A STUDY OF THE MORPHOLOGY, CYTOLOGY AND COMBINING ABILITY OF LINES OF *ZEA MAYS* L. IN RELATION TO THEIR ANCESTRY

by

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ABSTRACT

The cytology and morphology of a number of inbred lines and hybrids of *Zea mays L.* were studied with a view to determining the importance of divergence in these characteristics as an indication of phylogenetic relationships and of combining ability. The material investigated consisted of indigenous inbred lines and crosses among them, F_3 lines from a cross of a flint by a corn belt dent, and a few flint strains from South America and Mexico.

Counts of chromosome knob and seminal root numbers showed the lowest values for the northern flints, while the dent lines of the northern United States and Canada were intermediate between northern flints and the South American strains. On the basis of differences between northern flint and southern flint lines in chromosome knob and seminal root numbers, and the deviation of character associations revealed in these two groups, it was concluded that the southern flints are quite different from northern flints, and therefore phylogenetically distinct. Associations obtained, among indigenous inbred lines, between chromosome knob numbers and various morphological characteristics differentiating northern flint from dent type, showed that many associations present in the ancestral strains of maize have not been much altered even after prolonged breeding.

High grain yield, in both inbreds and hybrids, was associated with, large kernels, long ears and high tiller number. These, and an additional association of low ear-row number with hybrid yield, show that northern flints can contribute valuable breeding characteristics in addition to early maturity, since the only one of them considered undesirable in grain corn is high tillering. A number of other undesirable characteristics of the northern flints were found to be associated with early maturity, but the associations were not so strong as to inhibit the occurence of desirable recombinants in populations of manageable size.

Divergence in certain morphological characters differentiating dent and flint types was found to be a useful criterion of specific combining ability. One season's results in correlating combining ability and flint-dent differences showed that this correlation is of practical importance in predicting the performance of crosses. Lines derived directly from crosses of flint by dent had higher average combining ability than those derived from corn belt dent material. However, the advantage was too small to cast serious doubt on the hypothesis that corn belt dents trace their origin to similar stock in their remote ancestry. The heterotic effect produced by crossing divergent stocks suggests that lines with divergent genetic background may have utility in yield improvement, even though they are not themselves well adapted.

The desirability of maximising the genetic diversity while retaining the agronomic desirability of inbreds, and the problems involved in accomplishing this, are discussed.

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INTRODUCTION

The breeding of adapted corn hybrids for different regions of the North American corn belt has been among the most far-reaching developments in crop improvement of the present generation. Experimental findings reported in the literature indicate that crosses of unrelated inbreds of corn show greater heterosis than crosses of related lines. Anderson and Brown (2) pointed out that the common dent maize of the United States corn belt probably originated primarily from the mixing of Northern flints and Southern dents. They suggested that the heterosis utilised in commercial corn belt hybrids stems directly from the union of these genetically divergent corn forms. Hybrids are required that combine the early maturity of northern flint types with the higher yielding ability and superior plant characteristics of the corn belt lines, if corn is to develop greater importance as a grain crop in Western Canada and the northern part of the United States.

It has been shown by Anderson *et al*. (2) that there is relatively strong association among a number of characteristics of northern flint types of maize. Some of the characteristics are desirable, e.g. early maturity, low kernel row number, long ears and large kernels. A number of them are agronomically undesirable, e.g. low ear placement, profuse tillering, spindly tassels and long husk blades. On the other hand, varieties of dent type (particularly those of the central and southern United States where contamination with flint germ plasm is presumably slight or absent) are characterised by high ear placement, short shanks, low tiller number, compact sturdy tassel, high row number, short cylindrical ears, deep kernels and short husk blades.

Pure lines with flint ears and early maturity, but with plant characters resembling the dents have been isolated from flint-dent crosses, showing that the undesirable associations are not complete. However, in back cross programmes, utilizing flint sources as donors of earliness to reconstitute southern dent lines, considerable difficulty has been experienced in isolating early lines which do not carry one or more of the undesirable traits of the flint parent. The frequency of agronomically desirable types in a hybrid population involving flint and dent parentage of this type is not known, nor is it known how closely this ideal combination could be approached in a population of manageable size.

Recent investigation (26) has confirmed that low seminal root number is characteristic of flint types while high seminal root number is characteristic of the dents.

It has been reported that chromosome knob numbers are characteristic in various morphological groups of corn. Limited studies indicate that the northern flints have a low chromosome knob number compared to the southern dents. It has been suggested that the presence of knobs may indicate the presence of blocks of genes concerned with the expression of certain morphological features derived from an ancestral type. The extent of knob association with some morphological characters in the flints and dents is therefore of interest.

The primary purpose of this project was to provide information on the significance of the cytology and phylogeny of dent and flint maize types as they occur in the northern United States and Canada. The relationship of divergence in morphological characters and phylogeny to combining ability was studied. Information was sought concerning the possible association of high combining ability in terms of grain yield and early maturity coupled with certain undesirable traits of flint types.

LITERATURE REVIEW

The dark staining enlargements known as knobs are among the more important of the distinguishing features of maize chromosomes. They have been shown to occur at certain points on the chromosomes and are also used as one of the criteria in determining the relationship of various kinds of morphological groups of maize. McClintock (37) first established that the chromosomes of maize have these large bulky heterochromatic regions called knobs, visible in meiotic prophase, and located in definite and characteristic positions. Longley (32) studied knob number and position in a collection of maize varieties from thirty-three 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 was found in south-eastern varieties and a high frequency was observed on the chromosomes of most varieties from New Mexico and Arizona. On the basis of these findings, Longley suggested 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 (36) have suggested that the presence of chromosome knobs in maize is a result of hybridization 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 the new genus *Euchlaena*. These investigators pointed out that the so-called ''Andean'' or uncontaminated maize of South American highlands had only a 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 (44) who, in a study of knob numbers in maize from North, Central and South Americas, demonstrated a statistically significant relation between number of knobs and proximity to Central America, a region in which both *Tripsacum* and teosinte are found in abundance. Reeves found a range in chromosome knob numbers from 0.00 in a strain from Ecuador to 9.5 in one from Guatemala. Mangelsdorf and Cameron (35) found chromosome knob numbers in Guatemalan maize ranging from one to sixteen, with an average of 7.9, for 162 varieties. This was 1.35 lower than the average recorded by Reeves. Their data demonstrated a quite definite association of high knob number with each of cylindrical ears, straight kernel rows and denting and, to a lesser degree, with several other characters.

Mangelsdorf and Cameron (35) showed that, at low altitudes of 2000 to 5000 feet in north-eastern Guatemala where *Tripsacum* and teosinte occur, the native corn had relatively high numbers of chromosome knobs, while at a high altitude of about 8000 feet, the native corn had few knobs. They assumed that corn had acquired knobs from contamination with Tripsacum. Brown (5) found 0 to 12 knobs in members of a representative collection of United States maize consisting of northern flints, southern dents and corn belt inbreds. The greatest number of knobs was found in southern dents and the lowest in northern flints. The distribution of knobs in inbreds of corn belt origin is intermediate between those of northern flints and southern dents. He showed that chromosome knob number was positively correlated with kernel row number, degree of denting, absence of husk blades, many seminal roots and irregularity of kernel rows. Based on these results he suggested that the associations present in the ancestors of corn belt maize have not been extensively altered, even after centuries of breeding.

Vachani (56) observed chromosome knobs ranging from 2 to 8 in number with an average of 4.62 in twenty inbred lines of diverse origin used in the breeding programme at the Minnesota Experiment Station. His data showed no relation between chromosome knob numbers and morphological characters, although some ear characters approached the five percent probability level of deviation from independence. He stated that the group of inbreds sampled were of the low chromosome knob category, except for two, which had seven knobs or more.

Anderson and Brown (2) noted zero to two knobs among flint and flour varieties from New England and the north-eastern United States, the area in which the flint types presumed to be involved in the ancestry of corn belt maize were highly concentrated. They found five to twelve knobs in the open pollinated varieties of southern dent type, which are presumably least contaminated by northern flint germ plasm. The similarities in ear characteristics and low knob numbers (in the order of 3) observed in highland varieties of Guatemala were taken to indicate the Guatemalan origin of flint corn of the north-eastern United States. These investigators found a significant positive correlation between grain yield of single crosses with differences in morphological indices of the inbred, including chromosome knob numbers.

Welhausen *et al*. (59), in a study of races of corn in Mexico found that the most productive races of corn all show a strong introgression of teosinte. Furthermore they observed that races which were derived from the intercrossing of two other races, in general had a higher chromosome knob number than the average of the putative parents. In certain races of hybrid origin the knob number was higher than that of either one of the parents. Based on these observations, they pointed out that there might be some relationship between chromosome knob numbers and yield in corn. Welhausen et al. (59) reported chromosome knob numbers ranging from 1.75 to 9.10 in a study of 25 different varieties of corn adapted to different elevations in Mexico. Their data indicated that in lower altitudes, high-knob-number inbreds were the best combiners in top crosses while at higher altitude low-knob-number inbreds were the best combiners.

Suto (54) in a survey of morphological and cytological characteristics of 76 Oriental maize varieties obtained the following results: zero (or nearly so) chromosome knobs in European and North American flints from north Japan; 3 to 9 in ''Caribbean flints'' from southern Japan; 5 knobs in Persian flints from northern Nepal. Based on these morphological and cytological studies, he concluded that the Javanese type from Indonesia could have arisen through hybridization between races of Caribbean and Persian flints. Yamasaki et al. (62) found 7 to 8 chromosome knobs in Caribbean types of tropical flints from Japan and Indonesia; 3 to 5 in the North American corn belt types and a knobless group comprising the northern type of flints imported from the United States and Europe. These investigators presented data which showed a positive and significant association between degree of heterozygosity for chromosome knobs and grain yield among hybrids. However, there was significant negative correlation between the amount of precipitation in the serological reaction and each of heterozygosity of chromosome knobs and grain yield among 10 hybrids involving Japanese flint and corn belt dent inbred lines. From these results they suggested that the hybrid vigor of F_1 could be predicted either by serological index or by the number of heterozygotic pairs of chromosome knobs. They also suggested a similar use of serological index for those inbreds having no chromosome knobs.

Roberts et al. (49) reported average numbers of chromosome knobs ranging from 1.5 to 10.8 from the study of 21 races of maize from Colombia. Individual plants in the collection had up to 14 chromosome knobs. From the data on morphological and cytological characteristics in Colombian races of maize, they concluded that Colombia has been an important centre of origin of new races which have spread to other countries to become the progenitors of still other new races, including the world's most widely grown maize, the Corn Belt dent of the United States. Ricardo Ramirez et al. (46) obtained 1 to 2 chromosome knobs from the study of 11 races of highland maize of Bolivia and 3 to 13 chromosome knobs among non-Andean races of Bolivia. They indicated that the number of chromosome knobs increased from higher to lower altitudes, although the proportion to altitude was not always direct.

Ibrahim (20) found chromosome knob numbers ranging from 0 to 8 in open-pollinated varieties of maize from all over the world. These data indicated that varieties in the collection from regions of greater than 40° latitude North did not have any more than 3 knobs. This confirms the suggestion of Longley (32) that the number of chromosome knobs might give a clue to the geographical origin of varieties. He further reported that high number of chromosome knobs was strongly associated with denting, and with kernel row number. Grobman *et al.* (15) found low chromosome knob numbers in the great majority of highland races of Peru. The pattern of chromosome knobs observed was predominantly ''Andean'' according to the designation of pattern used by McClintock (38). This pattern is based on possession of a large intercalary knob on the long arm of chromosome 7 and, less frequently, a medium sized knob in the intercalary position on the long arm of chromosome 6. These authors reported 2 distinct groups of races of maize on the coast of Peru: (a) anciently derived races, and some more recent ones from highland floury source material, and (b) *Tripsacoid* races. The anciently derived races and highland floury races had chromosome knobs ranging from 0 to 3, while the *Tripsacoid* races had a range of 4 to 14 chromosome knobs. Based on their studies of cytological, morphological and physiological characteristics, these authors concluded that the central Andean maize domestication centre has undoubtedly contributed much more germ plasm to the middle American maize domestication centre than it, in turn received from the latter.

Murdy (41) in a cytological and morphological analysis of a maize chapalote population, showed association between specific chromosome segments marked by knobs with certain morphological characteristics e.g., small ear diameter, many tillers with a knob at 4L; similarly later pollen shedding,many stem internodes and narrow leaves with a knob at 6b.

Studies have been reported by a number of investigators on the relation between various characters of inbred lines and attributes of their hybrid progeny.

Kiesselbach (28) reported a relationship between the yield of inbred parents and that of their hybrid offspring.

Wolfe (61) found significant correlations between weight of grain per ear and the length of ear and circumference of the ear. Kempton (27) reported significant positive correlations between length of ear and each of number of kernel rows, height of plant and weight of seed among F_1 plants. In F_2, maturity was positively correlated with weight of kernel and height of plant. Kiesselbach (28) found F_1 crosses between high yielding corn strains to be, as a rule, better yielding than those between low yielding strains. On the other hand Richey (47) and Richey and Mayer (48) in a similar comparison found no such relationships. Hayes (16) found that yield was very strongly correlated with those characters of inbred lines which are concerned with the expression of vigour. Nilsson-Leissner (43) reported positive correlations (r = .19 to .74) between ear length, ear diameter, kernel row number and plant height of inbred lines and the same characters in their single cross progeny.

Jorgenson and Brewbaker (24) found positive significant correlations between yield of grain, ear length, ear diameter, kernel row number, height of stalk and weight of seed of inbred lines and the same characters in their single crosses. They concluded that selection of the most vigorous inbred lines was a desirable procedure from a practical breeding standpoint.

The most detailed and comprehensive correlation studies were those reported by Jenkins (21). He found that within the inbred lines, yield was correlated significantly and positively with plant height, number of ears per plant, ear length, ear diameter and shelling percentage, whereas it was correlated significantly and negatively with date of silking. Within the F_1 crosses, yield was correlated significantly and positively with date of tasseling, date of silking, plant height, number of nodes per plant, number of nodes below the ear, number of ears per plant, ear length, ear diameter and shelling percentage. He also found a significant positive relation between the yield of single crosses and the following characters of the parents: date of tasseling, date of silking, plant height, number of nodes per plant, number of nodes below the ear, number of ears per plant, ear length, ear diameter and yield.

Hayes and Johnson (17) reported highly significant positive correlations between the following characters of 110 inbreds and the same characters of the inbred variety cross: date silked, plant height, ear length, shank length. Within top crosses the grain yield was positively and significantly correlated with each of moisture content at husking and ear length, while there was a negative correlation between yield and percent of smut infection. They further found that yields of top crosses were correlated positively with the following characters of parental inbred lines: date silked, plant height, ear height, leaf area, stalk diameter and ear length. They obtained a multiple correlation coefficient of .67 between yield and 12 characters of the plant and ear, showing that 44.1 per cent of variability in the yield of top crosses was depended on these twelve characters of the inbreds.

Anderson (1), in studies of North, Central and South American maize varieties, found significant positive correlations between all combinations of the following characters: condensation of internodes in the tassel, increase in row number, length of tassel branches, ear length, and irregularity in formation of ear rows. Carter et al. (7) in a survey of maize in the south-western United States, found inter-relationships among ear tapering, kernel row number and depth of denting and referred to this as the Mexican complex. Kernel width, shank diameter and straightness of rows were also interrelated and were referred to as the eastern complex.

Robinson et al. (50) have presented both phenotypic and genotypic correlations involving a series of 8 attributes in crosses among F_2 plants derived from 3 single crosses. In only a few cases, did the two estimates of association differ appreciably. Ears per plant was the only attribute found to have high positive genetic correlation with yield. The only other characters found to have an appreciable genetic association with yield were plant height and ear height. These authors illustrated how genetic correlation may be used in construction and evaluation of selection indices.

