INHERITANCE OF SOME ENDOSPERM TYPES IN SORGHUM, *Sorghum bicolor* (L.) Moench

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CHAPTER I

INTRODUCTION

For a plant breeder to make progress in a breeding program he must have a genetically variable base population with which to work. A knowledge of the inheritance of various traits is required to make efficient gains in the improvement of any crop once the variability is available. Information on the genetics of sorghum, Sorghum bicolor (L.) Moench, has been accumulating since the early 1900's but is not nearly as extensive as that found for some other cereals.

In cereal crops the grain itself is of primary importance. The genetic composition of the grain can affect its value and usefulness for human consumption, livestock feed, or industrial products. Research has been conducted on the genetic controls of both physical and chemical properties of the grain. Such information is useful to the breeder in manipulating the genotype of the crop to obtain certain desirable characteristics.

The largest component of most cereal kernels is the endosperm, which is composed almost entirely of starch. Different endosperm types have been isolated and studied in corn, sorghum, and other cereals. The genetic controls for these various endosperm types have been studied extensively in corn, and to a lesser degree in other cereals. This information has been utilized by the breeder to alter the genotype of the grain and thus the carbohydrate content of the endosperm. By such methods material that is better suited for a specific commercial purpose can be obtained. Mutant endosperm types in corn have been used extensively in establishing the pathways of starch synthesis for endosperm formation. This is a prominent area of research at the present time.

Several of the same mutant endosperm types found in corn have been identified in sorghum. The mode of inheritance has proved to be the same or similar for some of these traits. Endosperm mutants could be just as useful in sorghum improvement as in corn. Information on the genetic control of endosperm synthesis could aid in improving the quality of sorghum grain and be useful in understanding the genetic-biochemical relationships of the crop.

The objective of this study was to investigate the genetic relationship of several endosperm types of sorghum.

CHAPTER II

LITERATURE REVIEW

Since numerous endosperm types have been studied intensively in corn the first portion of this review will be devoted to some of the findings on this crop.

King (33) defined the endosperm as being "triploid nutritive cells surrounding and nourishing the embryo in seed plants". This tissue is the largest single component of most cereal grains and is mainly starch or some other carbohydrate. In normal dent corn the endosperm comprises over 80% of the kernel. The starch granules are held in a proteinaceous matrix within the endosperm cells. This proteinaceous matrix is thicker in the outer horny endosperm than in the inner floury endosperm. The aleurone cells are the outer most layer of the endosperm and are much higher in protein than the remainder of the endosperm (3).

Zimmerman (5) states that the main transport material in higher plants is sucrose which is the first free sugar after photosynthesis. From the transport materials normal dent corn produces an endosperm which is about 25% amylose (straight chain) and 75% amylopectin (branched chain) (16). Mutants have been found which drastically alter this ratio, even to the point of little or no starch being present in the endosperm. Dunn, Kramer and Whistler (17) worked with endosperm mutants that ranged as low as 9% starch in the kernel. Creech and McArdle (16) discussed the following mutant endosperm types in corn:

sugary-1 (su_1), brittle-1 (bt_1), brittle-2 (bt_2), shrunken-2 (sh_2), sugary-2 (su_2), amylose-extender (ae), dull (du), and waxy (wx). The first five mutants greatly reduce starch and increase sugar content of the endosperm, especially sugary-1. The next three mainly effect the relative proportions of amylose and amylopectin found in the endosperm. Other mutants noted by Nass and Crane (38) are floury-1 (fl_1), non-horny (h), opaque-2 (O_2), and shrunken-1 (sh_1). Researchers have found that each of these mutants are conditioned by genes which are recessive to their normal alleles carried by regular dent corn.

Cameron (9) stated that Correns, East, and Hayes were among the early workers to investigate the inheritance of sugary-1 and that Eyster did much of the work on sugary-2. He also noted that Collins was among the first to report the inheritance of waxy in corn. All of the mutant types have been found to exhibit xenia when pollinated by normal dent corn. Hutchison (25) reported shrunken (sh_1) to be a simple recessive mutant linked to waxy with a crossover percentage of 21.8.

Zuber (56) described sugary endosperm (su_1 su_1 su_1) as being "translucent, wrinkled, and glassy textured" in appearance. He noted that the other sugary genotype (su_2 su_2 su_2) was less shrunken or wrinkled and had varying degrees of translucence. An allelic form of su_2 (su^{am}) was evident only when in the double homozygous condition with dull (du). The latter genotype was of particular interest to him because of its high amylose content (50%). Mangelsdorf (36) actually noted this unusual genotype first. The $su^{am}du$ endosperm is less wrinkled, less translucent and more starchy in appearance than su types. The dull condition (du) alone gives a phenotype which is slightly opaque or dull and frequently difficult to separate from normal.

Laughnan (35) studied the interrelationship of shrunken ($\underline{sh}_2$) and sugary ($\underline{su}_1$). He noted a 9:3:3:1 ratio of normal:sugary:shrunken: sugary-shrunken. He found that the homozygous shrunken ($\underline{sh}_2$) endosperm gave about a ten-fold increase of sugars (mainly sucrose) over normal dent kernels and about a four-fold increase over the sugary ($\underline{su}_1$) types. The total carbohydrate production was lowest for the double homozygous recessive genotype ($\underline{sh}_2$ $\underline{su}_1$). This double recessive genotype also showed a decrease in water-soluble-polysaccarides (WSP). He suggested that the $\underline{Sh}_2$ factor acts prior to Su in starch synthesis. Hutchison (25) had previously reported that the homozygous condition of the $\underline{sh}_1$ gene (different locus) caused a sharp increase in sucrose and reducing sugars and could be a block in synthesis of glucose polymers from sucrose.

Cameron and Cole (10) compared carbohydrate accumulation of $\underline{su}_1$, $\underline{su}_1$ du, and $\underline{su}_1$ $\underline{su}_2$ genotypes on several different genetic backgrounds. They found that $\underline{su}_1$ du and $\underline{su}_1$ $\underline{su}_2$ slowed starch accumulation compared to $\underline{su}_1$ alone in most cases. Sugars and WSP were not consistently different among these three genotypes in their study. Dunn et al. (17) noted that the triple recessive genotype ($\underline{su}_1$ $\underline{su}_2$ du) had only 9% starch and 77% of it was amylose. Cameron and Teas (11) reported that brittle-1 ($\underline{bt}_1$) and brittle-2 ($\underline{bt}_2$) increased sugar and decreased starch content in the endosperm.

Other mutants, as previously indicated, have been studied extensively for their effect on the ratio of amylose and amylopectin. The waxy (wx) type has probably been known the longest and studied the most intensively. Collins (13) first described the waxy endosperm in corn in 1909. Several others since then have found that the waxy endosperm type has all or nearly all amylopectin (branched chain type starch) in its endosperm.

Zuber (56) noted that many waxy (wx) mutants have been reported, but all of them are alleles, thus located at the same locus. Some of the mutants allowed a slight production of amylose in the endosperm. Nelson (39) obtained a large array of waxy mutants from different sources and was able to subdivide the waxy locus. He intercrossed the waxy mutants and by staining pollen with iodine solution (waxy-red, starchy-blue) was able to map 24 waxy "alleles" within the waxy locus. All of the waxy types he worked with were recessive to normal, but he did obtain a very low frequency of recombination in some waxy X waxy crosses by use of the pollen staining method and conventional genetic analysis. He also worked with three controlling elements which seem to function similar to those found in microorganisms. Ericksson (18) has completed an extensive literature review on the waxy character in cereals. He cited workers who found and worked with waxy endosperms in corn, sorghum, rice, and barley.

The amylose-amylopectin ratio may be altered genetically in the opposite direction. Kramer, Whistler and Anderson (34) identified a gene (ae) noted as an amylose extender which increased the proportion of amylose. Zuber *et al*. (57) found amylose content to range from 54 to 71% for ae endosperms and suggested that this variation could be due to modifier genes. He found that as the amylose content increased the total starch content decreased, just as Dunn *et al*. (17) noted for the triple recessive su_1 su_2 du endosperm type. Interaction of some of the other mutant alleles also increased amylose content but also reduced total starch production (56).

There has been considerable effort on corn to establish the genetic-physiological-biochemical relationship of these mutants. The work has been directed at locating and identifying the enzymes which may be present or absent when certain mutant genes are present. Specific genes could thus be identified as controlling synthesis of polysaccharides in maize endosperm. Enough information of this nature would enable researchers to establish a biosynthesis scheme.

Previous discussion has indicated possible roles of some of the endosperm mutant genes in control of carbohydrate biosynthesis. Creech and McArdle (16) and Creech (14,15) discussed these more extensively. The ae gene seems to be an early block between sugars and branched chain polysaccharides, resulting in sugar accumulation and reduced starch content. The du and su_2 genes appear to function in separate pathways for branched chain polysaccharides. The Wx allele of wx must be necessary for amylose synthesis since essentially no amylose is produced when the wxwxwx condition exists. The sh_2 gene must block a major pathway very early in conversion of sugars to starch. The su_1 gene could block the conversion of WSP to starch. Similar conclusions might be drawn from some of the other endosperm mutants in maize.

Nelson and Rines (40) found that waxy type seeds lacked a UDPG[1]-transferase system. Therefore, the amylopectin of the waxy types cannot be formed by the UDPG system. They further stated that two different starch formation paths probably exist, one to amylopectin and another via the starch granule-bound UDPG-transferase system to the straight chain polymer (amylose).

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[1]Uridine-diphosphate-glucose.

Tsai and Nelson (49) reported the isolation of four different phosphorylase enzymes (I, II, III, and IV) in developing maize kernels. They were physically separable and appeared at different times in endosperm development. In two shrunken mutant types they noted lower activity for I and II and somewhat less for III. These mutants conditioned a defective seed type with only one-third of the normal starch level. Their results indicated that phosphorylase enzymes have an important role in starch synthesis. More studies of this nature are being conducted and other enzymes are involved.

