest number of knobs encountered in this study were among the Old Southern Dents. Numbers in these varieties range from 5 to 12, with a rather strong mode at 7 to 8. Eleven and twelve knobs were found only in June Corn, which is of Mexican June type, and the variety Hickory King. Each of these corns are similar to some present-day Mexican varieties which are known to

TABLE 2

Numbers of chromosome knobs in Southern dent corns.

VARIETY	SOURCE	NUMBER OF CHROMOSOME KNOBS	VARIETY	SOURCE	NUMBER OF CHROMOSOME KNOBS
Gourdseed	Texas	6, 7, 8	Southern Snowflake	Virginia	5
Hickory King	Virginia	7	Southern Yel. Dent	Mississippi	4, 5
Hickory King	Georgia	6, 11, 12	Strawberry	Texas	8, 9
Hickory King	Tennessee	5, 7, 8	Va. Horsetooth	Virginia	4, 6, 7
Jellicorse	Virginia	9	Whatley's Prolific	Virginia	7, 8
June Corn	Louisiana	10, 11	Yellow Dent	Louisiana	6
Mexican June	Tennessee	7, 8	10-Row Dent	Arkansas	5
Mexican June	Tennessee	9	Cambren	Kentucky	6
Old White Dent (1)	Arkansas	5	Caraway's Prolific	Louisiana	6, 7
Old White Dent (2)	Arkansas	5	Cherokee	Georgia	5
Red Cob Chisholm	Texas	10	Clarks Yel. Dent	Texas	5, 6
Shoepeg	Louisiana	7, 8	Columbia Beauty	Tennessee	6
Shoepeg	Louisiana	6	Garretts 1	Kentucky	5, 6
Shoepeg	Louisiana	7	Garretts 2	Kentucky	7
Tenn. Red Cob	Tennessee	7, 8	Giant Yel. Dent	Texas	5
Tuxpan	Louisiana	7, 8, 9	Huffman	Tennessee	5
Tuxpan	Virginia	8	Jarvis Golden Prolific	Tennessee	5
White Dent	Arkansas	7	Jarvis Golden Prolific	Mississippi	4
Yellow Shoepeg	Louisiana	7, 8, 9, 10	Johnson Co. White	Missouri	7
Yellow Tuxpan	Louisiana	8	Latham's Double	Virginia	6
Neal's Paymaster	Arkansas	6	Mammouth Ensilage	Virginia	5
Neal's Paymaster	Mississippi	6	Mosby's Prolific	Mississippi	5
Sherman	Tennessee	5	Mosby's Prolific	Virginia	7, 8
Southern Ill. 1	Illinois	5	Mosby's Prolific	Louisiana	7
Southern Ill. 2	Illinois	6, 7	Mosby's Prolific	Tennessee	6

possess rather high numbers of chromosome knobs. It seems quite probable therefore that the Mexican June and Hickory King types of corn of the southern United States have come directly from Mexico without having undergone much change in plant or chromosome morphology. It is likewise relatively easy to find in central Mexico today varieties which closely approach in ear type the southern Gourdseeds and Shoepegs.

Knob numbers in corn belt inbreds range from 2 to 8 and their overall distribution is almost exactly intermediate between that of the Southern Dents and Northern Flints (fig. 5). This distribution, it would seem, might well be

TABLE 3

Numbers of chromosome knobs in dent corn inbreds.