Kopf (30), by study of inbred lines and their single crosses and backcrosses, found that intense red pigment of mid cob was associated with high yield, higher breaking strength, weight of cob and later silking date.

Mezzacapp (39) noted a positive correlation between grain yield and plant height among the top crosses of flint lines with synthetics. Zonjic (64) found that kernel weight of flint and dent hybrids was correlated with ear length and kernel percentages.

Ballesteros (4) reported a highly significant correlation coefficient between grain yield and ear length in single crosses involving inbreds of divergent origin in the Philippines. Murty et al. (42) from a study of open pollinated varieties in India obtained significant positive association between grain yield and the following characters: number of nodes, stalk girth, plant height, leaf area, weight of the ear, 100 kernel weight and ear length. They also found a negative significant correlation coefficient between grain yield and days to tassel.

Chao (8), by means of paracentric-inversions, showed that genes for earliness were located in the long arm of chromosome 3 of inbred Wf.9 and in chromosome 6 of a number of other strains. The genes for high number of ears were located on chromosome 6 of strain 3a and chromosome 3 in some other strains. He found high positive correlation between grain yield and number of ears.

Hoen *et al.* (18) in a study of flint and dent hybrids, found high positive correlations between number of husk blades with number of tillers and 1000 kernel weight. Ear height and number of kernel rows showed negative correlations with length of husk blades. Grain yield was positively correlated with ear number, number of kernel rows, kernels per row, 1000 kernel weight and degree of denting. Jugenheimer (25), in a study of 145 inbred lines, found a significant association of yield with plant height. Days to maturity was associated positively with each of plant height, ear height and 1000 kernel weight. Kramer *et al.* (31) found highly significant associations between the following characters of exotic inbreds and the same characters of top crosses with (Wf. 9 x Hy) x Inbred: plant height, date of silking, ear length, ear diameter, number of kernel rows per ear. Within the exotic inbred lines and within F_1 crosses among them the characters plant height, date of silking, ear length and ear diameter were inter-related in a positive manner. Within top cross progeny, yield showed a high positive correlation with plant height, days to silking, ear length and ear diameter.

Origin of Corn Belt Dent Maize

Wallace *et al.* (57) stated that the new varieties of corn belt dent, which presumably originated from prolonged and complex mixing of flint and gourd seed types, got their long cylindrical ears from flints, and their soft kernel from gourd seed, whereas the kernel row number was intermediate between the two groups. The intensified red cob colour was derived from gourd seed and the yellow kernel colour from flint varieties. It remained for selection of strains and yield tests of them to determine the most productive kinds out of this mixture, and for hybrid corn to make really efficient use of the germ plasm present in the corn belt dents.

Jones (23) reported that the flint and dent types of maize were intermediate between pop and floury types of maize, on the basis of proportion of soft and hard starch in the kernels of each type. Floury maize types had all soft starch and pop types only hard starch, while dent types had more soft starch than flints, which, after shrivelling, gives the characteristic appearance of the dent kernel. Flint maize had predominantly hard starch with very little soft starch near the embryos of the kernels. He observed the intermediate nature of F_1 grains of a cross between the Cuzco floury variety and a small seeded Rice pop corn.

He reviewed the observations of previous writers stating that gourd seed and northern flint varieties could probably both be grown in and about Virginia and presumably mixing of these types provided dents of primitive form and from these the modern types of dent corn might have developed. Anderson and Brown (2) presented evidence to show that the origin of Corn Belt Maize was from mixtures of northern flints and southern dents. The segregates in F_3 from a cross involving typical white gourd seed from Texas and a typical yellow flint from New York State, were within the range of variation of corn belt dents. From the study of character association in an opeh pollinated variety of Golden Dent, they showed association of: (1) wide kernel, (2) low row number, (3) short glumes, (4) few tassel branches, (5) long ears and (6) narrow cylindrical pith in the ear, all of these characterising the northern flints. The opposing combination (1) narrow kernel, (2) higher row number, (3) long glumes, (4) many tassel branches, (5) short ears and (6) wide central pith in the ear was shown to be associated with characteristic of Southern dents. They indicated that some of the characters which went in together from flints and dents were still in the open pollinated variety and tending to stay together on the average. They pointed out that the hybridization of southern dents, and northern flints represents mingling of two basically different germ plasm sources, based on the criteria of differences in taxanomic characters like spikelet shape and veination, spikelet arrangement, pubescence, internode proportion, leaf shape, rachis morphology, etc. Other distinguishing features of the southern dents from northern flints consisted of modifications of the entire inflorescence, such as condensation of the tassel in the southern dents, pairs of spikelets in whorls of 3 or mixtures of 3 or 2, and a short and flattened tassel rachis. On the contrary, northern flints were without condensation of the tassel, the pairs of spikelets were in whorls of 2, and the tassel rachis was slender and with long internodes. The consistent cytological differences between northern flints and southern dents were: the former have chromosomes which are essentially knobless at pachytene, the latter, on an average, nearly one knob per chromosome. This difference, they pointed out, must represent a difference in germ plasm. These authors (2) pointed out that differences in the chemistry of divergent germ plasm was indicated by a difference in smearing and ease of obtaining a sharp image at the pachytene stage. These authors suggested that the heterosis utilised in commercial corn belt hybrids stems directly from the union of these genetically divergent corn forms.

Experimental findings reported in the literature indicate that crosses of unrelated inbred lines of corn show greater heterosis than crosses of related lines (2, 9, 10, 14, 17, 19, 33, 40, 45, 62). Moll *et al*. (40), in discussing genetic diversity in relation to heterosis, observed that genetic differences between varieties have developed through geographical isolation accompanied by a combination of genetic drift and natural selection in different environments. They suggested that the degree of geographical separation and the degree of ancestral relation, in so far as these are known, could be used as an indicator of genetic diversity.

Galinat (11) pointed out that ancestral relationships in corn may be used to contribute to its' breeding. He suggested that consideration should be given to the natural association of pollen grain size and length of ear, as an aid in selection for increased ear length. He pointed out that by understanding the flow of germ plasm from corn's wild relatives teosinte and *Tripsacum*, one might be able to increase the pool of germ plasm among inbred lines which in turn would lead to increase their combining ability in the F_1 hybrids.

MATERIALS AND METHODS

Materials

For one phase of this study, forty-one inbred lines of corn were used, consisting of two distinct groups, i.e. dents and flints from the standpoint of kernel type. A number of these were developed from dent or flint varieties respectively, but some of each type were developed from hybrids between flint and dent lines or varieties. Most of the lines were relatively homozygous, having been intensively inbred. The degree of expression of morphological characters usually associated with either type varied widely in these lines. The lines within each group were chosen with a view to obtaining the greatest possible range in morphological characteristics in terms of maturity, plant height, ear height, tiller number, shank length, kernel row number, ear length and seminal root number. The source from which the inbred lines were obtained and the type of heterozygotes from which they were derived are given in Table 1.

Forty-eight crosses involving 12 inbred parents were used for the study of combining ability in terms of grain yield and morphological characteristics. The 12 inbred parents were crossed in a diallel series in all combinations except those in which the parents were closely related. The sources from which these inbred parents were

Table 1

Source and Origin of Inbred Lines

Serial number	Designation	Flint or Dent (based on denting)	Ancestral Origin	Institution from which obtained
1	61-66	Dent	Northern Flint Corn Belt Dent	University of Manitoba
2	61-67	Dent	"	"
3	61-69	Flint	"	"
4	61-71	Flint	"	"
5	61-73	Flint	"	"
6	61-74	Smooth Dent	"	"
7	61-75	Smooth Dent	"	"
8	61-76	Flint	"	"
9	61-77	Flint	"	"
10	61-78	Smooth Dent	"	"
11	61-79	Flint	"	"
12	61-80	Flint	"	"
13	61-81	Flint	"	"
14	61-82	Smooth Dent	"	"
15	61-83	Flint	"	"

Continued

Table 1 continued,

16	A.495	Dent	Corn Belt Dent	Minnesota Experiment Station
17	A.498	Dent	''	''
18	Howe's Alberta Flint	Flint	Northern Flint	Canada Dept. Agric.
19	K.71	Dent	N.Flint x C.B. Dent	University of Manitoba
20	M.14	Dent	N.Flint x C.B. Dent	Minnesota Experiment Station
21	Q.573	Flint	N.E.Flint	Macdonald College, Quebec
22	R.5	Dent	Corn Belt Dent	University of Manitoba
23	W.333	Flint	N.Flint	Wisc. Agric. Res. Stn., Spooner
24	15	Flint	N.Flint	''
25	152	Dent	Corn Belt Dent	Canada Dept. Agric.
26	K.D.54	Dent	''	University of Manitoba
27	K.N.11	Dent	''	''
28	V.3	Dent	''	Canada Dept. Agric.

Continued

Table 1 continued

29	W.D.	Dent	Corn Belt Dent	Wisconsin Agric. Research Stn., Madison, Wisc.
30	K.261	Dent	"	University of Manitoba
31	K.275	Dent	"	"
32	W.617	Flint	N.Flint x C.B.Dent	Wisc. Agric. Res. Stn., Spooner
33	M.7	Flint	"	Canada Dept. Agric.
34	M.17	Flint	"	"
35	K.126	Dent	"	University of Manitoba
36	K.98	Dent	"	"
37	Kfa	Dent	"	"
38	Ge	Dent	"	"
39	M.6	Flint	N.Flint	Canada Dept. Agric.
40	38	Flint	N.Flint	"
41	59-36	Dent	Corn Belt Dent	University of Manitoba

obtained are presented in Table 1 under serial numbers 26 to 37 inclusive.

One hundred twenty F_3 lines were selected from selfed plants in the F_2 population of the cross S.W.F. x B.14. These 120 lines were sampled to represent a range in maturity, tiller number, degree of denting and seminal root number. S.W.F. (Saskatchewan White flint) is a typical early flint line with low seminal root number and low chromosome knob number whereas B.14 is a late dent line of central corn belt origin with high seminal root number and relatively more chromosome knobs.

Twelve flint-type lines from South America and Mexico were obtained for the study of chromosome knob numbers, seminal roots and other morphological characteristics. These lines will be referred to hereafter as Southern lines.

Plan of Field Study

The 41 inbred lines used in the study were grouped in two experiments of 25 and 16 lines each. They were laid out respectively in 5 x 5 and 4 x 4 incomplete-lattice designs, with 3 replications, using a single row of 15 feet for each plot. The seeds were planted one foot apart with 3 feet between rows.

The 48 single-cross hybrids, with the F_1 double-cross hybrid Morden 88 as a control, were planted in a 4-replicate 7 x 7 incomplete-lattice design using single row plots 15 feet in length. The seeds were planted 1 foot apart with 3 feet between rows.

The 120 F_3 lines of the cross S.W.F. x B.14 were planted in single row plots, 15 feet in length, using intermittent parental checks after every 10 F_3 lines. Here also, planting within rows was 1 foot apart in rows 3 feet apart. Similarly the southern 12 lines were planted in single rows, using Morden 88 as a check. Standard plot techniques were used, including increased planting rates with thinning of seedlings to a uniform stand. The stand of the crop was satisfactory except in one inbred line R.5, which had to be replanted because of unsatisfactory germination for the first planting. Many of the F_3 lines were seriously damaged by a hail storm during July 1962, to the extent that a proportion of them did not provide reliable data. In addition, it was necessary to use the green house to collect pollen mother cells from the selected lines in this group. Damage by hail storm to the inbred lines, single crosses and Southern flints was negligible, as they were grown in a separate area.

Procedures in Collecting Field Data

Date of tasseling in each plant of corn, excluding border plants, was recorded as that when the first pollen shedding was observed. Similarly, the date of silking was recorded. The tasseling dates in inbred lines and F_3 progenies were observed daily. Characters such as plant height, ear height, tiller number, tassel branches, shank length, ear length, ear diameter, kernel row number and 1000 kernel weight were recorded when the plants were ripened in inbreds, single crosses and F_3 lines. Five plants in each replication were taken at random for observations of the above characters in inbred lines and single crosses. The average of all the replications of a specific item was taken for calculating coefficients of correlation. In the case of F_3 lines and Southern strains, all the plants except the bordern plants and those bordering gaps in rows were used for recording the above data. The average of all plants in each line was taken for calculating the coefficients of correlation. Grain yields of inbred lines and single crosses were adjusted to a uniform moisture basis. For the single crosses, moisture determinations were based on moisture loss on drying of all the ears taken from each plot at harvest, but for the inbred lines, a sample of 5 ears was used for determination of moisture percentages.

Determination of Seminal Root Development

Determinations of seminal root number in inbred lines and F_3 lines were done according to the technique outlined by Kajjari (26).

Determination of Chromosome Knob Number

Pollen mother cells were collected from each of the inbred lines, the Southern strains, and about 40 F_3 lines. The microsporocytes were killed and fixed in Farmer's fluid (glacial acetic acid one part: 95% alcohol three parts) for 24 hours. Preservation of samples was made in 70% alcohol at 0.0°C temperature. The acetocarmine smear technique, as outlined by Smith (53) for staining the pollen mother cells, was used for the study of chromosome knob numbers. The cells were gently pressed to flatten the chromosome threads as much as possible without rupturing the cells. The total number of knobs was counted for each line.

Association of Characters

The extent of association between characteristics within local inbred lines, single crosses, F_3 lines and Southern strains, was tested by calculating coefficients of correlation among them.

Before making tests of association, analysis of variance and F tests were applied to determine the statistical significance of differances among the metric characters of single crosses and inbred lines.

Within inbred lines and F_3, the data collected were used to test the extent of association between chromosome knob numbers and each of the morphological characteristics, including grain yield.

Similarly total correlation coefficients were computed between grain yield of the single crosses and the following characters of their inbred parents: maturity, plant height, ear height, chromosome knob numbers and grain yield. The average of the two parents was used in these calculations.

The F_1 yields were calculated, for the purpose of expressing them in terms of heterosis effects, in percent of the mid parent, higher parent and constant parent. The mid parent yield for each parental line was based on the average of all the mid parent yields of crosses with that particular parent in common. Similarly, the higher parent yield was calculated by taking the average of all the higher parents crossed with the parent in common.

Chi-square tests were applied to detect the interrelationships among the following characters of the F_3 lines: seminal root number, maturity period, tiller number, plant height, ear height, kernel row number, ear length and ear diameter.

Procedure in Calculating Inbred Indices on Morphological Characteristics

The extent of association between differences in morphological characteristics of inbred parents with the grain yield of single crosses was tested by computing the differences in terms of inbred indices for the following characteristics: ear length, 1000 kernel weight, tiller number and number of chromosome knobs. Only 39 single crosses were used for this purpose, since the chromosome knob number in one inbred could not be ascertained. The means for each character obtained from the replicated experiment were translated into numerical index values, based on a low value representing Northern flint tendencies and a high value Southern Dent tendencies. For example, the mean ear length values for the inbreds involved ranged from 11.1" to 17.0." These were arranged in Table 2, column 1, and the index number for each class indicated in column 5 of the same table. Index values for other characteristics were arranged similarly. A total index was determined as is shown by the example in Table 3, column 7. After index values had been determined for the 11 inbreds, the differences between the index numbers of various pairs of parents of crosses were worked out. The differences were then added, ignoring signs, as shown in Table 3, column 8. A scatter diagram was prepared taking the index of morphological differences among pairs of parents on the abscissa and grain yield on the ordinate. This diagram is presented in Fig. 8. Finally the total correlation coefficient was worked between index differences and grain yield.