Starch granules are stored initially in subcellular structures called plastids. Badenhuizen (5) indicated that these plastids have morphological features which are under genetic control. He further indicated (6) that enzymes which effect starch synthesis may be present in soluble forms or as multienzyme complexes in the membranes of the plastid envelope. Nucleic acids in the plastids themselves are involved in the formation of some of these enzymes. The enzymes involved with actual starch synthesis could be of this latter type.

Grogan and his associates (22) conducted a study of carotenoid pigments in the endosperm of corn. Their study involved both carotene and xanthophylls. They found reciprocal differences in white X yellow crosses and noted that the pollen (or ear) source had a significant influence on the content of carotene and xanthophylls in the first generation seed. The study indicated a lack of dominance and primarily additive gene action for the traits. Geometric gene action was indicated in the YYy and YYY endosperm genotypes by an increase of xanthophylls of 2.5 to 2.8 times for each additional gene in the sequence.

Sorghum

Grain sorghum is a cereal which frequently has been compared to corn, since both are used for similar purposes. With the advent of hybrids grain sorghum yields increased considerably, as did their total acreage. While grain sorghum is primarily a feed grain in the United States, about 75% of the world production is used for human food.

Sorghum grains are usually smaller than corn kernels, and a pound of sorghum contains 12,000 to 30,000 seeds. The grain colors are white, red, yellow, or brown resulting from complex gene action that involves both the pericarp and testa. As in corn the largest part of the caryopsis is the endosperm which normally is primarily starch. The starch of most sorghum endosperms has 22 to 25% amylose and the remainder is amylopectin. There are also waxy, sugary, and yellow endosperm types (42).

Several researchers have worked on the composition of sorghum kernels. Heller and Sieglinger (23) found sorghum to contain 8.80 to 13.10% protein, 2.40 to 3.00% fat, 1.40 to 1.50% crude fiber, and 71.80 to 75.10% N.F.E. Hubbard, Hall, and Earle (24) found the kernels to be 82% endosperm, 10% germ, and 8% bran. They further found the endosperm to be 82+% starch. Wall and Blessin (50) found comparable results in their studies.

Collier (12) studied caryopsis development in grain sorghum varieties and hybrids and found maximum dry weights of the kernels were reached in 24 to 35 days after bloom. Kersting, Stickler, and Pauli (31) found maximum accumulation of dry weight at 23 to 31% moisture and 35 to 45 days after pollination. The dry matter tended to decrease following maximum weight. Kersting, Pauli, and Stickler (32) made further chemical analysis of developing seeds starting three days after pollination. The sugar percent increased rapidly until twenty days after pollination and declined slowly after that, being 1 to 2% by the end of the season for most types. The percent starch increased rapidly after pollination to a maximum of about 64 to 79%. Decrease of maximum dry weight of the kernels was due to respiration.

Sanders (46) noted morphological and anatomical changes during the development of grain sorghum kernels, with special emphasis on endosperm development. He noted cell growth three days after fertilization. The outer layer was composed of cells with dense cytoplasm and large nuclei, but they were much smaller than other endosperm cells. These cells gave rise to the aleurone layer (endosperm epidermal layer) which is higher in protein and oil compared to the remainder of the endosperm. The subepidermal cells were irregular in shape and their cytoplasm content was low. These cells were higher in oil than the floury endosperm. The starch deposition began in the crown area and continued downward fairly rapidly. The original nutritive tissue of the ovule, the nucellus, was digested early and rapidly replaced by the endosperm. The cells of the endosperm expanded from the basal region, enveloping the embryo and crushing the nucellus in the crown region.

Further work on the nature of the starches found in sorghum endosperm was conducted by Barham *et al*. (7). They studied gel strength and found that kafirs and various normal endosperm types had a greater gel strength than glutinous (waxy) types. Overall they indicated that kafirs were better for food purposes. Norris and Rooney (41) did wet-milling studies on sorghum and found that the female parent of hybrids had a significant effect on starch yield, recovery, and protein content in wet-milling. Freeman, Kramer, and Watson (19) found gelatenization temperature of sorghum starch to be affected by both genetic and environmental factors. Waxy types had higher gelatinization temperatures than their normal counterparts. Workers in India describe "bold, white, pearly" grain types as the most desirable for cooking or bread (44).

Just as in corn there is variation in endosperm composition of sorghum. Rooney, Johnson, and Rosenow (45) indicated that starchy types, other than waxy, range from all-floury to all-corneous endosperm types, which give the extremes in density. Waxy, floury, corneous, and sugary types exist, similar to those found in corn.

Waxy endosperm types in sorghum are basically the same as those found in corn. They are also called glutinous sorghum because of the glue-like character of the cooked or wetted grain or flour. These types have been known in China for at least 300 years and have been used to some extent in industrial products in the United States. The waxy starch is entirely amylopectin in which the molecules are arranged with many branches (37).

Karper (28) first established the genetic relationship of the waxy endosperm to that of normal starchy types. He noted that the kernels which developed on a waxy type plant which was pollinated with starchy (normal) pollen had starchy endosperm. This xenia effect indicated the waxy condition to be recessive. His work showed that the waxy endosperm in sorghum was inherited as a simple recessive and designated the gene as wx.

Karper (28) made use of iodine solution to check endosperm classifications. The F_1 endosperm of a kernel which developed from a waxy floret, being pollinated with starchy pollen, stained blue with iodine, as does a normal starchy type. The waxy endosperms stained red to reddish brown when the iodine solution was applied. The pollen from waxy types also stained red, and the pollen from starchy (normal) types stained blue. F_1 plants from a waxy X normal cross produced equal amounts of blue and red staining pollen.

Webster (52) noted results similar to those of Karper. He also used the iodine (potassium iodide) solution for staining classifications. He further noted that the waxy locus was linked with a locus for normal or bloomless stalks and leaves (Bm, bm) with a crossover percentage of 2.7 + 0.36. In further studies Karper, Quinby, and Jones (29) noted linkage between the waxy locus and a locus for yellow seedling (y_2) with a crossover percentage of 26.5.

Jones and Sieglinger (27) studied the effect of the waxy gene on grain yields in Oklahoma. Their studies confirmed the mode of inheritance for waxy which both Karper and Webster had reported. They did note an average deficiency of 1.9% of the waxy type which they attributed to slower pollen tube growth of the waxy pollen resulting in somewhat less fertilization by this type. In their results on yield they found that starchy endosperm types generally yielded about 10% higher than waxy types, with heterozygotes being intermediate. The weight per 1,000 seeds was 0.77 grams in favor of starchy types. The starchy seeds outweighed waxy by an average of 1.2 pounds per bushel. They indicated that the depression of yield and grain weight could be due to a group of undesirable genes linked with the waxy locus, rather than the waxy gene alone.

Karper, Quinby, and Jones (29) and Karper and Stevens (30) have reported on the sugary endosperm type in sorghum. They noted that the

F_1 panicle of a cross between a sugary and a starchy type gave a 3:1 segregation of normal starchy seed to sugary endosperm types. Xenia was also shown when sugary flowers were pollinated from starchy type plants. These results indicated that a simple recessive gene, designated as su, was responsible for the sugary character.

Waxy endosperm flowers pollinated from sugary endosperm types resulted in F_1 seed (endosperm) which gave a blue (starchy) reaction with iodine solution. No linkage was found between waxy (wx) and sugary (su) endosperm types or between su and y_2 (yellow seedlings) (30).

The sugary seed types have been called "dimpled" by some Indian workers, and they are commonly used for food by parching and eating in the early dough stage (1). Sugary seeds wrinkle as they mature and varieties with corneous seeds and juicy stems wrinkle the most. The sugary seeds are about one-fourth smaller than normal seeds of sorghum. The seeds often contain twice as much total sugars as normal starchy seeds, and plants with sugary endosperm seed have juice higher in sugars.

Watson and Hirata (52) analyzed the carbohydrate content of some sorghum varieties of known genotype for the waxy and sugary loci. The homozygous condition of the su gene consistently lowered the percent starch and increased the sugars and water-soluble polysaccharides. One variety, Sugary Milo (Wx su), had only 31.5% starch but had 28.4% WSP and 2.68% sugar, which was mainly sucrose. Another variety, Sugary Feterita (Wx su), had considerably more starch (56.7%) and much less WSP (7.9%) than did Sugary Milo. This great difference would indicate some difference in genetic make-up.

Quinby and Martin (43) reported that in 1938 J. C. Stephens intercrossed three sugary lines. The F_1 from each cross was sugary, indicating that the same sugary gene was common to all three lines. The three lines were from diverse sources.

Quinby and Martin (43) mentioned two more endosperm types in sorghum, floury and pop sorghum. The floury type endosperm has been found in a number of the Kaoliangs. The pop sorghum types are common to India. Ayyanger and Ayyar (3) characterized the pop sorghum as having small grains with a hard, dense endosperm. Genetic information is not available on either of these two endosperm types.

Ayyanger and Narayanan (2) reported a hollow type grain which also had hollow peduncles. These hollow grains were like the normal until after the milk stage when they became hollow. As the grain ripened the top of the kernel would wrinkle or get a slight pitting. The inheritance of this trait was not reported. Ayyanger et al. (4) reported pearly to be dominant to starchy (chalky).

Jones and Sieglinger (26) reported a defective endosperm type which they found in an F_2 field hybrid progeny of Durra C.I. No. 696 in 1945. They indicated that this character showed xenia and was found to be inherited as a simple recessive with a chi-square probability of 0.59. They indicated that the endosperm of such seed was very shrunken and the seed germinated poorly.

Adapted yellow endosperm types of grain sorghum have been developed in the United States in recent years. They may have one-fourth or more as much carotenoid pigments as yellow corn (20). Sieglinger (47) stated that one could run a sample of 20 to 40 seeds of sorghum through a hand operated barley pearler and then observe the presence or absence of carotenoid pigments in the endosperm.