NO. CHROMOSOME KNOBS	INBRED STRAIN
1	GIPI*
2	B4AM1*, CI.61, G1P1*, Ind. 33-16, IW1*, JC3*, KG2*, K77AT1*, LDG, LE4*, SW19*, S32*, W61*, 101*.
3	A94*, BG6*, B4Y3*, CI.7, CI.61, Conn. 103, D31*, F3-2, G3K2*, I13*, JG3*, J61*, KYS, K43*, L24*, L317, Minn. 49, Ohio 28, Ohio 40b, SN2*, SW19*, W23, 38-11.
4	AE1*, AG1*, B4U2*, CI.187-2, Conn. 103, Conn. 105, IDT, Ind. B2, Ind. Lx2, Ky27, K4, K77, LE7UI*, Minn. 11, SO2*, SRS386*, T27GSA*, 104*, 106*.
5	A99*, CI.7, CI.187-2, F3K4*, Ill. M14, Ind. B2, IW1CM2*, K155, K201, LF5*, MD1*, MY1*, SO1*, SS2*, SY1*, WF9, WG1*, WP1*, 103*, 105*.
6	BH1*, BH2*, CI.2, CV1*, Ill. A, Ill. HY, LA, SS2*, W26, 102*.
7	F3B2*, H65*, Ill. R4, L21*, Os 420, SI1*, SK2*.
8	GN2BD1*.

* Inbred Strains developed by PIONEER HI-BRED CORN COMPANY.

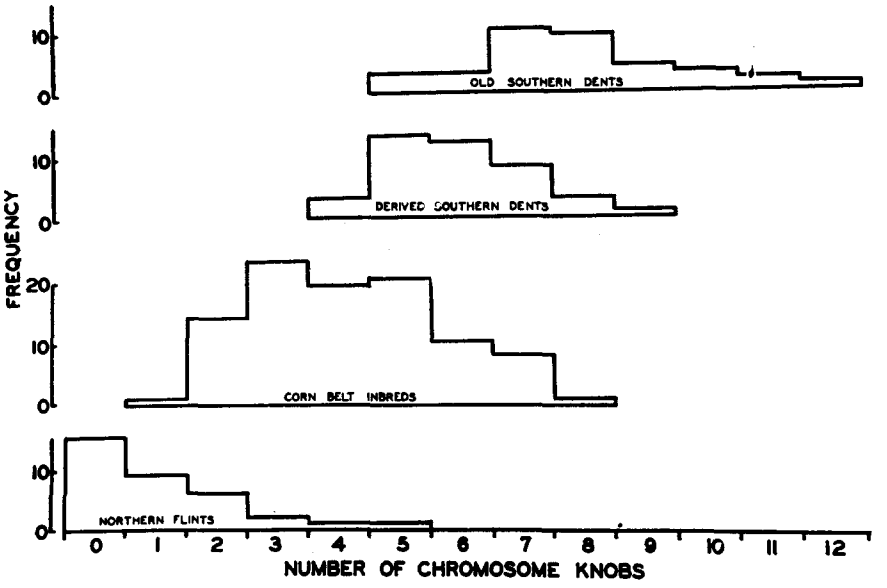

FIGURE 5.—Frequency distribution of chromosome knobs in United States maize.

taken as further substantiating evidence for the hybrid origin of corn belt maize in which the two parental types are represented by the Northern Flints and Southern Dents.

RELATIONSHIP BETWEEN NUMBERS OF KNOBS AND MORPHOLOGY

Even a cursory survey of figures 1 to 4 will suggest that numbers of chromosome knobs in United States maize do not vary at random but are instead associated with several morphological characters. A detailed statistical analysis of these relationships is being made and will be published at a later date. For this reason only the following more obvious associations between knobs and morphological characters will be referred to in this report.

Number of Rows of Kernels

Since the 8-rowed Northern Flints have but few knobs and the many-rowed Southern Dents have several, one might expect to find some correlation between knobs and row number in the maize of the corn belt. A positive correlation between these characters does exist although the value is not high. For 95 dent corn inbreds the correlation between knobs and row number is $r = +.20$ (significant at .05 level). For all the material herein reported upon including Northern flints, Southern dents and corn belt inbreds the correlation between these characters is $r = +.73$.