Table 2

Measurement of Four Morphological Characters Arranged to Index Number

Ear length cms.	1000 K. wt in grams.	Chromosome knob numbers	Tiller number	Index number given
1	2	3	4	5
16.6 - 17	251 - 260	0.1 - 1	2.76 - 3.0	1
16.1 - 16.5	241 - 250	1.1 - 2	2.51 - 2.75	2
15.6 - 16	231 - 240	2.1 - 3	2.26 - 2.50	3
15.1 - 15.5	221 - 230	3.1 - 4	2.01 - 2.25	4
14.6 - 15.	211 - 220	4.1 - 5	1.76 - 2.0	5
14.1 - 14.5	201 - 210	5.1 - 6	1.51 - 1.75	6
13.6 - 14.0	191 - 200	6.1 - 7	1.26 - 1.50	7
13.1 - 13.5	181 - 190	7.1 - 8	1.01 - 1.25	8
12.6 - 13.0	171 - 180	8.1 - 9	0.76 - 1.00	9
12.1 - 12.5	161 - 170	9.1 - 10	0.51 - 0.75	10
11.6 - 12.0	151 - 160	10.1 - 11	0.26 - 0.50	11
11.1 - 11.5	141 - 150	11.1 - 12	0.00 - 0.25	12

Table 3

Inbred Indices Based on Four Characters

S.N.	Inbred	Ear length	1000 kernel wt.	Tiller number	Chromosome knob no.	Inbred index	Sum of 4 differences without signs
1	2	3	4	5	6	7	8
1	K.D.54	12	12	12	4	40	
2	K.N.11	12	9	10	5	36	6
3	V.3	10	7	12	6	35	10
4	W.D.	8	8	7	4	27	
5	K.261	11	9	12	6	38	
6	K.275	7	9	11	5	32	
7	W.617	5	5	1	-		
8	M.7	3	7	6	4	20	5
9	M.17	5	9	5	4	23	
10	K.126	9	11	12	6	38	19
11	K.98	9	2	9	2	22	
12	Kfa	9	1	10	1	21	

RESULTS AND DISCUSSION

Chromosome Knob Numbers in Indigenous Inbred Lines, F_3 lines from a Cross (S.W.F. x B 14) and Southern Lines

The data on chromosome knob numbers of 41 inbred lines, used in the breeding programme at the University of Manitoba, are presented in Table 4. Some of the lines were from dent by flint crosses, but others were derived from stocks presumed to be either pure flints or pure dents. The average chromosome knob number of 36 of these inbred lines was 3.88, with a range of 0 to 8. The knob numbers for 5 of the lines could not be determined since these lines did not yield good pachytene figures. The lines 15, W333, Q573, 38, 61-66, 61-73, 61-74, 61-77, 61-79 and 61-80 had low knob numbers ranging from 0 to 2 (Fig. 1 and 2), although the majority of the remaining lines also had relatively low numbers within the range of 0 to 4. Of these lines, 15, W333, Q573 and 38 were pure flints, whereas the lines of the 61 family were derived from crossing V_3, a northern corn belt line, with the Northern flint line 38. The inbred lines M.14, K.71, K.98 and K.126 were also derived from the above cross. The line 59-36 was a sister selection of K.N.11. The group from V_3 x 38 parentage appears to recapture the range of the parents in knob number (one lower). The only line which had knobless chromosomes was 61-81. Only one line which had dent grains had the low knob number of one (Fig. 3). This

Table 4

Number of Chromosome Knobs, Seminal Roots and Other Morphological Characters of Indigenous Inbred Lines of Corn

S.No.	1	2	3	4	5	6
Name of inbred	61-66	-67	-69	-71	-73	-74
No. of chromosome Knobs	2	6	3	-	2	2
No. of Seminal Roots	1.30	2.05	-	1.51	1.56	1.60
Days to tasseling	71	67	67	69	69	68
Plant height inches	74.0	70.3	74.3	75.0	76.0	74.3
Ear height inches	23.3	21.3	17.6	16.6	19.6	18.0
Tiller No.	2.3	0.0	1.6	2.6	2.0	2.6
Shank length cms.	12.3	19.6	15.6	20.6	22.0	18.6
No. of Tassel branches	17.6	16.0	14.6	15.6	15.3	15.6
Ear length cms.	16.0	15.3	18.6	18.0	17.0	17.3
Ear diameter mm.	41.0	37.0	34.0	33.0	34.0	34.0
Kernel row number	19.0	15.0	14.0	14.0	14.0	14.3
1000 kernel weight gms.	208	161	170	204	234	203
Grain yield in Bushel per acre	24.6	21.9	24.9	23.1	22.2	23.2

continued

Table 4 continued,

S. No.	7	8	9	10	11	12
Name of inbred	61 -75	-76	-77	-78	-79	-80
No. of chromosome Knobs	3	6	1	3	2	-
No. of Seminal Roots	-	1.70	1.40	-	1.38	2.07
Days to tasseling	67	68	64	65	60	63
Plant height inches	74.3	74.0	51.3	63.3	52.0	65.0
Ear height inches	17.6	18.3	11.6	16.6	16.0	19.3
Tiller No.	3.0	2.6	2.6	2.3	2.3	2.6
Shank length cms.	21.3	18.6	15.3	16.6	8.0	12.3
No. of Tassel branches	15.0	14.3	14.6	14.3	15.6	11.3
Ear length cms.	17.6	17.6	11.3	16.0	14.0	12.3
Ear diameter mm.	34.0	35.0	39.0	39.0	36.0	43.0
Kernel row number	14.3	14.6	12.0	12.6	10.5	13.6
1000 kernel weight gms.	239	222	270	231	258	212
Grain yield in Bushel per acre	25.1	27.2	27.2	26.2	16.3	25.5

continued

Table 4 continued,

S. No.	13	14	15	16	17	18
Name of inbred	61 -81	-82	61-83	A.495	A.498	Howe's A.Flint
No. of chromosome Knobs	0	-	3	6	6	-
No. of Seminal Roots	-	1.48	1.35	2.52	3.04	1.0
Days to tasseling	63	59	60	75	73	50
Plant height inches	63.6	48.0	47.3	65.3	71.0	45.3
Ear height inches	21.0	12.3	14.6	24.6	25.5	2.0
Tiller No.	2.6	3.0	2.0	2.0	1.3	2.3
Shank length cms.	11.3	14.3	11.0	15.6	14.0	14.0
No.of Tassel branches	14.6	13.0	15.3	16.6	11.0	5.6
Ear length cms.	14.6	11.0	13.0	16.6	14.6	10.0
Ear diameter mm.	41.0	40.0	41.0	41.0	41.0	-
Kernel row number	12.6	14.3	15.3	15.0	17.0	8.0
1000 kernel weight gms.	237	219	198	178	182	-
Grain yield in Bushel per acre	32.3	15.4	17.4	16.4	27.2	-

Table 4 continued,

S. No.	19	20	21	22	23	24
Name of inbred	K.71	M.14	Q573	R5	W333	15
No. of chromosome Knobs	4	6	2	8	2	1
No. of Seminal Roots	3.21	3.46	1.01	-	-	1.00
Days to tasseling	68	86	68	76	77	64
Plant height inches	69.0	68.6	64.6	62.3	68.3	51.6
Ear height inches	19.0	24.6	20.3	22.6	29.3	16.3
Tiller No.	0.01	1.3	2.3	0.0	0.6	1.6
Shank length cms.	10.0	8.3	12.6	10.6	10.0	5.6
No.of Tassel branches	13.6	10.0	8.3	14.3	19.5	14.6
Ear length cms.	15.6	13.3	19.0	14.0	13.0	11.6
Ear diameter mm.	36.0	36.0	38.0	35.0	35.0	37.0
Kernel row number	17.0	17.0	11.3	13.3	12.3	12.3
1000 kernel weight gms.	166	228	213	231	154	146
Grain yield in Bushel per acre	16.0	6.3	18.5	6.8	12.6	9.7

Table 4 continued,

S. No.	25	26	27	28	29	30
Name of inbred	152	K.D.54	K.N.11	V.3	W.D.1	K.261
No. of chromosome Knobs	6	4	5	6	4	6
No. of Seminal Roots	2.64	2.86	2.93	4.39	1.80	3.76
Days to tasseling	75	68	62	66	62	63
Plant height inches	60.3	62.6	59.3	63.6	58.3	59.3
Ear height inches	18.6	17.3	20.0	18.3	16.3	17.3
Tiller No.	0.0	0.0	0.6	0.0	1.3	0.0
Shank length cms.	10.0	18.0	8.6	8.3	15.6	9.0
No.of Tassel branches	8.0	7.0	16.6	18.3	13.0	10.6
Ear length cms.	10.3	11.0	10.3	12.3	13.3	12.0
Ear diameter mm.	38.0	42.0	36.3	35.3	34.0	37.0
Kernel row number	16.0	16.0	15.6	12.6	12.6	14.6
1000 kernel weight gms.	180	145	174	197	190	180
Grain yield in Bushel per acre	11.1	21.8	17.0	14.4	26.2	19.5

Table 4 continued,

S. No.	31	32	33	34	35	36
Name of inbred	K.275	W.617	M.7	M.17	K.126	K.98
No. of chromosome Knobs	5	-	4	4	6	2
No. of Seminal Roots	3.40	1.47	1.68	2.57	2.82	4.20
Days to tasseling	62	66	65	66	66	64.0
Plant height inches	64.6	69.0	62.0	56.6	65.6	68.0
Ear height inches	17.6	18.6	15.3	11.0	18.0	22.0
Tiller No.	0.3	3.3	1.6	2.0	0.0	1.0
Shank length cms.	17.0	9.3	10.6	10.3	7.6	15.6
No.of Tassel branches	8.6	13.0	13.6	9.6	15.3	11.0
Ear length cms.	14.0	14.6	15.6	15.0	13.0	13.0
Ear diameter mm.	36.6	35.6	33.6	34.3	36.0	39.6
Kernel row number	14.3	14.3	13.6	13.6	17.3	15.3
1000 kernel weigh gms.	171	212	193	176	152	241
Grain yield in Bushel per acre	17.7	20.2	18.8	22.9	8.6	27.9

Table 4 continued,

S. No.	37	38	39	40	41	
Name of inbred	Kfa	Ge	M.6	38	59-36	Average
No. of chromosome Knobs	1	8	4	2	5	3.88
No. of Seminal Roots	1.45	3.37	1.06	1.17	3.87	2.15
Days to tasseling	68	66	69	65	69	
Plant height inches	50.0	56.6	58.0	60.6	59.0	
Ear height inches	12.0	12.3	12.0	14.6	24.3	
Tiller No.	0.6	0.0	0.6	3.0	0.3	
Shank length cms.	8.0	16.0	18.6	11.6	10.0	
No. of Tassel branches	11.3	11.6	15.3	12.0	15.3	
Ear length cms.	12.6	13.0	15.6	17.3	11.6	
Ear diameter mm.	39.3	36.3	32.3	29.0	35.6	
Kernel row number	12.3	14.0	12.0	8.6	16.0	
1000 kernel weight gms.	251	203	240	258	154	
Grain yield in Bushel per acre	23.8	16.7	24.8	22.3	20.0	

was Kfa, derived from a flint and dent hybrid, and with other characters showing flint tendencies.

The data are in general agreement with those of previous workers (2, 5, 20, 32, 56), although none of them reported an average as low as was found in this material. The lower average knob number can be readily explained based on the predominance of northern flint germ plasm in these lines; 31 of them are from flint or flint x dent sources. Moreover the recent survey made by Ibrahim (20) suggested that varieties from regions north of 40° latitude North have not more than 3 knobs, confirming the suggestion made by Longley (32) that the number of chromosome knobs on a strain of Indian corn give a clue to the geographical origin of the strain. Since even the dent lines studied owed their origin to material indigenous to the area above 40° latitude, the low average knob number tends to bear out Ibrahim's contention.

The chromosome knob numbers among 30 F_3 lines of the cross S.W.F. x B.14 are presented in Table 5. The average chromosome knob number was 3.23 with a range of 1 to 5. The flint parent S.W.F. had only 1 knob (Fig. 4) while the dent parent, B.14, had 8 chromosome knobs (Fig. 5). The average number of chromosome knobs observed in this sample of the F_3 population was somewhat below the average of the parents. There was no line which had a knob number equal to

Table 5

Number of Chromosome Knobs, Seminal Roots and Other Morphological Characters of F_3 Lines of the Cross S.W.F. x B.14.

S.No.	1	2	3	4	5	6
Progeny row no.	F_3(S.W.F. x B.14) -2	-4	-5	-9	-13	-16
No. of chromosome knobs	3	3	3	4	4	2
No. of seminal roots	1.50	2.05	-	1.80	2.67	1.22
Days to tasseling	63	71	74	61	68.1	68.
Plant height in inches	40.1	55.1	60.4	45.4	53.1	58.6
Ear height in inches	12.7	14.1	18.2	9.7	12.5	18.1
Tiller Number	1.27	0.2	2.28	1.93	0.27	1.53
Shank length in cms.	3.4	3.4	3.7	6.5	11.4	12.7
Ear length in cms.	-	-	-	15.9	16.3	17.9
Ear diameter mm.	-	-	-	36.0	39.0	39.0
Kernel row number	-	-	-	12.8	13.9	11.5

continued

Table 5 continued,

S.No.	7	8	9	10	11	12
	F_3(S.W.F.xB.14)					
Progeny row no.	-20	-25	-35	-36	-37	-38
No. of chromosome knobs	3	2	4	2	2	4
No. of seminal roots	2.30	1.41	1.92	1.32	1.10	-
Days to tasseling	69	70	71	63	60	65
Plant height in inches	56.9	51.4	66.1	56.0	46.1	59.3
Ear height in inches	16.1	13.1	12.0	10.5	7.4	14.4
Tiller Number	1.93	0.80	0.86	2.26	2.06	3.71
Shank length in cms.	8.4	8.5	9.7	7.8	11.5	16.0
Ear length in cms.	20.0	10.6	13.5	14.0	11.4	20.0
Ear diameter in mm.	40.0	31.0	34.0	33.0	34.0	41.6
Kernel row number	12.1	12.6	11.0	13.1	9.5	15.2

continued

Table 5 continued,

S. No.	13	14	15	16	17	18
Progeny row no.	F_3(S.W.F.x B.14) -41	-46	-50	-52	-54	-56
No. of chromosome knobs	3	4	4	2	3	3
No. of seminal roots	1.44	1.62	1.61	2.38	1.80	1.62
Days to tasseling	60	62	62	62	62	61
Plant height in inches	48.1	49.6	52.0	54.3	48.8	52.4
Ear height in inches	10.0	9.8	10.3	10.2	6.6	8.3
Tiller Number	1.66	1.80	2.20	2.27	1.87	1.80
Shank length in cms.	-	8.8	14.4	10.3	11.0	14.3
Ear length in cms.	-	18.0	15.2	16.3	15.1	14.4
Ear diameter in mm.	-	40.0	37.0	37.2	36.7	37.0
Kernel row number	-	10.2	12.6	11.7	11.0	10.4

continued

Table 5 continued,

S. No.	19	20	21	22	23	24
Progeny row no.	-57	-61	-64	-79	-80	-89
No. of chromosome knobs	5	5	4	3	4	5
No. of seminal roots	1.80	1.09	1.09	-	-	-
Days to tasseling	63	62	61	64	65	63
Plant height in inches	53.6	62.8	53.6	49.6	52.2	48.8
Ear height in inches	8.0	4.1	6.2	7.7	7.8	8.8
Tiller Number	3.07	3.67	2.87	0.80	0.33	1.4
Shank length in cms.	9.0	21.6	8.9	3.6	-	9.9
Ear length in cms.	13.9	18.3	15.5	18.1	-	12.0
Ear diameter in mm.	37.0	39.0	38.5	31.0	-	37.0
Kernel row number	11.7	11.2	11.8	10.0	-	12.6

continued

Table 5 continued,

S. No.	25	26	27	28	29
Progeny row no.	F_3(S.W.F.xB.14) -90	-97	-98	-99	-104
No. of chromosome knobs	5	1	3	3	2
No. of seminal roots	1.04	-	1.59	1.68	1.17
Days to tasseling	62	67	64	64	67
Plant height in inches	41.2	50.6	45.4	51.6	43.5
Ear height in inches	2.9	14.9	11.6	10.2	6.6
Tiller Number	2.87	0.93	0.83	2.40	1.60
Shank length in cms.	5.6	8.5	7.5	7.8	7.6
Ear length in cms.	11.1	16.1	15.7	17.5	12.4
Ear Diameter in mm.	39.0	41.0	51.0	40.0	34.0
Kernel row number	12.3	8.3	12.7	8.0	10.6

continued

Table 5 continued,

S. No.	30	Average	31	32
Progeny row no.	-120		S.W.F.Parent	B.14 Parent
No. of chromosome knobs	2	3.23	1	8
No. of seminal roots	1.91	1.57	1.06	3.90
Days to tasseling	63		50	88
Plant height in inches	44.0		48.3	68.9
Ear height in inches	4.6		7.9	24.9
Tiller number	2.13		3.07	0.07
Shank length in cms	-		19.2	7.8
Ear length in cms	-		16.0	15.6
Ear Diameter in mm	-		38.0	41.0
Kernel row number	-		8.0	16.0

that of the higher parent. The slightly lower number of knobs observed in this study than that expected based on the parental average, may be due to the non-randomness of the F_2 population sampled, since many late-maturing F_2 plants failed to mature seed here.