Blessin, Van Etten, and Wiebe (8) examined yellow endosperm type grain from sorghum. They estimated that common varieties had about 1.5 ppm of total carotenoids. Crosses of common varieties (non yellows) with "African Yellow Endosperm" varieties had 8 to 9 ppm. The carotenoid content was higher when the seed were protected from the weather after pollination. Further analysis showed that lutein, zeaxanthin, and beta-carotene were the three main types of carotenoids present. Crytoxanthin, hydroxy-alpha-carotene, and alpha-carotene were three major types found in yellow corn but not detected in grain sorghum.

Worzella *et al*. (54) investigated the inheritance of beta-carotene in grain sorghum hybrids. Beta-carotene in the grain of the parents varied from 0.22 to 3.23 milligrams per kilogram. The variation in carotene content of the F_2 segregates ranged between these values, but there was a preponderance of segregates with a beta-carotene content lower than the midparent value. They obtained positive correlation coefficients between endosperm color and beta-carotene content in the F_2. They concluded that relatively few genetic factors were involved in the inheritance of beta-carotene content in grain sorghum.

CHAPTER III

MATERIALS AND METHODS

Three endosperm types used in this study were obtained from a heterofertilization study conducted in 1966 and 1967 (21). They were noted as defective, shrunken, and dent mutants. The shrunken type should more properly be called sugary. Other endosperm types used in this study were designated as normal, yellow, and waxy.

A total of twelve different lines used in this study represented six different endosperm types. Two pure lines for each of the defective, dent, yellow, and normal endosperm types were selected for use in this study. Three lines of the sugary type and only one of waxy were selected. The lines and their endosperm types are indicated in Table I. The first five lines listed had normal appearing plump kernels. The remaining seven lines had mutant endosperm types which did not give plump kernels.

The two normal lines had starchy endosperms with an outer corneous portion and an inner floury portion. They gave a starchy, or blue, reaction to iodine solution. The two yellow endosperm types were normal except that they had a high concentration of carotenoid pigments in their endosperms. Dwarf Redlan appeared to be a normal endosperm type externally, but the endosperm was waxy (100% amylopectin) and gave a red reaction to iodine.

The other lines were visibly mutant types by external appearance.

TABLE I

LINES OF EACH ENDOSPERM TYPE WITH SOME DISTINGUISHING CHARACTERISTICS

Endosperm Type and Lines	Characteristics
Normal	
Wheatland	Large red grain, awnless, kafir-milo
BOK8	Early kafir, red grain, awnless
Yellow	
BOKY29	White grain, purple plant color
ROKY16	Red grain, tan plant color
Waxy	
Dwarf Redlan	Red grain, purple plant color, awnless
Defective	
Defective	Red grain, awns, durra derivative
Defective (R)	Red grain, awns, durra-milo derivative
Dent	
Dent (W)	White, dented, durra-type grain
Dent (R)	Red, frequently hollow grain
Sugary	
Sugary (R)	Red, dimpled grain, grain type
Sugary (W)	White, dimpled grain, short grain type
Sugary (F)	Brown, shriveled grain, forage type

Defective had a very collapsed seed with a degenerate endosperm which gave a starchy (blue) reaction to iodine. It had only one-fourth the volume of endosperm found in normal seeds. The dent type usually had a dent on the side of the kernel opposite the germ, but it frequently appeared plump and was hollow in the center of the endosperm. The sugary types (sugary, shrunken, or dimpled) ranged from seeds which were extremely shriveled and translucent to seeds which appeared normal but had a very depressed germ. For further description of these lines see Appendices A and B.

To conduct this study all possible crosses were made among these various endosperm types (not within a given endosperm type), including reciprocals. Some of the crosses were obtained from the heterofertilization study conducted at the Agronomy Research Station, Perkins, Oklahoma (defective X normal and some sugary X normal). The F_1 plants from this study were grown at Perkins in the Summer of 1967 and selfed.

The twelve parental lines were grown in 40-inch rows, 30 feet long, in the Summers of 1967, 1968, and 1969. Hand emasculated crosses were made among the indicated endosperm types in 1967 and 1968. Each cross (e.g. Dent (W) X BOK8) was made two or more times with an average of about twenty florets being emasculated for each cross. In addition to the emasculated crosses, pollinations with the parental lines were made at Perkins on the male steriles AOK8, A Wheatland, A Dwarf Redlan, and AOKY29 (1968 only) in 1967, 1968, and 1969. Each cross (e.g. AOK8 X Defective) was made three times and the resulting seeds on the male sterile parent were bulked. AOKY29 proved to be partially fertile and the crosses made on it were not useful.

The twelve parental lines were also grown in the greenhouse at Stillwater, Oklahoma in the Winters of 1968-69 and 1969-70 to make the emasculated crosses. Plants were grown in one-gallon cans, three plants per can. Plants of each of the parental lines were cut back and held over for the 1969-70 greenhouse and additional cans were planted to make whatever emasculated crosses were still lacking.

The seeds obtained from both the hand emasculated crosses and pollinations on male steriles were classified to obtain F_1 endosperm information. The seeds resulting from the emasculated crosses made in the field in 1967 and 1968 were planted in gallon cans in the greenhouse in 1968-69. The F_1 plants obtained from these seed were selfed, and the head or heads from each plant were harvested and threshed individually. The endosperm type of the seed harvested from these F_1 plants (F_2 endosperm) was then classified. A similar process was followed for F_1 plants obtained from 1967, 1968 and 1969 field plantings at Perkins and also for 1969-70 greenhouse material. Selfed heads (usually three) of each of the parental lines were saved from every planting in the field and greenhouse. Considerable difficulty was experienced in obtaining seeds from some of the hand emasculated crosses. Repeated attempts at some crosses failed to meet the objective of obtaining three F_1 plants per cross.

F_1 plants from pollinations on male steriles were grown in 1967, 1968, and 1969 at Perkins. Five heads were bagged in each of the F_1 rows (single row per cross). Notes were taken on male sterility, and if the F_1 plants were sterile, backcrosses, where possible, were made with both parents. If the F_1 plants were fertile, three selfed heads were harvested from each cross (e.g. A Wheatland X ROKY16).

In classification of the F_2 endosperms (kernels from F_1 plants) all seeds obtained from a given plant in the greenhouse plantings were classified. For classification of seeds from F_1 plants grown in the field at Perkins a sample was taken by use of a Boerner Sampler. The sample size ranged from about 200 to 700 kernels, depending on the cross. Initially all the seeds were classified from the F_1 plants grown in 1967 at Perkins, but this proved to be a tremendous task since some F_1 plants produced over 3,000 seeds.

The various categories of endosperm types (segregates) obtained from each cross are given in the results section. The only chemical test used in endosperm classification was the iodine (potassium iodide) test for waxy. The other endosperm classifications were made visually, based on the morphological characteristics of the seed and its endosperm. It was necessary to cut seeds appearing to be plump (normal) from crosses in which a dent endosperm line was one of the parents to check for hollow seed. A regular pocket knife was used for this.

In the crosses with the yellow endosperm lines a barley pearler was used to remove the seed coat to allow classification of the endosperm. In these crosses only the plump seeds were classified, since the mutant types would not pearl properly. The classifications for yellow endosperm were based on a set of standards ranging from one to eight, in which one had no apparent yellow coloration and eight had the most yellow coloration (highest concentration of carotenoid pigments). Category eight was a sample of seed from BOKY29, and category one was from Dwarf Redlan.

In 1969 at Perkins F_2 plants, which produced F_3 endosperms, were grown from seeds which had been classified for F_2 endosperm. These F_2 plants represented a sample of each endosperm type cross (e.g. defective X normal). Samples were not grown from all crosses (e.g. BOK8 X Dent (R)) since all crosses had not been obtained at that time. A single row was planted for each endosperm classification from a given F_1 plant. For example there were three rows for each Defective X B Wheatland F_1. The seeds planted in these three rows were defective, intermediate, and plump. These F_2 plants were selfed and the kernels were then classified for endosperm type in the Fall of 1969 to get a check on the F_2 endosperm classifications.

Kernel weights were taken on seed of each parental line and on seed harvested from the male steriles. A mean 100-kernel weight based on six (100-kernel) samples was calculated for each parental line. The kernel weight for the seed harvested from a given male sterile (e.g. A Wheatland X Defective) was determined for each year the cross was made and was based on two 100-kernel seed samples from a bulk of three heads. The weights were taken on seeds harvested from A Wheatland, AOK8, and A Dwarf Redlan. The crosses on AOKY29 could not be used because of a high percentage of selfs obtained from this male sterile. The 100-kernel samples were obtained with an electronic seed counter.

The F_2 endosperm data obtained from the hand emasculated crosses were tested for goodness of fit to a hypothesized ratio (49). The limited amount of backcross data was also analyzed in this manner. The F_1, F_2 and backcross data were used to determine the genetic relationship and mode of inheritance for the various endosperm types involved in this study.

CHAPTER IV

RESULTS AND DISCUSSION

Inheritance of Defective Endosperm

The defective endosperm type was first reported in 1951 by Jones and Sieglinger (26). They indicated the character was inherited as a simple recessive. Gorbet (21) found in 1966 and 1967 that the character did not appear to react as a simple recessive. When defective seeds from a segregating head were planted, a high percentage of the resulting plants segregated for the defective endosperm type. It was concluded that the inheritance of this character needed further study.

To obtain more information on the inheritance of this endosperm type two selected lines (Defective and Defective (R)) were crossed to two normal endosperm types. Reciprocal crosses were made by hand emasculations. The seeds obtained from the emasculated crosses in which the defective endosperm type was the female parent were only slightly more plump than the defective endosperm seeds. The reciprocal cross produced seeds which were essentially plump. This indicated some type of incomplete or lack of dominance.