Denting

For purposes of this study denting has been scored in the following manner:

0. No soft starch at crown of kernel
1. Soft starch but no denting
2. Soft starch and a small dent
3. Soft starch and a deep dent but no wrinkling of pericarp
4. Soft starch and wrinkling pericarp
5. Soft starch and the apex of the kernel collapsed

In a population comprising the Northern Flints and Southern Dents there is, of course, a very close relationship between knobs and denting. As is true in the case of row number some association between these characteristics still exist in corn belt inbreds. For 95 dent inbreds the correlation coefficient between knobs and denting is $r = +.20$, which value is significant at the 0.5 level. Even though this correlation is low it is perhaps significant that there should be any relationship between these characteristics since corn belt corn has undergone at least a century of very intensive selection for soft texture. The genetics of denting is complicated and is controlled by a number of genes which are probably distributed over several chromosomes. It is interesting, therefore, to find such a complex quantitative character associated with knobs, a factor which certainly has not been subject to intentional selection.

Husk Leaf Blades

Data on number and length of husk leaf blades ("flag leaves") are not available for all cultures included herein. Nevertheless, observations on a number

of varieties of Northern Flint and Southern Dent corn and approximately 75 dent inbreds reveal that flag leaves are closely associated with few or no knobs. Flag leaves are rarely found in Southern Dents but are extensively developed in most varieties of Northern Flints. This relationship carries over into corn belt inbreds. Those strains with longest flag leaves are found among the lowest knob groups whereas few strains with well-developed flag leaves have been found among inbreds with high numbers of knobs. It seems likely therefore that flag leaves are very closely associated with absence of knobs since more than a century of breeding and selection has failed to alter this association significantly.

Seminal Roots

While it is recognized that seminal root development in corn is greatly influenced by age of the seed and environmental factors, it is also apparent that there are inherent differences in numbers of seminal roots produced by different varieties of United States maize. In the Southern Dents the mean number of seminal roots per seed was found to be 4.70. The Northern Flints averaged 2.40. The average number of seminal roots for inbred strains in the 1 to 4 knob group was 2.54 whereas inbreds in the 5 to 8 knob group averaged 3.64. Thus there appears to be a rather close association between knobs and seminal roots in the open-pollinated Northern Flints and Southern Dents and some slight association between these characters in corn belt inbreds.

Ear Shape

The overall shape of the ear of maize is difficult to measure accurately. The ear may be cylindrical, it may be tapered from base to tip or it may be tapered from center to tip and at the same time contracted at the base. During this study it became evident that most strains could be placed in one of two categories (*pyramidal* or *cylindrical*) so far as shape of the ear is concerned. Although it is recognized that this classification is somewhat crude and not absolutely reliable, it has been found to be usable. Early in this study it became apparent that the knob number of corn belt inbreds could be predicted with some accuracy by observing the shape of the ears. It was found, for example, that if a strain possessed pyramidal ears the chances were good that it would have five or more knobs. If on the other hand the ears of an inbred were cylindrical or nearly so, it was usually found to have fewer than five knobs. The reasons for this association in corn belt material were clear when the Northern Flint and Southern Dent corns were analyzed. The ears of most Southern Dents are distinctly pyramidal whereas the low knob Northern Flints are typified by cylindrical ears. This association strongly expressed in the ancestors of corn belt corn has been maintained even in the highly selected inbred parents of today's hybrid corn.

Irregular Rows

Irregular rows of kernels covering usually a portion of the ear only are frequently found in the Southern Dents and certain high knob inbreds. Since these corns are basically straight rowed the occurrence of irregularity is the

result of some breakdown in the usual arrangement. An examination of a large number of ears suggests that at least three types of irregularity occur. That which is observed rather frequently is an irregular arrangement of rows due to the abortion of one member of a pair of paired spikelets. Another common occurrence is the dropping of a row or several rows of paired spikelets. This type of phenomenon seems to occur more frequently in the Southern Dents than in corn belt inbreds. A third type of irregular rowing and one which has been observed less frequently is that resulting from multiplication (CUTLER 1946).

The Northern Flints and dent inbreds with low numbers of rows of kernels tend to have very straight rows. There are, however, a few exceptional cases among these varieties in which a tendency toward irregularity does exist. In the majority of such cases examined the irregular rowing was found to be due to multiplication.