The data on chromosome knob numbers of the Southern lines are presented in Table 6. These lines were all of flint ear type. The number of knobs observed on the chromosomes of this group was high, with an average of 8.18 knobs. Here a line from Mexico had the highest number recorded (12 knobs) (Fig. 6) and the lowest in the group was a line from Argentina, which had 4 chromosome knobs. These data on the chromosome knob numbers agree with Wellhausen's (59) data for the Mexican lines and Reeve's (44) data for Guatemalan lines. However, they differ from Reeve's data for the lines from Argentina and Mexico. The reason for this difference cannot be stated positively. The limitation in number of varieties or lines sampled in relation to the diversity of forms occuring at lower and higher altitudes is probably mainly responsible. According to Mangelsdorf et al. (35) the forms occuring at lower altitudes had the greater number of chromosome knobs. In the present study and that of Reeves, information on the altitude from which the material was obtained was not available. This is unfortunate.

Table 6

Number of Chromosome Knobs, Seminal Roots and Other Morphological Characters of Southern Lines

S.No.	1	2	3	4	5
Source	Argentina	Uruguay	Guatemala	Guatemala	Paraguay
Name of lines	P.I 270297	P.I 186185	P.I 163558	P.I 163597	P.I 162927
No. of Chromosome Knobs	8	8	8	10	5
No. of seminal roots	2.6	3.0	6.3	7.3	4.0
Days to tasseling	late	75	82	88	late
Plant height in inches	-	56	100	98	80
Ear height in inches	-	19	64	64	57
Tiller Number	2.4	0.6	0.6	0.8	2.4
Shank length in cms.	-	6.6	-	-	-
No. of tassel branches	-	16	25	30	30
Ear length in cms.	-	11.3	-	-	-
Ear Diameter mm.	-	34.0	-	-	-
Kernel row number	-	18	-	-	-

continued

Table 6 continued,

S. No.	6	7	8	9	10
Source	Uruguay	Argentina	Argentina	Bolivia	Argentina
Name of lines	P.I 186229	P.I 198898	P.I 198902	P.I 214124	P.I 162702
No. of Chromosome Knobs	10	6	4	6	5
No. of seminal roots	3.5	4.2	2.7	3.0	-
Days to tasseling	77	73	79	65	68
Plant height in inches	78	90	71	77	85
Ear height in inches	38	49	34	31	26
Tiller Number	0.0	1.5	0.0	0.4	2.2
Shank length in cms.	6.9	9.4	12.6	9.8	10.2
No. of tassel branches	21	31	17	16	20
Ear length in cms.	13.2	16.0	12.8	15.8	17.0
Ear Diameter mm.	32.0	35.0	25.0	39.0	43.0
Kernel row number	13.3	15	11	12	19

continued

Table 6 continued,

S. No.	11	12	
Source	Mexico	Mexico	Average
Name of lines	P.I 217413	P.I 217409	
No. of chromosome Knobs	12	-	8.18
No. of seminal roots	-	3.5	4.03
Days to tasseling	72	89	
Plant height in inches	83	88	
Ear height in inches	48	52	
Tiller Number	0.6	2.0	
Shank length in cms.	16.2	-	
No. of tassel branches	28	-	
Ear length in cms.	10.6	-	
Ear diameter mm.	33.0	-	
Kernel row number	12	-	

However, the chromosome knob numbers reported here for the lines from Mexico, Guatemala and Uruguay were substantially higher than those found in the corn belt dents, which places them at the opposite end of the scale relative to the northern flints.

The data on seminal root numbers observed among inbred lines, F_3 lines and southern strains are presented in Tables 4, 5 and 6 respectively. The average number of seminal roots in the inbred lines was 2.15, with a range from 1 seminal root found in Howe's Alberta flint to 4.20 in K.98, which was derived from a cross of corn belt dent by northern flint lines. Similarly the average number of seminal roots observed among F_3 lines was 1.57 with a range of 1.02 to 3.33. The seminal root number for the southern lines was 4.03 with a range from 2.6 in an Argentine line to 7.3 for a line from Guatemala. These southern lines, which had flint grains, were characterised by having numerous seminal roots compared to those of indigenous lines and the F_3 progeny studied. A similar trend was observed for chromosome knob numbers. The data presented on seminal root numbers among F_3 progeny and indigenous inbred lines are in general agreement with those reported in the literature (5, 26, 29, 51, 52, 60). The seminal root numbers observed for Southern lines were higher than those reported by some of the above authors working with material from the same general areas. The Southern lines, therefore, although of flint grain type, were characterized by having numerous seminal roots and many chromosome knobs. This indicates that these maize lines are different entities, quite distinct from the northern flints.

Association of Chromosome Knob Number with other Characters

Total correlation coefficients were worked out among the characteristics shown in Table 7. Prior to making these calculations, frequency distributions were prepared from the data on each character and examined for normality of distribution. In F_3 lines, the distributions for seminal roots and days to tasseling were slightly skewed. Hence the correlations for these characters should be taken cautiously. The total correlation coefficient between number of chromosome knobs and each of grain yield and 1000 kernel weight was worked out for the indigenous inbred lines only. The correlation coefficients obtained among the characters of indigenous inbred lines are presented in Table 7. There was positive significant correlation between number of chromosome knobs with seminal root numbers, kernel row number and number of leaves, while significant negative dorrelations were obtained with grain yield and tiller number. This shows that there is a tendency among inbred lines with high knob number ot have a high kernel row number, many seminal roots, and few tillers. The correlation coefficients were moderate in size. The tiller number was negatively and significantly correlated with seminal roots. This means that plants with many seminal roots have a few or no tillers. These correlations are all among characteristics which are typical of dent lines. These interrelationships are in general agreement with those reported in the literature (5, 20 and 35) with the exception that Mangelsdorf et al. (35) showed high knob numbers to be related to straight rowing, which is a characteristic typical of northern flint maize.

The correlation between grain yield and number of chromosome knobs among the 41 indigenous inbred lines was negative and significant (Table 7). This shows that the lines with low numbers of knobs tended to yield more than those with high knob numbers. In fact one inbred line, 61-81, which had no chromosome knobs, gave the highest grain yield of 32.3 bushels per acre.

The total correlation coefficients between chromosome knob number and each of the morphological characters of thirty F_3 lines are presented in Table 8. In this group there was no relation between chromosome knobs and any of the morphological characters. The fact that only lines with low knob numbers were involved in the present study of F_3 lines could explain the lack of agreement with the results of Mangelsdorf and Cameron (35) and Brown (5). Hence it is too much to expect, as Vachani (56) has pointed out, that rather

Table 7

Total Correlation Coefficients Among Fourteen Characters of Forty-One Indigenous Inbred Lines

	Grain yield	Days to tasseling	Seminal root no.	Plant height	Ear height	Tiller Number	No. of leaves
Days to tasseling	-.293						
Seminal root no.	-.047	+.278					
Plant height	+.214	+.497^{xx}	+.205				
Ear height	-.207	+.703^{xx}	+.449^{xx}	+.243			
Tiller number	+.414^{xx}	-.262	-.566^{xx}	+.062	-.212		
No. of leaves	-.188	+.794^{xx}	+.401^{xx}	+.515^{xx}	+.690^{xx}	-.232	
Shank length	+.483^{xx}	-.039	-.089	+.449^{xx}	-.060	+.232	+.133
Tassel branch number	+.009	+.158	-.195	+.246	+.374	+.148	+.191
Ear length	+.322^{x}	+.243	-.278	+.633^{xx}	+.212	+.310^{x}	+.166
Ear diameter	+.064	+.206	+.278	+.012	+.446^{xx}	-.085	+.351^{x}
Kernel row no.	-.152	+.427^{xx}	+.517^{xx}	+.362^{x}	+.508^{xx}	-.262	+.439^{xx}
1000 kernel weight	+.312^{x}	-.088	-.400^{xx}	-.110	+.295	+.532^{xx}	-.109
Chromosome knob no.	-.379^{x}	+.265	+.563^{xx}	+.088	+.159	-.520^{xx}	+.449^{xx}

continued

Table 7 continued

	Shank length	Tassel branch nos.	Ear length	Ear diameter	Row number	1000 kernel wt.
Days to tasseling						
Seminal root no.						
Plant height						
Ear height						
Tiller number						
No. of leaves						
Shank length						
Tassel branch number	+.275					
Ear length	+.457^{xx}	+.244				
Ear diameter	-.100	+.052	-.134			
Kernel row no.	-.095	+.139	-.081	+.538^{xx}		
1000 kernel weight	+.153	-.015	+.212	-.085	-.552^{xx}	
Chromosome knob no.	-.062	-.118	-.187	-.001	+.336^{x}	-.304

x exceeds .308 significant value of 'r' at 5% level.

xx exceeds .398 significant value of 'r' at 1% level.

Table 8

Total Correlation Coefficients Among Eleven Characters in F_3 Lines of (S.W.F. x B.14)

	Days to tasseling	Plant height	Ear height	Tiller number	Shank length	Shank node number
Plant height	$+.454^{x}$					
Ear height	$+.679^{xx}$	$+.434^{x}$				
Tiller number	$-.577^{xx}$	+.092	$-.466^{x}$			
Shank length	-.143	$+.474^{x}$	-.050	$+.452^{x}$		
Shank node nos.	+.073	+.095	$+.499^{xx}$	+.086	$+.569^{xx}$	
Ear length	+.193	$+.528^{xx}$	$+.469^{x}$	+.077	+.182	-.154
Ear diameter	-.071	-.03	+.258	+.095	+.168	+.03
Row numbers	+.150	+.190	+.303	+.163	+.071	+.232
Seminal root nos.	+.209	+.133	+.375	$-.496^{x}$	-.287	+.258
Chromosome knob nos.	-.195	+.270	-.066	+.283	+.386	+.231

continued

Table 8 continued,

	Ear length	Ear diameter	Row number	Seminal root no.
Plant height				
Ear height				
Tiller number				
Shank length				
Shank node nos.				
Ear length				
Ear diameter	+.407[x]			
Row numbers	+.216	+.232		
Seminal root nos.	+.218	+.070	+.264	
Chromosome knob nos.	+.268	+.245	+.063	-.056

x exceeds .396 significant value of 'r' at 5% level

xx exceeds .505 significant value of 'r' at 1% level

For seminal root number .433 at 5%
.545 1%

low knob numbers (average 3.23) entering a particular cross would regularly associate with those genes having effect sufficient to establish positive correlation with the characters being studied, especially as most of these characters are of polygenic nature.

The data on the relation of chromosome knob numbers with morphological characters and maturity among southern lines are presented in Table 9. There was no relation demonstrated between chromosome knob numbers and the morphological characters studied, although the correlation coefficient between length of the ear and chromosome knob numbers was positive and approached the 5% probability level. In this case the chromosome knob number was high; the reason for lack of association of knob numbers with any of the morphological characters could be attributed, in part at least, to the small number of lines used in this study and also to the narrow range of chromosome knob numbers among this group.

Association among Morphological Characters in Inbred Lines, F_3 progeny and Single Crosses

Total correlation coefficients among 13 characters of 41 indigenous inbred lines, including grain yield, are presented in Table 7. Based on total correlation, days to tasseling was positively and significantly associated with plant height, ear height, number of leaves and kernel row

Table 9

Total Correlation Coefficients Among Thirteen Characters of Southern Lines

	Days to tasseling	Plant height	Ear height	Tiller number	Number of leaves	Shank length
Plant height	+.396					
Ear height	+.657^{x}	+.873^{xx}				
Tiller number	+.016	+.111	+.021			
No. of leaves	+.768^{xx}	+.830^{xx}	+.915^{xx}	+.033		
Shank length	-.014	+.369	+.509	-.312	+.025	
Shank node no.	-.380	+.489	+.456	+.060	+.112	+.835^{x}
Tassel branch no.	+.025	+.729	+.868^{x}	+.359	+.619	+.360
Ear length	-.576	+.560	-.051	+.632	+.205	-.262
Ear diameter	-.872^{x}	+.347	-.260	+.741	-.397	-.209
Row number	-.220	-.123	-.544	+.809^{x}	-.529	-.477
Seminal root no.	+.533	+.793^{xx}	+.794^{xx}	-.086	+.729^{x}	-.302
Chromosome knob no.	+.323	+.197	+.435	-.278	+.224	+.179

continued

Table 9 continued,

	Shank node no.	Tassel branches	Ear length	Ear diameter	Row number	Seminal root no.
Plant height						
Ear height						
Tiller number						
No. of leaves						
Shank length						
Shank node no.						
Tassel branch no.	+.339					
Ear length	-.157	+.032				
Ear diameter	+.148	+.020	+.649			
Row number	-.371	-.066	+.303	+.623		
Seminal root no.	-.041	+.508	+.569	+.361	+.290	
Chromosome knob no.	+.446	+.472	+.654	-.09	-.177	+.459

x exceeds .632 $\overset{@}{.754}$ significant value of r at 5% level

xx exceeds .765 $\overset{@}{.874}$ significant value of r at 1% level

@ (These figures pertain to chromosome knobs and ear characters.)

number. This suggests that early plants are of short stature with low ear placement and few kernel rows. The correlation coefficients were moderately high in the case of ear height and number of leaves, with a fair amount of predictive value. High seminal root numbers were correlated significantly with high placement of ears, many leaves, high kernel row number and few tillers. Interrelation was found (based on significant total correlation) among late maturity, high placement of ears, high kernel row number and many leaves. Similarly low seminal root number, large kernels and many tillers were interrelated. Shank length was positively associated with ear length and plant height. With few exceptions, these interrelations suggest that the morphological characters typical of northern flint corn on the one hand, and dent corn on the other, have tended to retain their ancestral associations in these lines. However, the association in many instances was low, although significant statistically.

Grain yield among indigenous inbred lines was positively associated with tiller number, shank length, ear length and 1000 kernel weight. However, the correlation coefficients, though statistically significant, were of low predictive value. In the present study the positive association of grain yield with plant height agrees with the findings of a number of authors (21, 25, 42, 50). Jenkins (21) and Murty (42) found that grain yield was negatively associated with maturity while others (17, 25), reported positive association of these characters. The present data agree with those of Jenkins and Murty, but the association was not significant. Some workers (21, 42) reported that grain yield was positively associated with ear length, and the same was to be born out by the present data. The characters - long shanks, many tillers, long cob, large kernel and few chromosome knobs, typical of flint lines, were associated with high grain yield in these inbred lines.