In view of the F_1 endosperm types obtained, the F_1 plant (F_2 endosperm) results, and noting the lack of complete dominance found in the heterofertilization study (21), an intermediate endosperm classification was established. The hypothesis was that this intermediate phenotype had one dominant factor with two recessive factors (Ddd). Then the plump genotypes would be DDD and DDd while the defective endosperm genotype would be ddd. The F_2 endosperm classifications were then expected to fit a ratio of 2:1:1 (plump:intermediate:defective) in contrast to a 3:1 (plump:defective) for complete dominance. On this basis the parental genotypes were DDD (plump) and ddd (defective). The complete data for this and all other crosses with chi-square tests are given in Appendix C.

The F_2 data (endosperms) given in Table II were taken on the basis of incomplete dominance with one locus or pair of alleles controlling the character. The results given for each cross (e.g. Defective X Wheatland) represents the pooled data from three F_2 samples of seed from three F_1 plants. In general the analysis indicated a reasonable fit to this hypothesis for crosses with both defective endosperm lines. Only in the case of the Defective X Wheatland cross was the hypothesis rejected at the .05 level of probability. It should be noted that the reciprocal of this cross, Wheatland X Defective, gave a probability value of .83, which was the best fit among the various crosses of this type. The .07 probability value obtained for the Wheatland X Defective (R) also indicated a rather poor fit. All other crosses gave probability values near or above .20, and two crosses gave values above .50.

In the data given in Table II there were no apparent consistent differences between reciprocal crosses. Based upon the hypothesized mode of inheritance of the defective endosperm trait, differences between reciprocal crosses would not be expected. No maternal effects or unusual types of gene action were indicated.

There was a tendency for the intermediate class in Table II to be

TABLE II

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF DEFECTIVE X NORMAL ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes				Values	
Female	Male		Plump	Intermediate	Defective	Total	χ^2	P
Expected Ratio - 2:1:1								
Defective X Wheatland		(O)[1]	2034	960	904	3898	9.023	.01
		(E)[2]	1949	974.5	974.5			
Defective X BOK8		(O)	1867	941	872	3680	3.379	.18
		(E)	1840	920	920			
Defective(R) X Wheatland		(O)	1283	670	633	2586	1.214	.56
		(E)	1293	646.5	646.5			
Defective(R) X BOK8		(O)	983	467	452	1902	2.390	.30
		(E)	951	475.5	475.5			
Wheatland X Defective		(O)	437	208	217	862	0.355	.83
		(E)	431	215.5	215.5			
Wheatland X Defective(R)		(O)	507	218	216	941	5.672	.07
		(E)	470.5	235.25	235.25			
BOK8 X Defective		(O)	658	298	304	1260	2.545	.27
		(E)	630	315	315			
BOK8 X Defective(R)		(O)	203	95	87	385	1.478	.48
		(E)	192.5	96.25	96.25			

[1]Observed values.

[2]Expected values.

less than one-half the plump class, and for the defective class to be smaller than the intermediate class. These deviations from expected contributed to the low probabilities obtained for some of these crosses. Losses during threshing due to the light weight of the defective seed could have contributed to this deficiency.

The defective gene is detrimental to fitness as evidenced by its very poor germination (15% or less). Considering this the homozygous defective condition could also have caused a shortage of seed with this genotype, as noted in Table II.

It should be mentioned that the genetic background of the plant did effect the expression of the defective trait. The seeds of the Defective(R) endosperm line were not as collapsed as the regular Defective line. This indicated that other genes which affected the morphology of the kernel influenced the expression of the defective character. This expression carried over into the crosses so that the parental type was considered in the classification of the F_2 endosperm types.

Both of the defective endosperm lines used in this study proved to be restorer types. The F_1 plants obtained from pollinations on the male steriles (A Wheatland and AOK8) were fertile. Therefore no backcross data were obtained.

Table III gives the endosperm classification of F_2 plants (F_3 endosperms) obtained from seeds classified for F_2 endosperm (from F_1 plants). These data were a check on the F_2 endosperm classifications. Based upon the genetic controls described for this character seeds classified as defective should have been homozygous (ddd) and thus should have produced plants which were homozygous for the defective endosperm trait. The seeds classified as intermediate should have been

TABLE III

CLASSIFICATION OF ENDOSPERM TYPE OF F_2 PLANTS FROM DEFECTIVE X NORMAL ENDOSPERM CROSSES, PERKINS, 1969

Cross		Type of Seed Planted	Number of Plants Classified as		
Female	Male		Defective	Segregating	Plump
Defective X Wheatland		Defective	32	3[1]	0
(5 heads)		Intermediate	5[1]	88	0
		Plump	0	69	70
Defective X BOK8		Defective	28	9[1]	0
(5 heads)		Intermediate	3[1]	59	3[1]
		Plump	0	70	63
Defective(R) X Wheatland		Defective	63	5[1]	0
(6 heads)		Intermediate	11[1]	60	2[1]
		Plump	3[1]	63	59
Defective(R) X BOK8		Defective	12	2[1]	0
(3 heads)		Intermediate	1[1]	42	0
		Plump	0	61	55
BOK8 X Defective		Defective	14	1[1]	0
(1 head)		Intermediate	2[1]	13	0
		Plump	0	9	11
Wheatland X Defective		Defective	18	0	0
(1 head)		Intermediate	3[1]	12	0
		Plump	0	10	6

[1]Plants which should not have resulted from the indicated type seed.

heterozygous (Ddd) and should have produced plants which segregated for the defective endosperm type. The seeds classified as plump should have been of two types, DDD and DDd, one of which should have given plants homozygous for plump kernels and the other should have given plants with kernels segregating for the defective character. These two types were expected to be in approximately equal proportion. The plants which should not have resulted from the indicated endosperm type are marked with a superscript numeral. These plants could have resulted from seeds which were misclassified for endosperm type, or from hetero-fertilization (21).

When considering the results obtained in Table II and III jointly, the hypothesized mode of inheritance, one factor with incomplete dominance, seemed to fit the data. One would have liked lower chi-square values than obtained for some crosses but in general the values indicated a reasonable fit to the 2:1:1 ratio.

Inheritance of Sugary Endosperm

Sugary endosperm was reported by several workers (1,29,30). All of the researchers found the sugary character in sorghum to be inherited as a simple recessive (su). They noted differences in the morphological expression of the character ranging from very shriveled grain to slightly dimpled types. Since different loci affecting the sugary character had been located in corn (10,14,35), a check on this in sorghum would be of value.

Three different sugary lines, which varied greatly in morphology of plant and seed type, were used in this study. The Sugary(F) line was a typical sugary line with very small shriveled seed and sweet juicy stalks. The other two sugary lines, Sugary(R) and Sugary(W), had less shriveled grain, and usually the seed had a slight dimple in the top and a depressed germ. Each line was crossed to the normal endosperm lines Wheatland and BOK8. In all cases the endosperm of the seed obtained from the emasculated female parent was plump in appearance with a starchy endosperm. The same was true for the seed obtained from the male steriles of A Wheatland and AOK8 when pollinated with any of the three sugary lines. These results indicated that the sugary character was recessive to normal starchy (plump).

Table IV gives the results from classification of the F_2 endosperm of the sugary X normal crosses with chi-square and probability values. The classifications were made on the basis of sugary being inherited as a simple recessive giving a 3:1 ratio of plump to sugary. As noted by the probability values these data gave a good fit to this ratio and confirmed the work which had been reported by others. The values were all very acceptable with the lowest probability value obtained from the Wheatland X Sugary(F) cross (P = .19).

One backcross was made for the sugary cross. An F_1 plant of Sugary(W) X BOK8 was male sterile so pollen was applied from the Sugary(W) parent. Twenty-one seeds were obtained with ten classified as sugary and eleven classified as plump which gave a probability value of 0.87 for a 1:1 expected ratio.

Some of the sugary X normal crosses were very difficult to obtain. Most of the time the Sugary(W) line was male sterile under greenhouse conditions. This was convenient for crosses in which it was the female parent but very difficult for crosses in which it was to be the pollen parent. This same situation often occurred in the field. Frequently the F_1 plants were male sterile under greenhouse conditions. In addition the Sugary(F) line was very difficult to emasculate.

Since the morphological expression of the sugary endosperm character varied so greatly, the three sugary lines were crossed among themselves to check for possible differences among lines in the genes

TABLE IV

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF SUGARY X NORMAL ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes			Values	
Female	Male		Plump	Sugary	Total	χ^2	P
Expected Ratio - 3:1							
Sugary(R)	X Wheatland	(O)[1]	285	105	390	0.769	.40
		(E)[2]	292.5	97.5			
Sugary(R)	X BOK8	(O)	921	307	1228	0.0	1.00
		(E)	921	307			
Sugary(W)	X Wheatland	(O)	1602	514	2116	0.567	.47
		(E)	1587	529			
Sugary(W)	X BOK8	(O)	178	65	243	0.397	.55
		(E)	182.25	60.75			
Sugary(F)	X Wheatland	(O)	2858	915	3773	1.128	.30
		(E)	2829.75	943.25			
Sugary(F)	X BOK8	(O)	2375	828	3203	1.236	.28
		(E)	2402.25	800.75			
Wheatland	X Sugary(R)	(O)	691	248	939	0.997	.32
		(E)	704.25	234.75			
Wheatland	X Sugary(W)	(O)	672	233	905	0.163	.72
		(E)	678.75	226.25			
Wheatland	X Sugary(F)	(O)	1505	546	2051	2.875	.19
		(E)	1538.25	572.75			
BOK8	X Sugary(R)	(O)	682	225	907	0.017	.90
		(E)	680.25	226.75			
BOK8	X Sugary(W)	(O)	755	238	993	0.564	.48
		(E)	744.75	248.25			
BOK8	X Sugary(F)	(O)	419	125	544	1.187	.28
		(E)	408	136			

[1]Observed values.

[2]Expected values.

controlling the character. F_1 plants from Sugary(F) X Sugary(R) and Sugary(F) X Sugary(W) were grown in the greenhouse in the Winter of 1969-70. The seeds from each of the F_1 plants were examined for possible segregation but none was evident, indicating the same gene controlled the sugary trait for all three lines. Stephens (43) reported similar results when he intercrossed three diverse sugary lines. It would appear that other genes not directly concerned with the sugary character modify its expression.