There is, therefore, in this material a tendency for irregular rows to occur in combination with high numbers of chromosome knobs. However, this association would be altered if the Caribbean flints of the Gulf Coast and the Indian varieties of southwestern United States were included in the survey. These two types of corns are in general typified by high numbers of knobs and straight rows, an association that is exactly the opposite of that found in the Southern Dents, Northern Flints and corn belt inbreds.

DISCUSSION

Data on knob numbers in maize are now available for a rather large number of varieties of South, Central and North America. Only for a collection of Guatemalan corn, however, has information on knob numbers been correlated with morphological data. MANGELSDORF and CAMERON (1942) have shown that for 162 varieties of Guatemalan maize there is an association of high and low numbers with several plant and ear characters. Their data demonstrate quite definite associations between high knob number and cylindrical *vs.* pyramidal ears, straight rows *vs.* irregular rowing, denting *vs.* flint and flour endosperm, glabrous leaf sheaths *vs.* pubescent sheaths, and several other plant and ear characteristics. Although our present knowledge of corn in the western hemisphere may not yet permit a fair comparison of United States maize with that of Guatemala, it is interesting to note that only in two instances do the results of this study conflict with the correlations reported by MANGELSDORF and CAMERON. High numbers of knobs in the United States material included in this study are positively correlated with irregular rowing and not with straight rows. Among United States corns those varieties with most consistent straight rows are found in the Northeastern Flints with very few knobs while the strongest tendency for irregular rowing occurs in certain Old Southern Dents and high knob inbreds of the corn belt. The second case in which these data conflict with the observations on Guatemalan corn is that of pubescence. Although pubescent leaf sheaths are not commonly found in United States maize, it is interesting to note that the only variety included

here which exhibited marked sheath pubescence was Tuxpan, one of the Old Southern Dents with 7, 8, and 9 knobs. The most glabrous varieties of United States corn are found among the almost knobless Northeastern Flints.

It is not probable, however, that this bit of conflicting evidence has any great significance. Our present knowledge of United States corn suggests that Guatemalan varieties have played a very minor role in the origin of United States varieties. Although we cannot yet completely abandon the idea of a Guatemalan origin of Northern Flints the evidence for such a hypothesis is indeed meager. In contrast, there is abundant evidence that a large segment of United States corn (most southern varieties exclusive of Caribbean flints) has stemmed directly from Mexico, and since Mexican and Guatemalan maize are very different entities it is probably incorrect to make direct morphological and cytological comparisons between Guatemalan and United States varieties. The work of MANGELSDORF and his collaborators suggests that the presence of chromosome knobs in maize is the result of contamination with Tripsacum. If this hypothesis can be applied to United States corn one would expect the Northern Flints, which externally exhibit more Tripsacum influence than any other group of varieties included in this survey, to possess many knobs. Actually, they have fewer knobs than any other group of United States maize. This may mean one of two things. Either the assumed tripsacoid nature of the Northern Flints is a superficial one or these flints are the result of the admixture of a knobless maize with a low knob Tripsacum, such as *T. australe*. It would seem, therefore, that more data are needed before one can safely regard knobs as a reliable indicator of Tripsacum germ plasm in Zea. It does appear, however, that knobs may represent one of the better indicators of relationships in corn.

SUMMARY

1. Chromosome knob numbers were determined for representative collections of United States maize consisting of Northern Flints, Southern Dents, and corn belt inbreds.

2. Knob numbers range from 0 to 12 with the greatest number being concentrated in the Southern Dents, the lowest in the Northern Flints. The distribution of knobs in inbreds of the corn belt is intermediate between the Northern Flints and Southern Dents.

3. High numbers of knobs are positively correlated with the following external features of the ear and plant: High row numbers, denting, absence of husk leaves, many seminal roots, and irregular rows of kernels.

4. The fact that similar relationships between knobs and morphological characters can be shown in the open pollinated Northern Flints and Southern Dents and in corn belt inbreds suggests that associations present in the ancestors of corn belt maize have not been extensively altered even after a century of breeding.

5. The present data are discussed briefly in light of the Tripsacum hypothesis. It is suggested that more data are needed before one can safely use knob numbers as an index to the amount of Tripsacum germ plasm in Zea.

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