The total correlation coefficients among 10 morphological characters in all possible combinations for 30 F_3 lines are presented in Table 8. Similarly Chi-squares with corresponding probability levels for independence among these characters for 110 F_3 lines are presented in Table 10. Based on the total correlation coefficients, the days to tasseling was positively associated with plant height and ear height, but negatively associated with tiller number. Similarly seminal root number was negatively associated with tiller number. Plant height was associated positively with ear height, shank length and ear length. On the basis of the Chi-square tests, applied to the larger group of F_3 lines the above relations were found to hold and a few additional associations were obtained which were not shown by the total correlation coefficients on the smaller sample. On this basis, days-to-tasseling was associated positively with each of seminal

Table 10

Chi-Square Values for Independence Among Ten Characters and Corresponding Probabilities in F_3 Lines Derived from (S.W.F. x B.14)

	Seminal Root no.		Days to tassel		Tiller number	
	X^2	P	X^2	P	X^2	P
Days to tassel	8.67^x	.02-.01				
Tiller number	3.28	.5-.25	34.28^x	.005		
Plant height	4.56	.2-.1	11.86^x	.1-.05	6.76	.7-.5
Ear height	.17	.99-.97	22.8^x	.005	17.78^x	.05-.02
Shank length	2.34	.5-.25	17.69^x	.025	13.98	.25-.1
Shank node no.	.11	.95-.90	6.17	.5-.25	4.74	.9-.7
Ear length	1.93	.75-.5	8.67	.25-.1	7.37	.7-.5
Ear diameter	7.20^x	.1-.05	9.12	.25-.1	6.34	.7-.5
Row number	3.27	.2-.1	8.15^x	.1-.05	7.88	.5-.25

continued

Table 10 continued,

	Plant height		Ear length		Shank length	
	X^2	P	X^2	P	X^2	P
Days to tassel						
Tiller number						
Plant height						
Ear height	34.5^{xx}	.005	5.24	.25-.1		
Shank length	17.57^{x}	.05-.02	7.60	.7-.5	16.37	.5-.25
Shank node no.	2.78	.97-.95	4.58	.9-.7		
Ear length	21.47^{xx}	.025-.01				
Ear diameter	10.91	.5-.25	13.88	.25-.1	6.22	.7-.5
Row number	10.5	.25-.1	6.09	.5-.25	3.13	.9-.7

x significant at the .05 level

xx significant at the .01 level

root number and kernel row number but negatively with shank length. This shows that late plants tend to have many kernel rows, short shanks and numerous seminal roots besides being tall, with highly placed ears and few tillers. High tillering was associated with low ear placement and long shanks. Although the associations were significant statistically they were small with low predictive value. However, they are suggestive of a tendency for the characteristics of flint corn and those of dent corn to stay associated.

The correlation coefficients among 12 characters in the southern flint strains are presented in Table 9. Based on total correlation coefficients, days to tassel was associated positively with each of ear height and number of leaves but negatively with ear diameter. Seminal root number was positively associated with plant height, ear height and number of leaves. Plant height, ear height and seminal root number were all interrelated in a positive manner. Ear height was also associated with large numbers of tassel branches. These relations indicate that late lines in this group tend to have high placement of ears, many leaves and slender ears. Similarly lines with numerous seminal roots tend to produce tall plants with high placement of ears with many leaves. The plants with many tillers tend to produce many kernel rows. The interrelationships observed in this group of lines differs from those found among northern flint and dent inbreds as well as in the F_3 progeny of the flint-dent cross studied in that maturity was negatively related with ear width, and tiller number was positively related with kernel row number. Tiller number showed a significant negative association with seminal root number among the northern flints, but such a relationship was not found among southern lines. Based on these limited data it may be said that the southern flint lines are quite distinct types as compared to both flint and dent lines of northern origin.

Total correlation coefficients among eleven characters of 48 single crosses are presented in Table 11. The following significant correlation coefficients were found among characters of the F_1 hybrids: Grain yield was positively correlated with each of tiller number, ear length and 1000 kernel weight, while it was negatively correlated with kernel row number. Similar associations were found among the parental inbred lines, except for kernel row number, which did not show any correlation with grain yield among inbred lines. This suggests that the genes responsible for these characters are linked and dominant in effect.

Correlation coefficients between grain yield of single crosses and morphological characters of their inbred parents were computed and are presented in Table 12.

Table 11

Total Correlation Coefficients Among Eleven Characters of Forty-eight F_1 Hybrids Involving Twelve Inbred Parents

	Grain Yield	Maturity expressed in moisture basis at husking	Plant height	Ear height	Tiller numbers	Shank length
Maturity in terms of moisture	+.149					
Plant height	+.134	+.137				
Ear height	+.176	-.154	+.279			
Tiller number	+.619^{xx}	-.04	+.018	+.237		
Shank length	-.040	+.087	+.025	-.186	-.354^{x}	
Tassel branch no.	+.161	+.067	-.036	+.017	+.047	-.473^{xx}
Ear length	+.477^{xx}	+.058	+.361^{x}	+.126	+.714^{xx}	-.314^{x}
Ear diameter	+.039	+.364^{x}	+.063	+.190	-.544^{xx}	+.517^{xx}
Row number	-.415^{xx}	+.146	-.085	+.197	-.527^{xx}	+.147
1000 kernel weight	+.705^{xx}	-.069	-.037	+.004	+.547^{xx}	+.026
Hetero-chromo knob pair	-.573^{xx}					

continued

Table 11 continued,

	Tassel branch numbers	Ear length	Ear diameter	Row number
Maturity in terms of moisture				
Plant height				
Ear height				
Tiller number				
Shank length				
Tassel branch no.				
Ear length	+.147			
Ear diameter	-.063	-.568^{xx}		
Row number	+.076	-.562^{xx}	+.467^{xx}	
1000 kernel weight	+.103	+.508^{xx}	-.211	-.658^{xx}
Hetero-chromo knob pair				

x exceeds .282 significant value of r at 5% level

xx exceeds .365 at significant value of r at 1% level

x for chromosome knob and yield exceeds .317 significant value of r at 5% level

xx exceeds .408 significant value of r at 1% level

Table 12

Correlation Coefficients Between Grain Yield of F_1 and Each of Twelve Characters of the Inbred Parents

S. No.	Inbred characters	Correlation coefficient
1	Days to tasseling	+.275
2	Plant height	$-.471^{xx}$
3	Ear height	$-.424^{xx}$
4	Tiller number	$-.424^{x}$
5	Shank length	-.260
6	Tassel branches	+.011
7	Length of ear	+.01
8	Ear diameter	+.038
9	Kernel row number	$-.507^{xx}$
10	1000 Kernel weight	$+.539^{xx}$
11	Grain yield	$+.335^{x}$

x exceeds .317, significant value of r at 5% level.

xx exceeds .408, significant value of r at 1% level

Based on the significant correlation coefficients, grain yield of the single crosses was negatively associated with each of plant height, ear height and kernel row number of inbred parents. On the other hand, it was positively related to 1000 kernel weight and ~~of~~ grain yield of inbreds. This indicates that inbreds with short stature, low placed ears, few kernel rows, large kernels and high yield are the best combiners. The results of the present study differ from those reported in the literature (17, 21) in that the correlations of grain yield of F_1 with plant height and ear height were negative, while it was reported by previous workers (17, 21, 22) to be positive. Similarly there was no relation between ear length of parents and single cross yield, while many authors (17, 21, 22) have reported such relationships. The divergence of these results may be explained by the difference in environmental conditions under which the lines were selected and the type of source material best adapted to this environment.

The consistent associations of the following morphological characters with grain yield among inbred lines as well as among F_1 hybrid combinations suggest that the germ plasm of the two different morphological groups of maize involved in this part of North America are still partially intact: ear length, 1000 kernel weight, tiller number and chromosome knob number (the first 3 characters are physical components of yield). If this assumption is true, it should be possible to classify inbreds on the basis of morphological differences according to their flint and dent tendencies. The importance of genetic diversity in bringing about heterotic effect in hybrids is well known. Thus it should be possible to predict with some accuracy the relative degree of heterosis, to be expected from crossing two inbred lines, on the assumption that morphological diversity is related to diversity in yield genes. With this objective in view, the morphological characters, 1000 kernels weight, tiller number, ear length, and chromosome knob number, of the inbreds were used to determine whether hybrid vigor, expressed in terms of grain yield, could be predicted on the basis of the morphological character differences of inbreds involved in making the F_1 hybrids. The morphological indices and their differences were prepared and are presented in Table 3. The details of procedure in obtaining the indices for each character are shown in Table 2. The morphological differences of inbreds involved in each single cross and the grain yield of F_1 were plotted on the scatter diagram presented in Fig. 8. The correlation coefficient between grain yield of F_1's and index differences was +.393 and was significant statistically. This suggests that morphological differences could be used to predict the single cross yield, to a certain extent.

Combining ability among single crosses involving inbreds from flint and dent types

The mean grain yields of the parent inbred lines and of F_1 intercrosses among them are shown in Table 13. Each F_1 tested greatly exceeded both its respective parents in total grain yield. The mean yield of all 48 single crosses was 63.4 bushels per acre, which was equal to that of the double cross Morden 88, used as a control. There were 8 single crosses which gave significantly higher yield than Morden 88. Out of these highest yielding F_1s, seven had a parent in common, Kfa, which was derived from a hybrid of Northern flint and corn belt dent. The eighth single cross was between M7 and W.D., the former a flint line derived from a cross of northern flint and corn belt dent, while the latter was derived from corn belt dent. On the basis of the average yield of all F_1 hybrids for each inbred (last column, Table 13), Kfa gave the highest mean yield in crosses. The next best combining parent was W.617. The inbred line K.98 showed the lowest prepotency in terms of average mean yield of its' hybrids. This shows that the first two lines (Kfa and W.617) had the highest general combining ability while K.98 had the lowest. The two inbreds which were the poorest combiners, producing about identical hybrid yields at the bottom of the scale, were themselves the highest and lowest yielding of the inbreds studied, suggesting little relation between inbred yield and combining ability. A comparison of combining

Table 13

Mean Grain Yields (Bushels per acre) of the Parent Inbred Lines (diagonal) and Their F_1 Intercross Combination

Parents	K.D.54	K.N.11	V.3	W.D.	K.261	K.275	W.617
K.D.54	(21.8)	-	63.8	60.0	59.6	56.4	65.6
K.N.11		(17.0)	69.5	67.0	59.3	61.2	64.4
V.3			(14.4)	66.1	-	-	69.3
W.D.				(26.2)	-	60.9	-
K.261					(19.5)	-	68.5
K.275						(17.7)	68.1
W.617							(20.2)
M.7							
M.17							
K.126							
K.98							
Kfa							
Morden 88							

continued

Table 13 continued,

Parents	M.7	M.17	K.126	K.98	Kfa	Mean F_1
K.D.54	61.4	-	-	64.6	67.8	62.4
K.N.11	68.6	-	63.0	49.8	80.0	64.8
V.3	49.1	55.9	55.0	-	82.0	63.8
W.D.	70.8	68.5	61.6	59.5	-	64.3
K.261	58.5	68.5	46.3	54.5	76.2	61.5
K.275	59.3	59.0	45.7	59.3	77.3	60.8
W.617	64.8	63.2	65.2	66.9	-	66.2
M.7	(18.8)	57.7	-	-	77.8	63.1
M.17		(22.9)	-	-	75.6	64.1
K.126			(8.6)	-	74.5	58.8
K.98				(27.9)	-	59.1
Kfa					(23.8)	76.4
Morden 88						63.4

Least significant difference 6.3 bus. at 5% level

8.3 bus. at 1% level

ability in relation to the origin of the lines involved is shown in Table 14. The values in the table were obtained as follows: the parental inbred lines were divided into two groups based on their origin from flint and dent crosses on the one hand, and from dents on the other. Average yield of crosses within each group and between groups was then calculated. The inbreds from group A (northern flint x corn belt dent) crossed within group A gave the highest general average F_1 yield. The remaining three averages were very similar, but crosses within group B gave the lowest average. When individual average yields of hybrids from each inbred were examined within groups and between groups, it was found that five inbreds in group B and two in group A gave higher grain yields when crosses were made between groups rather than within groups. However, the lines M.7, K.126, K.98, M.17 and V.3 gave higher yields when crosses were made within the groups. The higher yields obtained from crossing lines within group A than those from crossing between the two groups indicates that the lines in group A were presumably at least as different from one another as they were from B lines. Examination of Table 14 shows that half of the lines in group A were of flint type and the remaining half were of dent type. This divergence in germ plasm, represented by flint and dent groups, tended to show higher combining ability than those of crossing the corn belt dents with corn

Table 14

Average Yields of F_1's (for each inbred) Whose Parents Are Within the Same Group and For F_1's Whose Parents Are In Different Groups

Group	Inbred	Origin	Group A	Group B
A	W.617 flint	N.flint x C.B.dent	65.02	67.2
	M.7 flint	"	66.7	61.2
	K.126 dent	"	69.8	54.3
	K.98 dent	"	66.9	57.5
	Kfa dent	"	75.9	76.7
	M.17 flint	"	65.5	63.0
		Mean	68.2	63.3
B	K.D.54 dent	Corn Belt dent	64.8	59.9
	K.N.11 dent	"	65.2	64.3
	V.3 dent	"	62.3	66.5
	W.D.[illegible] dent	"	65.1	63.5
	K.261 dent	"	62.1	59.4
	K.275 dent	"	61.5	59.5
		Mean	63.3	62.4

belt dents. However, one inbred line V.3, was primarily responsible for reducing the average of B types crossed with A to a figure close to that for crosses within B. This can be explained on the basis that V.3 is closely related to two of the three A type lines with which it was crossed. It appears that some of the lines in group A which were developed by crossing northern flints and corn belt dents acquired flint or dent germ plasm along with associated genes for vigour which tended to stay together, as was shown in presenting the section on association of characters among indigenous inbreds and F_3 lines. These results are in general agreement with other experimental findings reported in the literature that unrelated inbred lines are better combiners than related ones (9, 10, 14, 17, 19, 22, 40, 62). Brown and Anderson (6) hypothesized that the origin of corn belt dent was due to primarily to the deliberate mixing of northern flints with southern dents. They suggested that much of the heterosis utilised in commercial corn belt hybrids stems directly from the union of these divergent corn forms. The results of the present study suggest that lines derived from crosses of flint and dent types had greater combining ability than those from dent alone. However, the results were from a limited sample size of inbred lines.