Table V gives the classification of endosperm type of F_2 plants from sugary x normal starchy endosperm crosses. If the sugary endosperm character were conditioned by a completely recessive condition of the su gene, seeds classified as sugary should have given plants all of which were homozygous for the sugary endosperm seed. Eight plants were obtained from these classifications which were segregating for sugary. These seeds must have actually been heterozygous for the su gene. They were misclassified or were the result of heterofertilization.

The seeds classified as plump should have been of three types, SuSuSu, SuSusu, or Sususu. The first genotype should have given plants which were homozygous plump while each of the last two genotypes should have produced plants segregating for the sugary endosperm character. On this basis the seeds classified as plump should have given a two to one ratio of segregating sugary plants to homozygous plump plants and no homozygous sugary plants. The results in Table V agree with this. No homozygous sugary endosperm plants were obtained from plump seed, and the ratios of segregating to homozygous plump endosperm plants were approximately 2:1. These results substantiated the mode of inheritance described for sugary.

TABLE V

CLASSIFICATION OF ENDOSPERM TYPE OF F_2 PLANTS FROM SUGARY X NORMAL ENDOSPERM CROSSES, PERKINS, 1969

Cross		Type of Seed	Number of Plants Classified as		
Female	Male	Planted	Sugary	Segregating	Plump
Sugary(W) X Wheatland		Sugary	24	0	0
(5 heads)		Plump	0	38	15
Sugary(F) X Wheatland		Sugary	45	1[1]	0
(5 heads)		Plump	0	51	26
Sugary(F) X BOK8		Sugary	39	6[1]	0
(3 heads)		Plump	0	33	18
BOK8 X Sugary(R)		Sugary	14	1[1]	0
(1 head)		Plump	0	11	5
Wheatland X Sugary(F)		Sugary	15	0	0
(1 head)		Plump	0	10	6

[1]Plants which should not have resulted from the indicated type seed.

Relationship of Sugary and Defective

All possible crosses were made between the defective endosperm and the sugary endosperm lines to test for linkage and/or any common genetic controls of the two characters. When sugary endosperm lines were emasculated and then pollinated with one of the defective lines, the resulting seed were plump. When one of the defective lines was used as the seed parent and a sugary line was used as the pollen parent, the resulting seed were intermediate endosperm types. These results were expected according to the genotype and expression of the respective endosperm types.

Table VI gives the proposed genotypes and relative frequencies of F_2 endosperm types obtained from sugary X defective crosses under the assumption of single independent gene action. While there were differences in the F_1 endosperm types for reciprocal crosses, the F_2 endosperm types should be essentially the same for crosses in either direction.

TABLE VI

PROPOSED GENOTYPES AND FREQUENCY OF F_2 ENDOSPERM TYPES OBTAINED FROM SUGARY (susu DD) X DEFECTIVE (SuSu dd)

Male Gametes	Female Gametes			
	SuSu DD	susu DD	SuSu dd	susu dd
Su D	SuSuSu DDD[1]	susuSu DDD[1]	SuSuSu Ddd[3]	susuSu Ddd[3]
su D	SuSusu DDD[1]	sususu DDD[2]	SuSusu Ddd[3]	sususu Ddd[2]
Su d	SuSuSu DDd[1]	susuSu DDd[1]	SuSuSu ddd[4]	susuSu ddd[4]
su d	SuSusu DDd[1]	sususu DDd[2]	SuSusu ddd[4]	sususu ddd[5]

[1]Plump endosperm type - 6.

[2]Sugary endosperm type - 3.

[3]Intermediate endosperm type - 3.

[4]Defective endosperm type - 3.

[5]Sugary-defective endosperm type - 1.

The phenotypes given at the bottom of Table VI were expected to be in a ratio of 6:3:3:3:1 assuming no linkage. Due to the difficulty of consistently indentifying all of these phenotypes, some classes were combined. The intermediate and sugary types were put in one class, and the defective and sugary-defective types were combined into one group. The resulting ratio was 6:6:4.

The F_2 endosperm classifications of sugary X defective crosses are given in Table VII. The chi-square probability values indicated a reasonable fit of the data to a hypothesized ratio of 6:6:4. The probability value for one cross, Sugary(W) X Defective, was rather low (.05). All other values were greater than 0.11. Six of the twelve crosses gave chi-square probability values above .50. Since these data gave a good fit to the 6:6:4 ratio no linkage was indicated between the genes controlling these two endosperm types.

Table VIII contains the classification of endosperm type of F_2 plants from sugary X defective crosses. Six plants did not fit the proposed scheme. Seeds classified as defective or sugary-defective should have produced plants with seed that were of the same type as those which were planted. The five plants which were segregating for defective must have actually been intermediate endosperm types. The one plant from plump seed which had sugary endosperm seed must have been misclassified. It apparently was a sugary endosperm type seed or the result of hetero-fertilization. The remainder of the plants had endosperm classifications which fit the genotypes proposed for the seed. The sample size was not large enough to check expected ratios from a given endosperm type seed.

It was very evident that both the defective and the sugary mutants

TABLE VII

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF SUGARY X DEFECTIVE ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes				Values	
Female	Male		Plump	Sugary Intermediate	Sug. Def.[1] Defective	Total	χ^2	P
Expected Ratio - 6:6:4								
Defective X	Sugary(R)	(O)[2]	411	404	251	1066	1.263	.53
		(E)[3]	399.75	399.75	266.5			
Defective X	Sugary(W)	(O)	422	428	295	1145	0.398	.82
		(E)	429.37	429.37	286.25			
Defective X	Sugary(F)	(O)	692	659	470	1821	1.435	.48
		(E)	682.87	682.87	455.25			
Defective(R) X	Sugary(R)	(O)	365	371	231	967	0.659	.72
		(E)	362.63	362.63	241.75			
Defective(R) X	Sugary(W)	(O)	477	461	276	1214	3.608	.16
		(E)	455.26	455.26	303.5			
Defective(R) X	Sugary(F)	(O)	623	616	428	1667	0.443	.84
		(E)	625.13	625.13	416.76			

TABLE VII (Continued)

Cross			Number of Seed in Classes				Values	
Female	Male		Plump	Sugary Intermediate	Sug. Def.[1] Defective	Total	χ^2	P
Sugary(R)	X Defective	(O)	125	130	73	328	1.419	.47
		(E)	123	123	82			
Sugary(R)	X Defective(R)	(O)	418	401	235	1054	4.474	.12
		(E)	395.24	395.24	263.49			
Sugary(W)	X Defective	(O)	1260	1152	842	3254	6.11	.05
		(E)	1220.26	1220.26	813.51			
Sugary(W)	X Defective(R)	(O)	165	146	99	410	1.334	.51
		(E)	153.75	153.75	102.5			
Sugary(F)	X Defective	(O)	250	257	167	674	0.222	.89
		(E)	252.74	252.74	168.49			
Sugary(F)	X Defective(R)	(O)	299	284	192	775	0.408	.82
		(E)	290.63	290.63	193.76			

[1]Sug. Def. = sugary-defective.

[2]Observed values.

[3]Expected values.

TABLE VIII

CLASSIFICATION OF ENDOSPERM TYPE OF F_2 PLANTS FROM SUGARY X DEFECTIVE ENDOSPERM CROSSES, PERKINS, 1969

Cross		Type of Seed Planted	Number of Plants Classified as[1]					
Female	Male		Def. Sug. Def.	Sug.	Seg. Def.	Seg. Sug.	Seg. Both	Plp.
Sugary(W) X Defective (2 heads)		Defective, Sug. Def.	24		5[2]			
		Sugary Intermediate		23	18			
		Plump		1[2]	13	19	14	9

[1]Def., Sug. Def. = defective, sugary defective; Sug. = sugary; Seg. Def. = segregating defective; Seg. Sug. = segregating sugary; Seg. Both = segregating both sugary and defective; Plp. = plump.

[2]Plants which should not have resulted from the indicated type seed.

affected the quantity of carbohydrate present in the endosperm of the sorghum kernel. Also the sugary endosperm is known to greatly alter the kind of carbohydrate present in the endosperm. Researchers in both corn and sorghum have found the sugary endosperm to be much higher in sugars and lower in starch. It is not known at the present time just how the defective gene effects the quality or proportion of various carbohydrates in the endosperm. The iodine test on dissected seed of the defective endosperm type gave a starchy or blue reaction. This indicated that the starch was still in the approximate ratio (amylose to amulopectin) as that of normal kernels or at least had enough amylose present to give the normal or blue reaction to iodine. The small amount of starch which was present in the defective endosperm seeds appeared to be more floury than that found in the normal plump kernels.

Inheritance of Dent Endosperm

The dent (or hollow) endosperm type was selected from the sorghum breeding nursery at Perkins, Oklahoma. The two lines of this type used in this study were selected from the same segregating population. They differed somewhat in the expression of the dent character. The line with white seed, Dent(W), characteristically had a dent in the upper backside of the seed due to a lack of endosperm. The line with red seed frequently did not dent but was hollow instead. No genetic information had previously been reported on this character. Ayyanger (2) reported a hollow seed type found in some material in India, but no genetic information was given on the character.

The two dent endosperm lines were crossed to the two normal endosperm lines, just as with the previous mutant endosperm types.

Reciprocal crosses were made in all instances. The seed obtained from emasculated crosses in either direction had plump or normal endosperms (F_1 endosperms). This indicated the dent character to be recessive to normal endosperm.

Table IX gives the results from classification of F_2 endosperms of the dent X normal endosperm crosses with the chi-square and probability values. The classifications and chi-square tests were based upon the dent endosperm type being inherited as a simple recessive with a 3:1 ratio of plump to dent endosperm seed. The chi-square probability values indicated a reasonable fit to the expected ratio. The BOK8 X Dent(R) cross was the only probability value below .10. On the other hand only two of the crosses, Dent(R) X Wheatland and Wheatland X Dent(W), gave probabilities above .50.