The average yields of the F_1 intercrosses relative to their respective mid-parent, higher parent and constant parent yields, were 325.1, 268.5 and 320.6 respectively (Table 15). A considerable heterosis was observed for the inbred line Kfa on the basis of percent yield relative to the higher parent. The inbred line V.3, although it recorded the second lowest in yield as an inbred, produced hybrids which gave an average yield of 63.8 bushels per acre, which was comparable to the check Morden 88. This line when combined with the high combining inbred Kfa, gave the highest yield of 82 bushels per acre (Table 13). This line also, gave a higher degree of heterosis based on the percent yield of F_1 relative to the mid parent and higher parent yields. The other lines which gave a high expression of heterosis were K.N.11, K.126, M.7 and W.617. The lines K.98 and W.D. were relatively low in heterosis effect. The lowest yielding inbred, K.126, had low combining ability on the basis of its mean F_1 yield, but relative to the mid parent, high parent and constant parent it showed a considerable amount of heterosis effect. Thus, it appears that there is evidence of great diversity, on the basis of differences in heterotic response from intercrosses, among the parental inbreds used. The highest yield was obtained when Kfa, which had predominantly flint characteristics with dent grain, was crossed to V.3, which was a line with corn belt dent characteristics and a fair amount of combining ability. The yield of V.3 as

Table 15

Grain Yield of Inbred Parents and Their Mean F_1 as Determined In All Cross Combinations Together With F_1 Means Expressed as Percent of Mid Parent, Higher Parent and Constant Parent

Serial No.	Parent	Grain yield bus./acre		Percent relative to		
		Parental	Mean F_1	Mid Parent	Higher Parent	Constant Parent
1	K.98	27.9	59.1	244.7	211.8	211.8
2	W.D.1	26.2	64.3	286.8	230.5	245.4
3	Kfa	23.8	76.4	369.3	321.0	321.0
4	M.17	22.9	64.1	301.6	256.4	279.9
5	K.D.54	21.8	62.4	291.5	240.4	286.2
6	W.617	20.2	66.2	340.0	273.5	327.7
7	K.261	19.5	61.5	310.4	263.7	315.3
8	M.7	18.8	63.1	322.1	281.7	335.6
9	K.275	17.7	60.8	315.8	255.5	343.5
10	K.N.11	17.0	64.8	339.8	294.5	381.2
11	V.3	14.4	63.8	365.8	296.5	443.0
12	K.126	8.6	58.8	413.8	296.9	683.7
	Mean	19.9	63.8	325.1	268.5	320.6
	Morden 88 (check)	63.8	-	-	-	-

an inbred was very low, indicating lack of adaptability. This indicates that lines divergent in genetic material may have utility in yield improvement, even though they are themselves not particularly well adapted to local conditions. However, this conclusion is based on the results of only one year. Griffing _et_ _al_. (1954) presented data to show that the inclusion of 25% Mexican germ plasm in the genetic background of corn belt inbreds increased general combining ability of lines considerably. Moll _et_ _al_. (40) found genetic diversity of parent varieties associated with greater heterosis in varietal crosses from 3 different geographical regions. In this study the data suggest that the amount of heterosis is associated with amount of genetic divergence.

GENERAL DISCUSSION

The data pertaining to chromosome knob number were in general agreement with those reported in the literature (2, 5, 20, 32, 56). These data indicated that northern flint lines had low number of chromosome knobs while southern lines, even though of flint type, had very high numbers. Corn belt dent lines were intermediate in knob numbers. A similar trend was observed from the study of seminal root development. The northern flints were characterised by having no secondary seminal roots (usually one rarely two or three seminal roots) while southern flint lines had numerous seminal roots and the corn belt dent lines were intermediate. Such a trend was also found among northern flints and corn belt dents by previous workers (26, 29, 51, 52, 60). No reference to previous seminal root counts on southern lines was found. The consistent trend in numbers of chromosome knobs and seminal roots may be considered as indices of phylogenatical differences among the 3 types of lines studied. It would have been desirable to obtain serological data for these lines as an additional relationship but this was beyond the scope of the study. Low chromosome knob numbers have also been reported for the Andean corn of South America and for high altitude races of north-western Guatemala (2, 35). Anderson et al. (2) suggested the Guatemalan origin of Northern flints based on the similarities in terms of low chromosome knobs and morphological characters of northern flints and highland maize from Guatemala. Unfortunately no strains known to be of this origin were included in the present study.

Based on the data obtained, the dent lines observed here are intermediate between northern flints and corn belt dents, from the point of view of the phylogenetical characteristics studied. Anderson _et_ _al_. (2) suggested that the corn belt dents probably originated by hybridization of southern dents and northern flints, on the basis of cytological, genetical and morphological evidence obtained by analysing the characters of lines from the corn belt. Jones (23) and Wallace _et_ _al_. (57) had pointed out that corn belt dents were intermediate between the flints and the soft grained gourd seed of the southern United States, based on the proportion of hard and soft starch content of the kernel. From morphological and cytological studies Suto (54) concluded that Javanese types from Indonesia could have arisen through hybridization between races of Caribbean and Persian flints. In a study of several inbred lines in each of the classes of commercially grown maize, Kajjari (26) showed that pop corn lines had the lowest number of seminal roots as a group and that dent lines had the highest number, while the flint and sweet lines were intermediate in this characteristic. There is general agreement that pop corn is in the lowest level of evolution among cultivated maize types, although there is not real proof of this. This is based on the observations that the pop lines appear to have more characteristics of wild relatives than do other types. Next in line of evolution are the flints and then the dents. The study of seminal roots would suggest that this sequence is logical. Additional data would be desirable on morphology, including floral development, before it would be possible to generalise with any confidence. However, the lines derived from corn belt sources were rather similar in phylogenetic characters to those derived from flint and dent hybrids, suggesting that the conclusion of Anderson et al. (2) with regard to origin of corn belt dent may be valid.

From the study of association of grain yield and chromosome knobs among indigenous lines, it was found that lines with low numbers of knobs, which is characteristic of northern flints, were high in grain yield. Similarly there was negative significant correlation between numbers of chromosome knobs of the inbred parents and the grain yield of their single crosses (Table 11). This suggests that inbreds with low knob numbers are good combiners. These interrelationships can be explained on the basis that lines of northern flint type are best adapted to the local conditions in Manitoba. Adaptation to environment was similarly used by Welhausen (59) to explain the fact that at higher elevations in South America, low knobbed lines were better combiners than high-knobbed ones.

It is difficult to see any relation between South American lines adapted to high elevations and the flints adapted to Manitoba conditions, based on the results obtained in this study. Very recently Galinat(12) reported that a population of maize which was segregating T. dactyloids and T. floridanum chromosomes, acquired from Tripsacum several characteristics which resemble those of northern flints. Galint did not indicate the number of chromosome knobs of these segregates in his studies. Mangelsdorf et al. (36) had suggested that the number of chromosome knobs in maize represented the amount of introgression from Tripsacum. The morphological characters of northern flints are Tripsacoid in many respects, but they have low numbers of chromosome knobs. Mangelsdorf (34) suggested that heterosis in maize was due to introgression of germ plasm from Tripsacum. Grobman (see Mangelsdorf (34)) pointed out that some varieties of modern maize might have acquired heterosis resulting from the interaction of genes from teosinte and Tripsacum. These observations on the Tripsacoid appearance of northern flints which are characterised by having low chromosome knobs and are better in combining ability suggest that northern flint lines might have acquired Tripsacum germ plasm through hybridization with a knobless or low knobbed Tripsacum species such at T. australe. They might on the other hand, have hybridized with T. maizer, since the latter species was observed to resemble Andean varieties of corn and north-eastern U.S. flints in having few or no knobs (58). Further investigations are required to furnish more convincing evidence with respect to the hypothesis that introgression of Tripsacum into northern flints has actually occurred.

The southern flint lines in contrast to the northern flint lines, had high numbers of chromosome knobs and seminal roots, suggesting lack of relationship between these two flint groups.

High numbers of chromosome knobs were associated with many seminal roots, many kernel rows, few tillers and many leaves among indigenous inbred lines. These are all characteristics typical of dent maize. Similar relations were reported by other workers (2, 5, 20, 35). However, selection is not practiced for chromosome knob number and seminal root number in breeding programmes. In spite of this fact, the association of numbers typical of dent corn on the one hand and flint on the other, have persisted. This indicates that, although the chromosome knobs may themselves have no genetic effect they are presumably linked with genes which are responsible for the expression of these morphological characters. As a result blocks of genes or segments of chromosomes tend to be transmitted together during inbreeding from the ancestral type to the derived lines (Fig. 7).

Besides these associations of phylogenetical characteristics, there was a consistent association of the following morphological characters with grain yield, both among indigenous inbreds and among F_1 hybrids involving 12 of these inbreds: tiller number, 1000 kernel weight, ear length. Based on these consistent associations of morphological characters and grain yield, indices were worked out based on the morphological difference representing the flint and dent tendencies of these characters. The index differences between inbred parents were tested for correlation with the grain yields of corresponding single crosses on the assumption that they might represent genetic diversity. The correlation coefficient was positive and significant statistically, suggesting that these morphological differences could be used as a guide for eliminating the low yielding single crosses on the basis of low index differences (Fig. 8). However, the correlation coefficient was rather low and would have only a moderate amount of predictive value. This low correlation may be explained on the basis of the influence of flint germ plasm among the Corn belt dent lines used in this study.

The total correlation coefficients obtained in F_2 (S.W.F. x B.14) and Backcross (S.W.F. x B.14^2) material are shown in comparison with those obtained in F_3 (S.W.F. x B.14) in Table 16. The F_2 and backcross data were

Table 16

Total Correlation Coefficients Among Five Characters in F_2, Backcross and F_3 of the Cross S.W.F. x B.14

Characters Correlated	Total Correlation Coefficients		
	F_2	Back Cross	F_3
Seminal root number with maturity	$+.243^{xx}$	$+.078^{x}$	$\overset{@}{+.209}$
" Pl. height	$-.027$	$-.006$	$+.133$
" ear height	$-.075$	$-.048$	$+.375^{x}$
" tiller number	$-.097^{x}$	$-.036$	$-.496^{x}$
Maturity with Plant height	$+.375^{xx}$	$+.130^{xx}$	$+.454^{x}$
" ear height	$+.274^{xx}$	$+.182^{xx}$	$+.679^{xx}$
" tiller number	$-.138^{xx}$	$-.366^{xx}$	$-.577^{xx}$

x significant at 5% level

xx significant at 1% level

@ significant association at the 5% level by test of chi-square for independence.

taken from the Master's thesis submitted by Kajjari (26). A consistent association was found between seminal root number and maturity period in F_2, F_3 and backcross populations. Although the correlation coefficients were significant statistically, they were low. However, these results suggest that seminal root number would be a useful guide in screening very large populations from this type of cross when one of the plant breeding objectives is early maturity. Late maturity, tall plants, high placement of ears and low tiller number were significantly interrelated in F_2, F_3 and the backcross of the hybrid, as well as in the group of indigenous inbred lines studied. These relations were moderate. The results indicate that late maturity was associated with a number of desirable characters besides low tillering. Since the associations were not at a higher level, it should be possible to recover early lines with very few tillers, and otherwise desirable, by handling large size populations, using low seminal root number as an aid in selection for earliness. Based on this limited study the line Kfa, with smooth-dent grain, but with other morphological characters showing a moderate tendency towards flint type, gave the highest grain yield among the single crosses tested, when crossed with the unrelated corn belt dent line V.3, and also had the highest general combining ability (Table 13). Second in average combining ability was W.617, which had predominantly flint characteristics. These lines were both derived from hybrids between flint and dent types. The performance of these two lines along with the relatively desirable characteristics of the other lines of flint and dent parentage, suggest that this is a relatively good source from which to breed lines with early maturity, good combining ability, and at least reasonably satisfactory plant characteristics.

Among inbred lines, high grain yield was associated with large kernels; many tillers, long shanks and long ears. These are among the characteristics of flint types. Their association with yield may be explained on the basis that flint types are best adapted to Manitoba conditions, assuming that high yield is a reliable indication of adaptation. There was no relation between kernel row number and grain yield among the indigenous inbred lines. The reason for this non-association cannot be stated positively. Kernel row number is one of the physical components of yield, as mentioned by Grafius (13). Grafius pointed out that the physical components of yield (total number of ears, kernel row number, number of kernels per row and weight per kernel), may be extraneous, and total yield may be closer to the primary effects of genes than the expression of any of the components on the basis of inconsistent relations between the components of yield and yield itself. Tiller number, ear length, and 1000 kernel weight were interrelated in a positive manner, while kernel row number was negatively correlated with each of tiller number, ear length and 1000 kernel weight among inbred lines. Grafius postulate may be valid. On the other hand, perhaps the lack of association of row number with yield is an indication that there was, in this material at least, equal compensation for loss of row number by increase in kernel size.

The strength of conclusions to be drawn from this study are limited by the fact that yield tests were conducted only one season and that not all the possible 66 single crosses from the 12 inbred lines were used. Unfortunately, the breeding nursery was destroyed by hail in 1962, making repetition of crosses impossible. Also the sample of lines was restricted by maturity to a relatively narrow range, both among indigenous lines and segregates from the cross studied. In the single crosses, lines with low average combining ability such as K.98 and K.126, when crossed with other relatively low-combining lines, such as K.261 and K.275, gave low yields (Table 13). On the other hand, the low-combining K.126 crossed with the high combining line Kfa, gave a high yield. Similarly K.98, a line with low general combining ability when crossed with the high combining line W.617, gave a fairly high yield. The low combiners mentioned above have desirable plant characteristics. This suggests that specific combining ability is highly important under the conditions in which this breeding programme is carried out.

It was found that lines with the highest general combining ability were bred directly from flint x dent hybrids. The advantage was not so great, however, that it would cast any serious doubt on the contention that corn belt lines may have originated from similar material in their remote ancestry. Some loss of heterotic value from the original hybridization would be expected if many generations of selection to a specific type intervened between the hybridization and the ultimate inbreeding.

There was some indication that genetic diversity based on origin of lines, contributed to heterosis. There was also an indication that the greater the genetic diversity of inbreds the greater the heterosis among single crosses. This was also found to be so from previous literature reported (14, 31, 40, 45). These results suggest that by maximising the genetic diversity of parents, the maximum heterosis could be obtained in hybrid combination. Galint (11) suggested that this could be done by increasing the germ plasm from wild relatives, such as teosinte and *Tripsacum*. Griffing *et al*. (14) suggested introduction of Mexican germ lines into breeding programmes of corn belt maize to maximise the genetic diversity. These suggestions and findings depend in part on the major problem of knowing the wild ancestors of corn. Regardless of difficulties in identifying the germ plasm source, the incorporation of exotic material is essential to increase the genetic diversity. Efforts already made by northern corn belt breeders to introduce gourd seed types for diversity might be intensified. It may also be worthwhile to introduce southern flint lines in the breeding programme to increase the genetic diversity and at the same time maintain the agronomic standards of the inbred lines. Since southern flint lines were found to be different from northern flints morphologically it is highly probable that they are also different genetically in genes for vigor as well as morphology.

SUMMARY AND CONCLUSIONS

The primary object of this study was to obtain information on the significance of cytology and phylogeny of dent and flint maize types as they occur in the northern United States and Canada. The relationship of divergence in morphological characters and phylogeny to combining ability was studied. The basic material used consisted of indigenous inbred lines of flint and dent origin, developed through the breeding programme at the University of Manitoba, and a group of F_3 lines from a cross of a northern flint by a corn belt dent. Some South American and Mexican flint stocks were also included in the study.

The average chromosome knob number among indigenous inbred lines was 3.88 with a range from 0 to 8. The F_3 lines had an average of 3.23, and range of 1 to 5 knobs. Somewhat higher chromosome knob numbers averaging 8.8 and with a range of 4 to 12 were found among southern flint lines. Seminal root numbers followed a somewhat similar pattern, with an average of 2.15 among indigenous lines, 1.57 among F_3 segregates and 4.03 among southern lines. Southern flint lines were characterised by having numerous seminal roots and many chromosome knobs, suggesting that these lines are quite different from northern flints, which had very few chromosome knobs and seminal roots. The dent lines were intermediate between southern flints and northern flints in these characteristics. Among indigenous inbred lines, high chromosome knob numbers were associated with high kernel row numbers, many seminal roots and few tillers. These are the characteristics typical of dent lines, suggesting that the association present in the ancestral strains of maize have not been much altered even after prolonged breeding. There was no association between chromosome knobs and the morphological characters of either the F_3 lines or the southern flints. On the basis of these phylogenetical relations the origin of dent maize was discussed.

There was a positive association between days to tasseling and each of plant height, ear height, number of leaves and chromosome knob numbers among indigenous inbred lines. There was association of many seminal roots with each of high kernel row number, high placement of ears, many leaves and few tillers. With few exceptions the same relations were found among F_3 lines. The characteristics found to be associated were, in general, those typical of northern flints on one hand, and corn belt dents on the other, suggesting that the ancestral associations tended to remain intact. However, the correlations were moderate. Among southern lines, plants with many seminal roots tended to produce tall plants, with high placement of ears and many leaves. Plants with many tillers had many kernel rows. The interrelations observed in northern flints and corn belt dents differ from those found among southern lines in which maturity was negatively correlated with ear diameter and ear number was positively correlated with tiller number. Tiller number showed negative association with seminal root numbers among northern flints, but such a relationship was not found among southern lines. These differences suggest that the two flint collections constitute quite distinct groups.

Grain yield among single crosses was positively correlated with each of tiller number, ear length, and 1000 kernel weight but negatively associated with row number. Similar associations were found among the parental inbred lines except for kernel row number, suggesting that the genes responsible for these characters are linked and dominant in effect.

The average levels of index values, representing differences between parental inbred lines in characteristics which distinguish flint from dent were correlated with levels of grain yields of the corresponding F_1 hybrids. The correlation was significant statistically and large enough to be of some practical importance in determining the genetic diversity.

The possibility is discussed whether the combining ability of inbred lines derived in part from northern flint germ plasm could be due to introgression of Tripsacum, in view of their Tripsacoid characteristic but low chromosome knob numbers.

A consistent association was found between seminal root number and maturity period in F_2, F_3 and backcross population of the cross of corn belt dent line B.14 and the northern flint S.W.F. Associations were also found among low tiller number, tall plants and high placement of ears among the same three populations and also the indigenous inbreds. The significance of these associations in maize breeding programmes for this area is discussed.

The inbred lines Kfa and W.617 showed the highest average combining ability of lines tested, while K.98 had the lowest. Low combiners when crossed with high combiners gave high yield, while low combiners when crossed with low combiners gave low yield, suggesting that specific combining ability is highly important under the conditions in which this investigation was carried out.

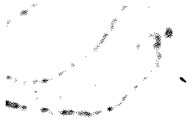
Inbred lines from group A (northern flint x corn belt dent) gave a higher average F_1 yield, when crossed within group A, than when crosses were made between group A and group B (corn belt dent), or when crosses were made within group B. This showed that lines derived from crosses of flint and dent types had greater combining ability than those from dent alone. It was found that lines with highest combining ability were bred directly from flint x dent hybrids. Although the advantage was not so great, it would show that the corn belt dent lines may have originated from such material in their remote ancestry.

A considerable heterosis effect was shown by the inbred line Kfa, on the basis of the percent yield relative to the higher parent. The highest yield from an individual cross was obtained when Kfa, which had predominantly flint characteristics with dent grains, was crossed with V.3, a line with corn belt dent characteristics and a fair amount of combining ability. V.3 produced a low yield as an inbred. These results indicate that the lines with divergent genetic background may have utility in yield improvement, even though they are themselves not particularly well adapted to local conditions.

There was an indication that the greater the genetic diversity of inbreds the greater the heterosis among single crosses. The desirability of maximising genetic diversity of parents as a factor in obtaining a high expression of heterosis is discussed.

FIG. 1

Pachytene cell of the flint line W.333 showing chromosome knobs. (760X.)



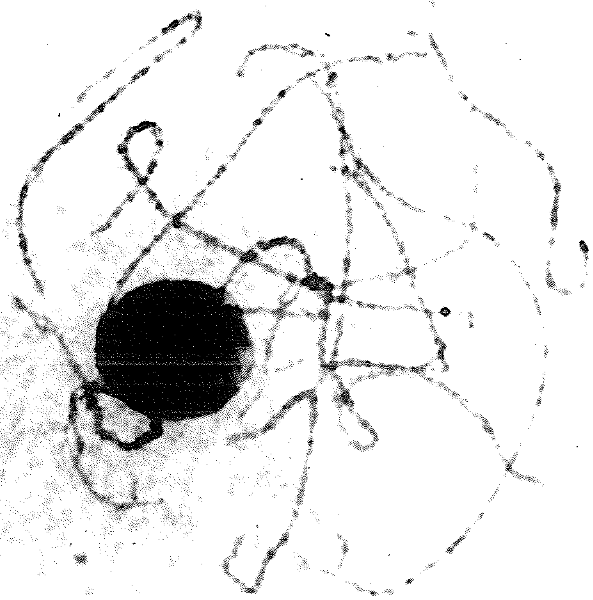


FIG. 2

Pachytene cells of the flint line 38 showing chromosome knobs. (740X.)

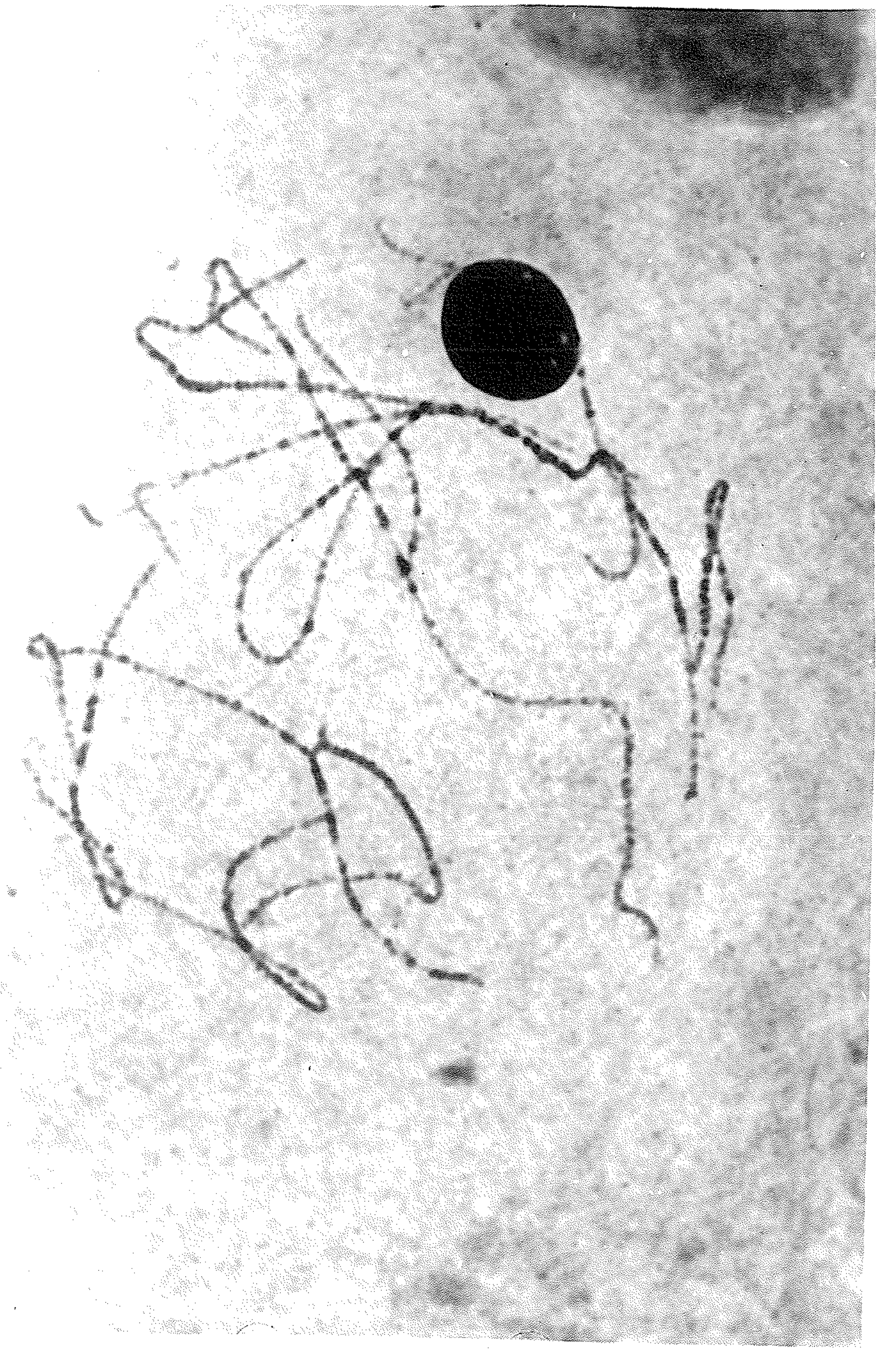


FIG. 3

Pachytene cell of the smooth dent line Kfa showing chromosome knob. (600X)

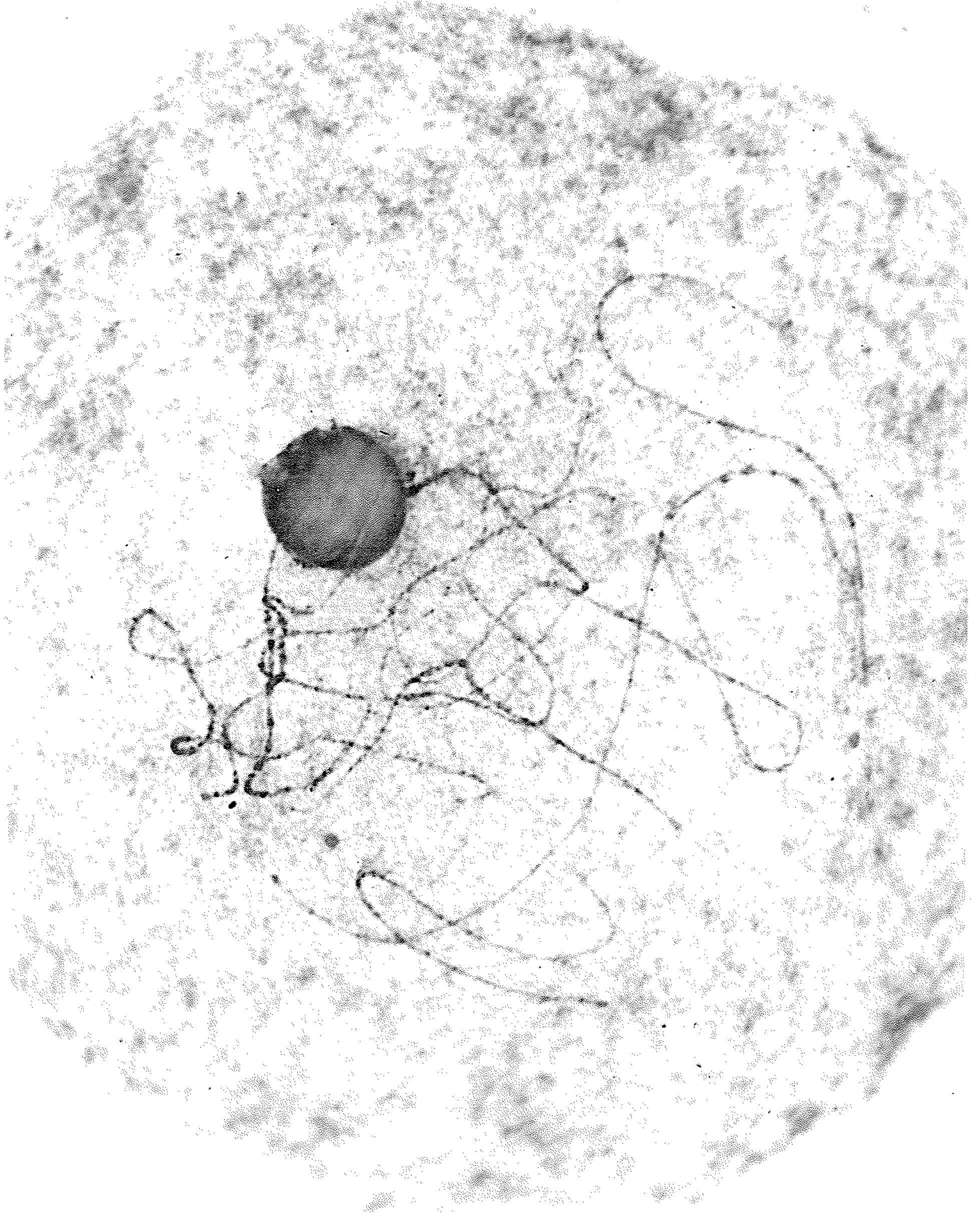


FIG. 4

Pachytene cell of the flint parent S.W.F. showing chromosome knobs. (780X)

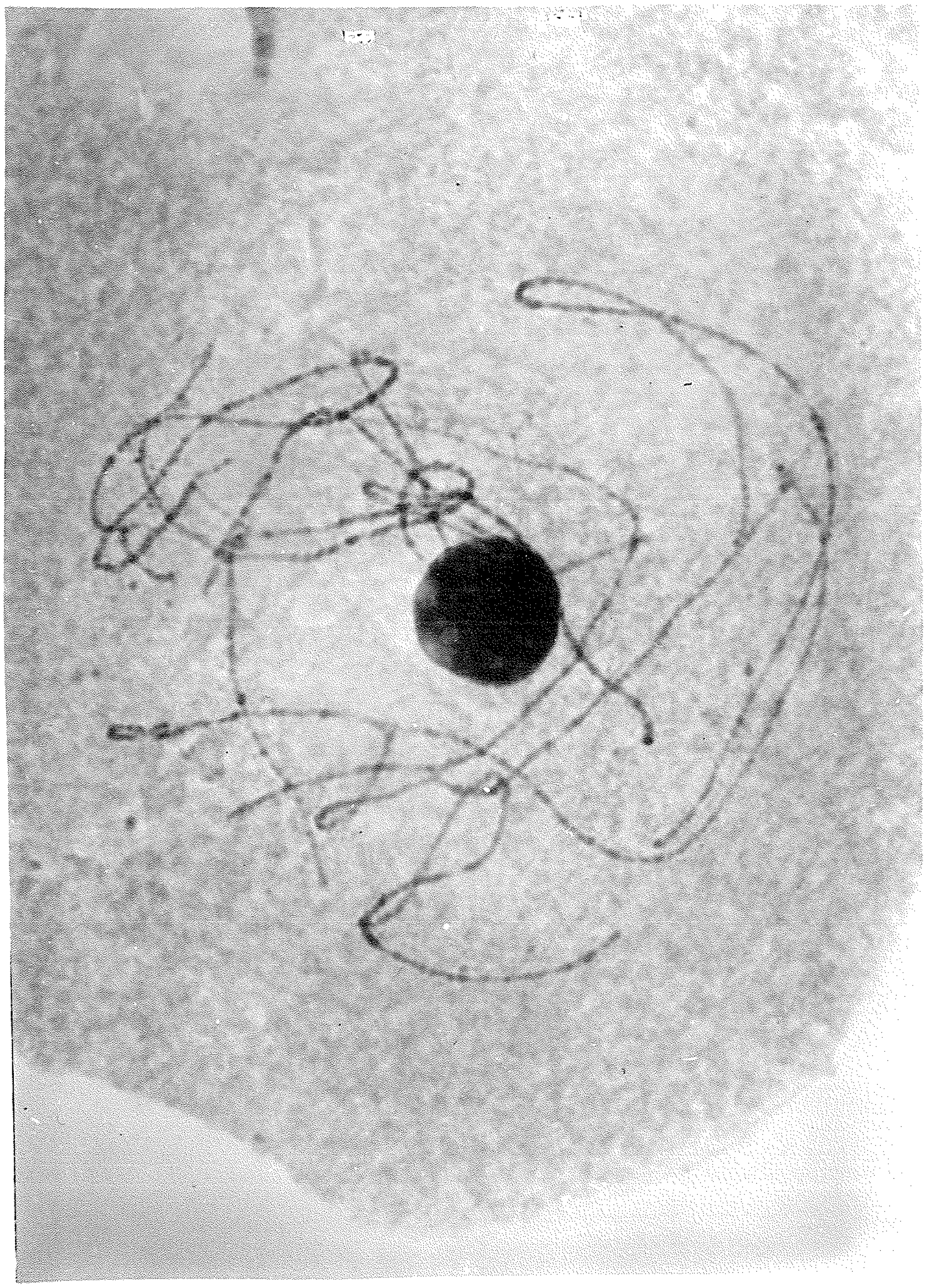


FIG. 5

Pachytene cell of the corn belt dent line B.14 showing chromosome knobs. (720X)