Considerable difficulty was encountered in obtaining several crosses of the Dent(R) parent. It frequently was male sterile under greenhouse conditions and occassionally in the field. F_1 plants from it were also male sterile or partially male sterile for some crosses. Several backcrosses were attempted on these sterile F_1 plants but the dent parent was usually so sterile only a few seeds were obtained. The backcross seeds could be classified into normal and dent endosperm types but not enough seeds were obtained for a chi-square test.

F_2 plants obtained from a BOK8 X Dent(W) cross agreed with the F_2 endosperm data. Of fifteen plants obtained from seeds classified as dent endopserm types only one failed to produce kernels with an expected endosperm. This plant segregated for dent and plump endosperm seeds. Homozygous plump and segregating dent plants were obtained from the seeds classified as having plump endosperm. The ratio of these two

TABLE IX

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF DENT X NORMAL ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross (Female X Male)		Number of Seed in Classes: Plump	Dent	Total	Values: χ^2	P
Expected Ratio - 3:1						
Dent(W) X Wheatland	(O)[1]	686	247	933	1.081	.31
	(E)[2]	699.75	233.25			
Dent(W) X BOK8	(O)	215	86	301	2.048	.16
	(E)	225.75	75.25			
Dent(R) X Wheatland	(O)	242	75	317	0.304	.65
	(E)	237.75	79.25			
Dent(R) X BOK8	(O)	174	71	245	2.069	.16
(2 heads)	(E)	183.75	61.25			
Wheatland X Dent(W)	(O)	879	281	1162	0.372	.56
	(E)	870	290			
Wheatland X Dent(R)	(O)	805	287	1092	0.957	.33
	(E)	819	273			
BOK8 X Dent(W)	(O)	329	123	452	1.180	.29
	(E)	339	113			
BOK8 X Dent(R)	(O)	866	323	1189	2.975	.09
	(E)	891.75	297.25			

[1]Observed values.

[2]Expected values.

types was expected to be close to 2:1 (segregating to homozygous plump) and this was the exact ratio obtained (12:6). These data thus supported the F_2 endosperm classifications and the simple recessive mode of inheritance for the dent endosperm character. The controlling gene could be designated as dt.

Relationship of Dent and Defective

The dent X defective crosses can be explained almost exactly as the sugary X defective endosperm crosses. Both dent and sugary endosperm types were shown to be inherited as simple recessives in the previous discussion. When dent endosperm lines were pollinated (emasculated crosses) with defective endosperm pollen, plump seeds with starchy endosperm resulted. When defective endosperm types were emasculated and pollinated with dent endosperm pollen, intermediate endosperm type seeds were produced. The same difference in F_1 endosperm for reciprocal crosses was noted previously with the defective endosperm type.

For genotype and frequency expectation of F_2 endosperm types obtained from the dent X defective crosses refer to Table VI and substitute the dent genes Dt and dt for the sugary genes Su and su, respectively. The only change would be the description of the phenotypes. The plump, intermediate, and defective endosperm types could be described the same. Instead of sugary endosperm types one would have dent endosperm types, and instead of sugary-defective types there would be dent-defective endosperm types. The expected ratio of the phenotypes would be 6:3:3:3:1 of plump:dent:intermediate:defective:dent-defective. Again difficulty was experienced in completely identifying all those phenotypes so the dents and intermediates were put in one class, and the defectives and dent-defectives were put together in a class. This again altered the ratio to 6:6:4.

The F_2 classification with chi-square and probability values for a 6:6:4 ratio are given in Table X. The chi-square probability values

TABLE X

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF DENT X DEFECTIVE ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes				Values	
Female	Male		Plump	Dent Int.[1]	Dent Def. Def.[2]	Total	χ^2	P
Expected Ratio - 6:6:4								
Defective X Dent(W)		(O)[3]	442	443	304	1189	0.205	.89
		(E)[4]	445.87	445.87	297.24			
Defective X Dent(R)		(O)	473	490	314	1277	0.422	.82
		(E)	478.87	478.87	319.24			
Defective(R) X Dent(W)		(O)	462	482	317	1261	0.436	.81
		(E)	472.87	472.87	315.24			
Defective(R) X Dent(R)		(O)	469	486	206	1261	0.668	.72
		(E)	472.87	472.87	315.24			
Dent(W) X Defective		(O)	430	406	284	1120	0.762	.70
		(E)	420	420	280			
Dent(W) X Defective(R)		(O)	279	263	203	745	2.353	.30
		(E)	279.37	279.37	116.24			
Dent(R) X Defective		(O)	418	425	268	1111	0.515	.79
		(E)	416.63	416.63	277.76			
Dent(R) X Defective(R)		(O)	177	196	129	502	1.023	.62
		(E)	188.26	188.26	125.5			

[1]Int. = intermediate.

[2]Def. = defective.

[3]Observed values.

[4]Expected values.

indicated a good fit for all of the crosses of this type to the expected ratio. These data indicated independent assortment of the factors controlling these characters, and gave additional support to the inhertance described for both the dent and defective endosperm types.

As previously mentioned all of the plump seeds from dent crosses had to be cut with a knife to check for the hollow condition. This was especially necessary for the crosses in which the Dent(R) line was involved because it appeared to have a somewhat thicker and stronger (less brittle) outer corneous endosperm layer than the Dent(W) line did. This could be the reason for the Dent(R) seed not denting as consistently as the seed from the Dent(W) line.

Classifications of endosperm type of F_2 plants from the dent X defective endosperm crosses supported the results of the F_2 endosperm classifications. The genotypes of the embryos of the seeds (classified for F_2 endosperm) planted for these F_2 plants are given in Table XI. The sample of F_2 plants came from a Dent(W) X Defective(R) cross. The seeds that were classified as defective or dent-defective produced thirteen plants with only this type of seed, as expected. Plants from seeds classified as dent or intermediate produced five plants which were segregating for defective endosperm, seven plants homozygous for dent, and five plants segregating for both. The plump seed produced five plants segregating for defective, five plants segregating for dent, six plants segregating for both, and two plants with plump seeds. No unexpected plants occurred.

TABLE XI

EMBRYO GENOTYPES AND RELATIVE FREQUENCY OF SEEDS EXPECTED FOR F_2 ENDOSPERM TYPES FOR DENT X DEFECTIVE CROSSES

Endosperm Type	Embryo Genotype	Relative Frequency
Defective	dd DtDt	1
	dd Dtdt	2
Dent-Defective	dd dtdt	1
		4
Dent	DD dtdt	1
	Dd dtdt	2
Intermediate	Dd DtDt	1
	Dd Dtdt	2
		6
Plump	DD DtDt	1
	DD Dtdt	2
	Dd DtDt	1
	Dd Dtdt	2
		6
	TOTAL = 16	

Relationship of Dent and Sugary

The dent and sugary endosperm types have both been shown to be conditioned by a simple recessive. The phenotypic expressions of the two mutant endosperm types were quite different. There was no real reason to suspect any common genetic controls. The crosses between the two endosperm types were made primarily to check for linkage.

All possible crosses were made among the lines involved, two dent types and three sugary lines. Xenia was noted in the F_1 endosperm for crosses in either direction, with the F_1 endosperm being normal or plump.

Table XII contains the F_2 endosperm classifications of dent X sugary endosperm crosses with chi-square and probability values. The double homozygous recessive phenotype could not be distinguished from the sugary endosperm type, thus they were combined into one class. This made the expected ratio 9:3:4. Eight of the twelve crosses gave responses which agreed with the hypothesized ratio. Four of the crosses gave probability values below the .05 level, which indicated a poor fit. One cross, Dent(R) X Sugary(F), did not fit the hypothesized ratio at all. The probability value for this cross was essentially zero, since the chi-square calculation was 56.59. In all of the crosses except two, Sugary(F) X Dent(W) and Dent(R) X Sugary(R), there was a deficiency of plump endosperm types. This was carried to the extreme in the Dent(R) X Sugary(F) cross. Since plump endosperm seed were recombinants, this would indicate possible linkage. Yet the evidence is not consistent since most of the crosses fit the 9:3:4 ratio. Some other factors may have caused the extreme lack of fit for the Dent(R) X Sugary(F) cross, especially since the reciprocal cross gave a reasonable fit (P = .26).

Looking at the data from the three individual F_1 plants for the Dent(R) X Sugary(F) cross (Appendix C), one of three F_2 samples (one F_1 plant) gave a reasonable fit to the 9:3:4 ratio (P = .12). The other two F_1 plants are the main source of discrepancy. No concrete explanation of this can be offered at the present time.

Table XIII gives the classification of endosperm type of F_2 plants

TABLE XII

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF DENT X SUGARY ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes				Values	
Female	Male		Plump	Dent	$\overline{su}\ \overline{dt}$ Sugary	Total	χ^2	P
Expected Ratio - 9:3:4								
Sugary(R)	X Dent(W)	(O)[1]	581	200	265	1046	0.216	.89
		(E)[2]	588.4	196.13	261.51			
Sugary(R)	X Dent(R)	(O)	273	109	135	517	2.848	.24
		(E)	290.79	96.93	129.24			
Sugary(W)	X Dent(W)	(O)	2567	941	1173	4681	6.231	.04
		(E)	2633.04	877.68	1170.24			
Sugary(W)	X Dent(R)	(O)	49	21	26	96	1.13	.59
(2 heads)		(E)	54	18	24			
Sugary(F)	X Dent(W)	(O)	228	70	84	382	2.223	.33
		(E)	214.9	71.62	95.51			
Sugary(F)	X Dent(R)	(O)	307	119	131	557	2.662	.26
		(E)	313.29	104.43	139.24			
Dent(W)	X Sugary(R)	(O)	437	159	209	805	1.281	.56
		(E)	452.80	150.93	201.24			
Dent(W)	X Sugary(W)	(O)	147	55	64	266	0.666	.72
		(E)	149.65	49.88	66.51			
Dent(W)	X Sugary(F)	(O)	725	298	330	1353	9.651	.01
		(E)	761.04	253.68	338.24			
Dent(R)	X Sugary(R)	(O)	326	114	138	578	0.586	.76
		(E)	325.15	108.38	144.5			
Dent(R)	X Sugary(W)	(O)	478	192	211	881	9.224	.01
		(E)	495.54	156.18	220.24			
Dent(R)	X Sugary(F)	(O)	622	336	348	1306	56.59	0
		(E)	734.65	244.87	326.5			

[1]Observed values.