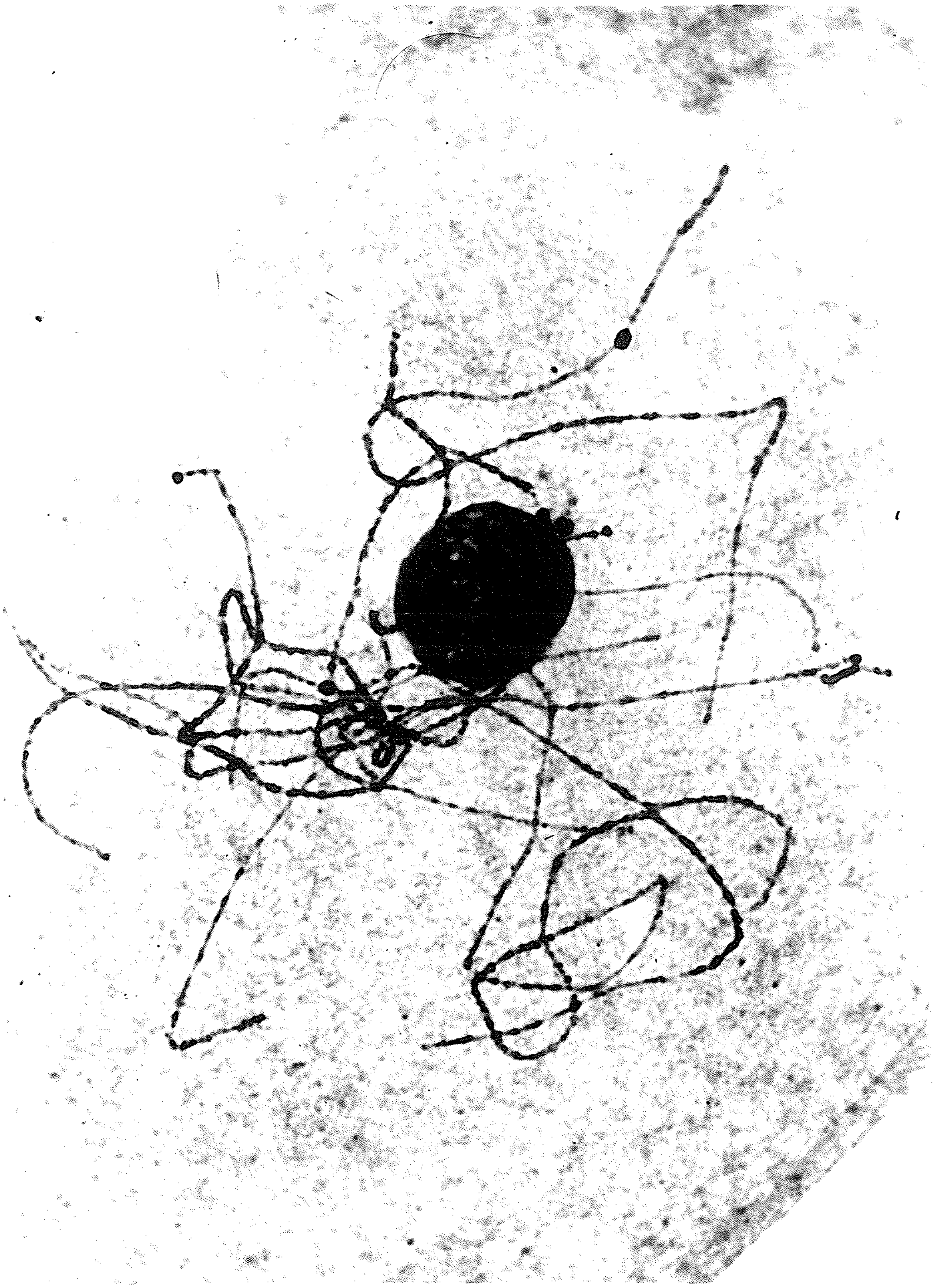


FIG. 6

Pachytene cell of the southern flint line from Mexico (P.I. 217409) showing chromosome knobs. (800X)

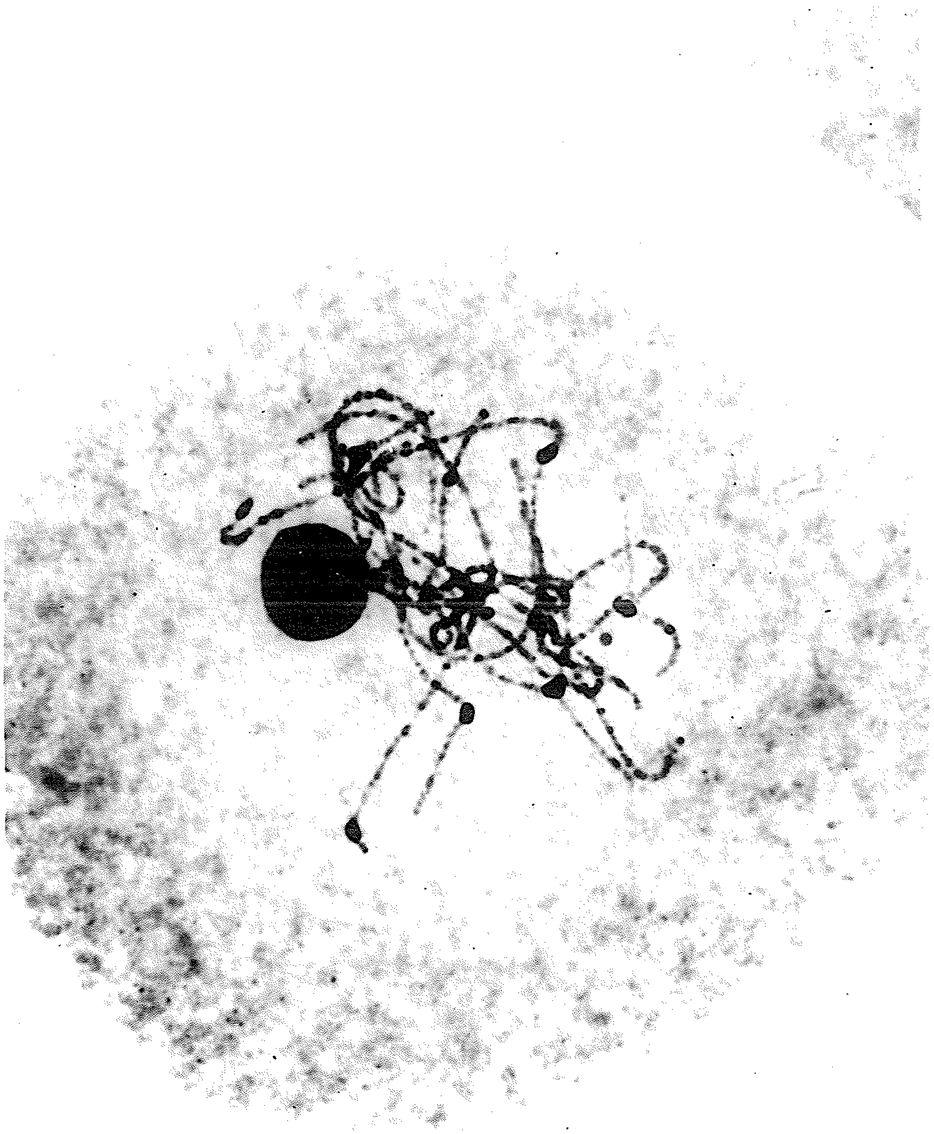
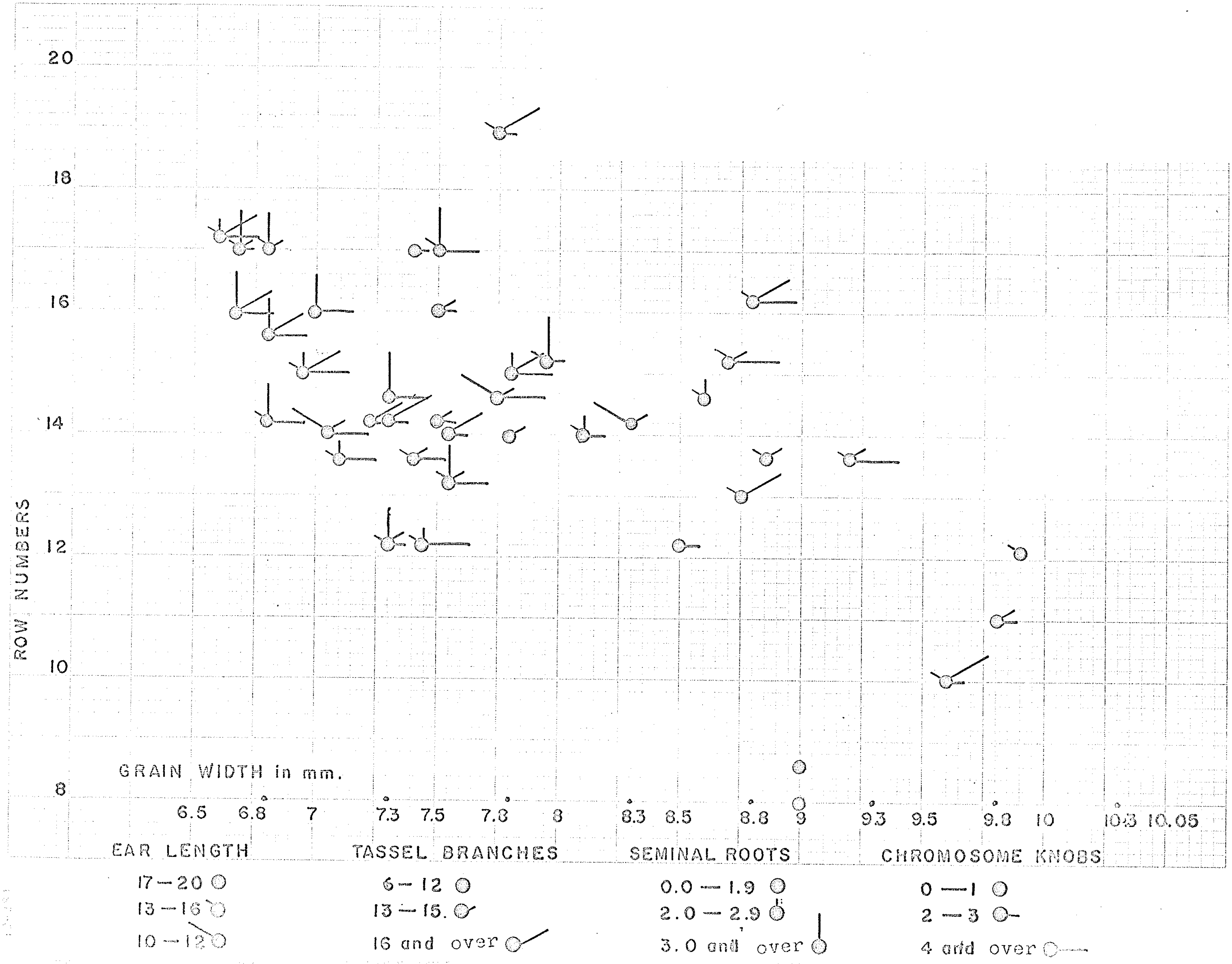


FIG. 7

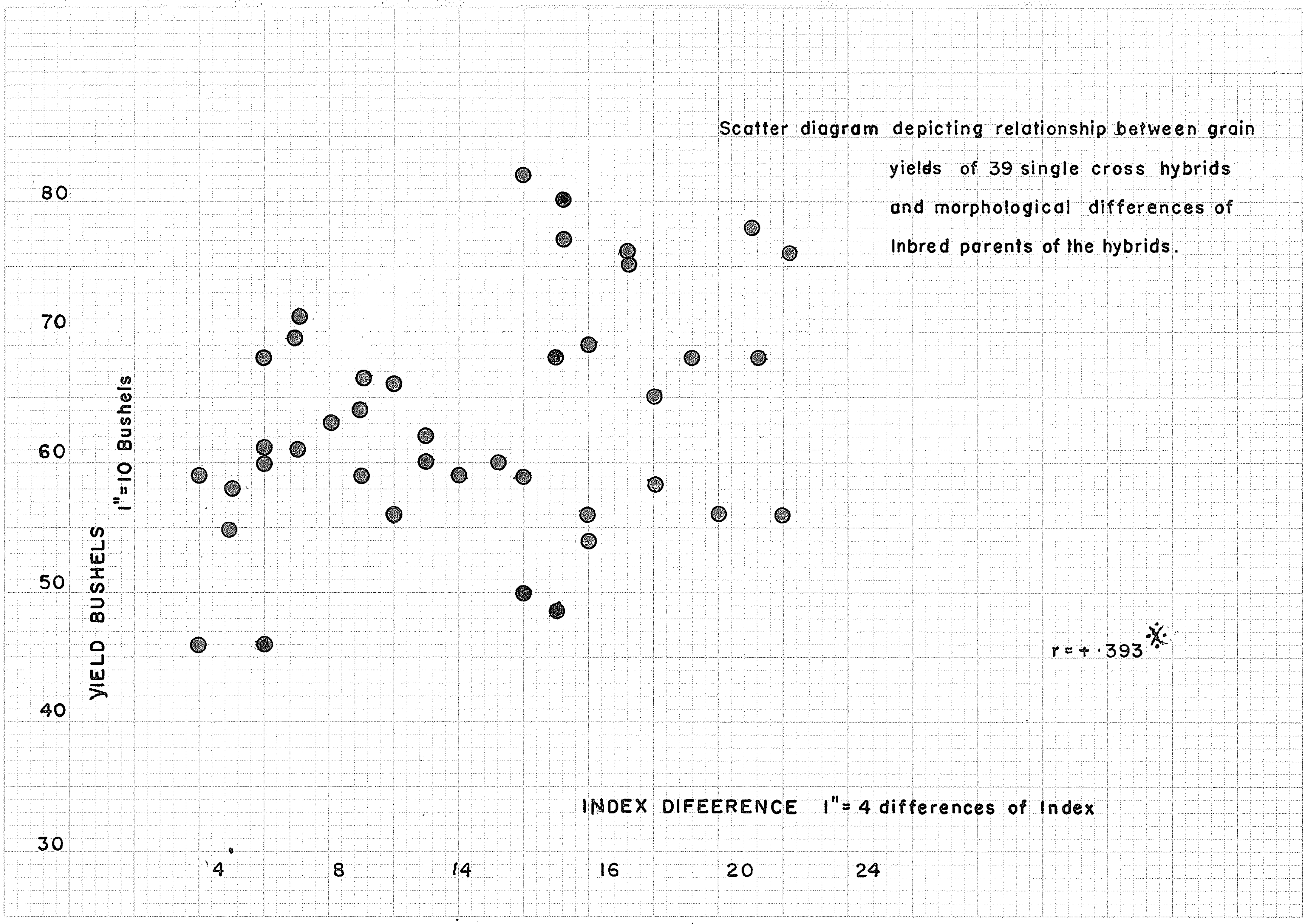
Pictorialized diagram showing relationship between numbers of rows of kernels, kernel width, tassel branches, seminal roots, ear length and chromosome knobs among indigenous inbred lines.



ROW NUMBERS
20
18
16
14
12
10
8
GRAIN WIDTH in mm.
6.5
6.8
7
7.3
7.5
7.8
8
8.3
8.5
8.8
9
9.3
9.5
9.8
10
10.3
10.05
EAR LENGTH
17 — 20
13 — 16
10 — 12
TASSEL BRANCHES
6 — 12
13 — 15.
16 and over
SEMINAL ROOTS
0.0 — 1.9
2.0 — 2.9
3.0 and over
CHROMOSOME KNOBS
0 — 1
2 — 3
4 and over

FIG. 8

Scatter diagram dipicting relationship between grain yields of 39 single cross hybrids and morphological differences of inbred parents of the hybrids.



Scatter diagram depicting relationship between grain yields of 39 single cross hybrids and morphological differences of Inbred parents of the hybrids.

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