[2]Expected values.

TABLE XIII

CLASSIFICATION OF ENDOSPERM TYPE OF F_2 PLANTS FROM DENT X SUGARY ENDOSPERM CROSSES, PERKINS, 1969

Cross		Type of Seed Planted	Number of Plants Classified as[1]					
Female	Male		Su. Dt. Sugary	Dent	Seg. Su.	Seg. Dt.	Seg. Both	Plp.
Sugary(W) X Dent(W)		Su. Dt. Sugary	24					
		Dent	4	15				
		Plump		1[2]	11	11	16	7
Sugary(R) X Dent(R)		Su. Dt. Sugary	17					
		Dent	5	14				
		Plump			5	4	6	2
Dent(W) X Sugary(F)		Su. Dt. Sugary	28		1[2]			
		Dent	11	26		1[2]		
		Plump			10	8	12	5

[1]Su. Dt. = sugary dent; Seg. Su. = segregating sugary; Seg. Dt. = segregating dent; Seg. Both = segregating sugary and dent; Plp. = plump.

[2]Plants which should not have resulted from the indicated type seed.

from the dent X sugary endosperm cross. Most of the data in this table supported the 9:3:4 ratio expected for the F_2 endosperms. A few plants, as indicated, occurred which failed to fit the scheme proposed. Only three plants resulted which were not expected from the seed classification indicated. Again these could have been misclassification or the result of heterofertilization. In general the results from this table supported the F_2 endosperm classifications given in Table XII.

Inheritance of Waxy Endosperm

Waxy endosperm refers to those endosperms in which the starch is essentially 100% amylopectin. The normal endosperm of sorghum has starch with about 75% amylopectin and about 25% amylose. The waxy endosperm gives a red color reaction to potassium iodide while the normal or starchy endosperm gives a blue reaction. The results of this test were used in this part of the study to make the endosperm classifications. The seeds were cut approximately in half and the iodide solution applied to the endosperm. Classifications were then made on the color expression.

The inheritance of waxy endosperm was previously reported by Karper (28). This study was conducted to offer further confirmation of this inheritance and to check the relationship of waxy and the other endosperm types involved in this study. The initial check on the inheritance of waxy was obtained from the waxy (Dwarf Redlan) X normal endosperm crosses. The F_1 endosperm of reciprocal crosses gave a blue (starchy) reaction to iodine indicating xenia with waxy as the recessive condition.

Table XIV gives the classifications of F_2 and backcross endosperm

TABLE XIV

CLASSIFICATIONS OF F_2 AND BACKCROSS ENDOSPERM TYPES OF WAXY X NORMAL ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes			Values	
Female	Male		Blue	Red	Total	χ^2	P
Expected Ratio - 3:1							
D. Redlan X Wheatland		(O)[1]	419	127	546	0.881	.35
		(E)[2]	409.5	136.5			
D. Redlan X BOK8		(O)	455	138	593	0.945	.33
		(E)	444.75	148.25			
Wheatland X D. Redlan		(O)	644	203	847	0.483	.78
		(E)	635.25	211.75			
BOK8 X D. Redlan		(O)	327	109	436	0.012	.90+
		(E)	326	110			
Expected Ratio- 1:1							
F_1(A Wheatland X D. Redlan) X D. Redlan		(O)	33	39	72	0.50	.50
		(E)	35.5	35.5			
F_1(A D. Redlan X BOK8) X D. Redlan		(O)	26	22	48	0.334	.60
		(E)	24	24			
F_1(A Wheatland X D. Redlan) X D. Redlan		(O)	46	40	86	0.418	.53
		(E)	43	43			

[1]Observed values.

[2]Expected values.

types of waxy X normal crosses with chi-square calculations. With complete dominance the expected ratio for the F_2 endosperm classifications was 3:1. The first four crosses in the table give information indicating a good fit to this ratio with chi-square probability values ranging from 0.33 to 0.90+.

The next three crosses in Table XIV gave backcross data. In this case male sterile F_1 plants were obtained utilizing male sterile lines. The endosperm types from the backcross were expected to segregate in a 1:1 ratio of blue:red. The backcross of the same type F_1 plant to the normal endosperm parent gave all starchy endosperm (blue). These results supported the simple recessive mode of inheritance for the waxy character, and thus agreed with the original report by Karper (28).

Relationship of Waxy and Defective

Waxy has been shown to be conditioned by a single gene pair. It has been indicated in previous discussion that the defective endosperm type is also conditioned by single gene pair. Crosses were made between the two defective endosperm lines and the waxy endosperm line (Dwarf Redlan) to check for linkage and any type of interaction which might occur between the genes controlling the two traits.

Pollinations with Dwarf Redlan (waxy) on emasculated defective endosperm type plants resulted in intermediate endosperm type seed which were nonwaxy (starchy, blue). The reciprocal cross produced F_1 endosperms which were plump and gave a blue or starchy reaction to the iodine test. These results were expected based on the mode of inheritance for these characters.

Table XV contains the F_2 endosperm classifications from the

TABLE XV

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF WAXY X DEFECTIVE ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes							Values	
			Plump		Intermediate		Defective				
Female	Male		Blue	Red	Blue	Red	Blue	Red	Total	χ^2	P
Expected Ratio - 6:2:3:1:3:1											
Defective	X D. Redlan	(O)[1]	394	121	179	59	188	59	1000	1.869	.86
		(E)[2]	375	125	187.5	62.5	187.5	62.5			
Defective(R)	X D. Redlan	(O)	504	184	250	75	238	65	1316	7.145	.21
		(E)	493.5	164.5	246.75	82.25	246.75	82.25			
D. Redlan	X Defective	(O)	265	87	117	38	127	41	675	1.791	.88
		(E)	253.14	84.38	126.57	42.19	126.57	42.19			
D. Redlan	X Defective(R)	(O)	261	92	129	38	136	40	696	1.513	.90
		(E)	261	87	130.5	43.5	130.5	43.5			

[1]Observed values.

[2]Expected values.

waxy X defective crosses with the chi-square calculations. With complete dominance in one of the characters and incomplete dominance for the other trait, the expected ratio was 6:2:3:1:3:1. This ratio would represent plump(blue):plump(red):intermediate(blue):intermediate(red): defective(blue):defective(red) if the two loci were not linked. The seed were first classified for the defective endosperm character and then the iodine test was applied within each of the classes. The results gave an exceptionally good fit to the expected ratio. The chi-square probability values were close to .90 on three of the four crosses. The .21 probability value obtained for the fourth cross was at an acceptable level. These results indicated that the factors controlling the defective and waxy characters were independently inherited with no apparent linkage, and gave further support to the mode of inheritance previously discussed for the two endosperm types.

The endosperm classifications of F_2 plants from the defective X waxy crosses are given in Table XVI. These data were somewhat inconclusive. The plants marked with a superscript numeral in the table were not expected from the seed type planted. It appeared that some of the seed classified as defective were actually intermediate endosperm types. Five such plants are indicated in the table. The other plant classifications were as expected. Since the defective endosperm seed germinate so poorly, distribution of segregates may be distorted. The results obtained for the F_2 plants did not give strong support to the F_2 endosperm classifications but the data did not completely contradict it either.

The genes controlling waxy and defective appeared to function independently with no noted interactions. Linkage was not indicated,

TABLE XVI

CLASSIFICATION OF ENDOSPERM TYPE OF F_2 PLANTS FROM WAXY X DEFECTIVE ENDOSPERM CROSSES, PERKINS, 1969

Cross		Type of Seed Planted	Number of Plants Classified as[1]								
Female	Male		Def.(B)	Def.(R)	Def.(Seg.)	Seg.(B)	Seg.(R)	Seg.(Both)	Plp.(B)	Plp.(R)	Plp.(Seg.)
Defective X D. Redlan		Def.(B)	1		1	2		1[3]			
		Def.(R)		1			2[3]				
		Int.(B)[2]				5		5			
		Int.(R)					7				
		Plp.(B)				3		5	3		2
		Plp.(R)					4			6	

[1]Def.(B) = defective(blue); Def.(R) = defective(red); Def.(Seg.) = defective(segregating blue and red); Seg.(B) = segregating defective(blue); Seg.(R) = segregating defective(red); Seg.(Both) = segregating defective, blue and red; Plp.(B) = plump blue; Plp.(R) = plump red; Plp.(Seg.) = plump, segregating blue and red.

[2]Int. = intermediate.

[3]Plants which should not have resulted from the indicated type seed.

nor was epistasis of any kind. Defective-waxy types were observed at the expected frequency.

Relationship of Waxy and Sugary

The waxy endosperm type was also crossed with the three sugary endosperm lines, including reciprocals. When either endosperm type was emasculated, the resulting F_1 seeds from cross pollinations were plump. Xenia was thus expressed for both endosperm types. Sugary(R) and Sugary(W) lines also produced starchy F_1 endosperm when crossed with Dwarf Redlan. This was expected since each mutant endosperm type was expected to be carrying the normal dominant allele of the other endosperm type.

The waxy X Sugary(F) crosses were plump, however they were waxy, rather than starchy. This indicated that the Sugary(F) line must also carry the alleles for waxy (*wx*). The genotype of the Sugary(F) thus appeared to be *sususu wxwxwx* rather than *sususu WxWxWx*.

The results of the F_2 endosperm classifications of waxy X sugary are given in Table XVII. The initial hypothesis was to expect a 9:3:4 ratio of plump starchy(blue):plump waxy(red):sugary. The sugary classification or last category consisted of the sugary genotype *sususu Wx--* plus the double homozygous recessive genotype *sususu wxwxwx*. Of the six crosses indicated in the table, only two, Sugary(W) X Dwarf Redlan and its reciprocal gave a reasonable fit to the 9:3:4 ratio. The crosses with Sugary(F) gave a 3:1 ratio of plump waxy to sugary with no apparent segregation for the waxy condition. E_1 is the expected value for the 9:3:4 hypothesis, and E_2 is the expected values for the 3:1 ratio.

TABLE XVII

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF WAXY X SUGARY ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes				Values	
			Plump		Sugary			
Female	Male		Blue	Red		Total	χ^2	P
E_1 = Expected Ratio of 9:3:4								
E_2 = Expected Ratio of 3:1								
Sugary(R)	D. Redlan	(O)[1]	572	87	230	889		
		(E_1)	500.05	166.68	222.24		48.71	<.001
		(E_2)	666.74		222.24		0.279	.87
Sugary(W)	D. Redlan	(O)	248	75	110	433	0.581	.76
		(E_1)	243.54	81.18	108.24			
Sugary(F)	D. Redlan	(O)	---	612	194	806	0.372	.58
		(E_2)	---	604.5	201.5			
D. Redlan	Sugary(R)	(O)	849		272	1121	0.324	.60
		(E_2)	840.75		280.25			
D. Redlan	Sugary(W)	(O)	346	117	143	605	0.606	.75
		(E_1)	340.29	113.43	151.24			
D. Redlan	Sugary(F)	(O)	---	1150	349	1409	0.04	.87
		(E_2)	---	1056.75	352.25			

[1]Observed values.

The two crosses of Sugary(R) X Dwarf Redlan did not produce the expected results. On the basis of F_1 endosperm classifications for this cross the expected F_2 ratio was 9:3:4, just as obtained for the Sugary(W) X Dwarf Redlan crosses. However, the plump seed had a deficiency of the waxy (red) endosperm types (top line in Table XVII). The sugary type gave no detectable reaction to the iodine test so waxy types (double homozygous recessives) were not identified. In the recriprocal cross, Dwarf Redlan X Sugary(R), the same results were obtained. Only a sample of the 849 plump seeds were classified for waxy. From this sample 297 seeds were classified as starchy (blue), and 32 seeds were classified as having waxy (red) endosperms. The results again indicated a great shortage of the waxy types. Both of the crosses gave a reasonable fit to a 3:1 ratio for plump:sugary with chi-square probability values of 0.87 and 0.60, respectively.

A definite explanation of the shortage of waxy endosperm seeds from the Sugary(R) crosses was not obvious. Linkage would have resulted in an excess of waxy types since the waxy parent was plump, but this was not the case. There could have been some type of genetic interaction with some locus or loci other than the sugary locus. If this was the case the other sugary lines must have been of a different genotype for the interaction locus (loci). Some researchers (39) have identified "controlling element alleles" which alter the expression of the waxy character in corn. It could be that some other genes of this nature were operating, although they have not been previously reported in sorghum. It could have been that an embryonic lethal was involved causing the shortage of the waxy types in this particular cross.

The waxy locus has been shown to be rather complex in corn (39,18). More than one allele has been identified and located within the "locus". It could be that the waxy locus in sorghum is just as complex. Several different waxy lines would be needed to determine such a condition.

Relationship of Waxy and Dent

Reciprocal crosses were made between Dwarf Redlan (waxy) and the two dent endosperm lines. The crosses of the dent lines as seed parents showed xenia with the F_1 endosperm being plump and starchy. The reciprocal crosses produced plump, starchy seed also.

On the basis of the F_1 endosperm response and the previous information on the mode of inheritance of the two endosperm types the expected ratio for the F_2 was 9:3:3:1, assuming independent segregation of two loci with complete dominance. Table XVIII gives the results obtained from F_2 endosperm classifications. Of the four crosses indicated in the table only one, Dent(R) X Dwarf Redlan, gave a reasonable fit to the 9:3:3:1 ratio with a chi-square probability value of 0.32. The sample size for this cross was quite small compared to the other crosses. Calculations for a 3:1 (plump:dent) ratio gave acceptable fits for all crosses except for the Dwarf Redlan X Dent(W) which had a chi-square probability of 0.001.

The results obtained from these crosses were very similar to those from the waxy X Sugary(R) crosses described in the previous section. There was a substantial shortage of the waxy endosperm types. These waxy X dent crosses allowed classification of the double mutant, dent and waxy, endosperm type which was not identifiable in the waxy X sugary crosses. A shortage of waxy types similar to that noted in the plump class for the waxy X sugary crosses occurred in both the plump and dent classes for the waxy X dent crosses in all cases. Again no satisfactory explanation can be offered for these results. It appears that the same factors causing the waxy shortage in the sugary cross may be influencing the results in the waxy X dent crosses since the ratios of normal

TABLE XVIII

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF WAXY X DENT ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross: Female	Cross: Male		Number of Seed in Classes: Plump: Blue	Plump: Red	Dent: Blue	Dent: Red	Total	Values: χ^2	Values: P
E_1 = Expected Ratio of 9:3:3:1									
E_2 = Expected Ratio of 3:1									
Dent(W) X D. Redlan		(O)[1]	194	24	69	10	297		
		(E_1)	167.06	55.68	55.69	18.56		>16.27	<.001
		(E_2)	222.75		74.25			0.405	.54
Dent(R) X D. Redlan		(O)	43	7	11	4	65		
		(E_1)	36.55	12.18	12.18	4.06		3.46	.32
		(E_2)	48.73		16.24			0.128	.73
D. Redlan X Dent(W)		(O)	889	128	370	42	1429		
		(E_1)	803.80	267.94	267.94	89.31		>16.27	<.001
		(E_2)	1071.75		357.25			11.19	.001
D. Redlan X Dent(R)		(O)	270	32	105	12	419		
		(E_1)	235.71	78.57	78.57	26.19		>16.27	<.001
		(E_2)	314.25		104.75			1.911	.18

[1]Observed values.

starchy to waxy are very similar. The ratios ranged from near 7:1 to about 9:1 (starchy:waxy) for both waxy X sugary and waxy X dent crosses. If another locus or loci caused the shortage of waxy types, the two dent lines could be the same or similar to the Sugary(R) line in genotype at these loci.

Two backcrosses on male sterile F_1 plants (Dent(R) X Dwarf Redlan) with Dwarf Redlan pollen were made. The seeds obtained were all plump and segregating for waxy. One cross gave 33 starchy (blue) endosperm seeds and 45 waxy (red) endosperm seeds with a chi-square probability of 0.18 for a 1:1 ratio. The other backcross gave 44 starchy and 48 waxy and a chi-square probability of 0.70 for the 1:1 ratio. These data gave support to the simple recessive mode of inheritance for the waxy character. Backcrosses were not made using the dent endosperm type. The dent parent was also male sterile at the particular time the male sterile F_1 plants were available in the greenhouse.

The overall results obtained from the waxy endosperm crosses were not consistent for all crosses. The waxy X normal and waxy X defective crosses gave results which indicated the waxy character was controlled by a simple recessive gene. The waxy X sugary and waxy X dent endosperm crosses cast some doubt on the simple recessive inheritance as giving a complete explanation of the situation. From these latter crosses it appeared that some other genes must have been interacting with the waxy locus to cause a shortage of the waxy type.

Inheritance of Yellow Endosperm

Crosses were made with two yellow endosperm lines, ROKY16 and BOKY29, to study the inheritance of carotenoid pigments in sorghum. In order to study the responses of these crosses color standards of endosperm types in a scale ranging from one to eight were established, with one having the least amount and eight having the greatest amount of carotenoid pigments. Category one of these standards was composed of seeds from Dwarf Redlan, which appeared very white when pearled. Category two was composed of pearled seeds from B Wheatland, and these seeds showed a very slight expression of yellow. The third standard category was obtained from seeds of A Wheatland X BOKY29 pollinations (F_1 endosperm, one dose yellow). The fourth category was seeds from the reciprocal cross of the seeds in category three or AOKY29 X B Wheatland (two doses yellow). The fifth category was seeds from F_1 (A Wheatland X BOKY29) X BOKY29, or a heterozygous yellow F_1 plant backcrossed to the yellow parent (averages two doses of yellow). Category six was composed of seeds from the ROKY16 parent. The seventh category was kernels from the BOKY29 parent. The final class was also BOKY29 but the seeds were grown under greenhouse conditions which gave more pigmentation and smaller kernels.

Worzella et al. (54) indicated beta-carotene in grain sorghum to be controlled by relatively few genetic factors. They used an F_2 generation to find a positive correlation between endosperm color and beta-carotene content. Their results gave F_2 segregates which ranged between the parental values for carotene but a preponderance of the segregates were lower in beta-carotene than the midparent value.

As noted by the composition of the eight categories previously discussed, xenia was noted in pollinations with yellow endosperm parents. When nonyellow endosperm parents were pollinated with yellow endosperm lines, yellow coloration resulted in the crossed seed. And when yellow endosperm parents were pollinated with nonyellow lines, a reduction of pigment resulted in the crossed seed. These results indicated that dominance, if present, was not complete.

Figures 1 and 2 give the data obtained from the classification of F_2 endosperm from the yellow X normal crosses. The horizontal axis represents the eight yellow endosperm classes, as previously described. The vertical axis represents the number of seed in any given category. Figure 1 exhibits the distribution obtained from reciprocal crosses of Wheatland X ROKY16. The results were essentially the same no matter which line was used as the female parent. The mode for both crosses was class three. The cross in which ROKY16 (yellow parent) was the seed parent gave slightly more individuals above the mode, relatively, than did the reciprocal cross. The cross in which ROKY16 was the seed parent gave one segregate in category eight, while the reciprocal cross gave more in class eight.

The parental values for carotenoid pigments were class two for Wheatland and class six for ROKY16. Since the midparent value would be class four and the mode was class three, slight dominance is indicated in the direction of Wheatland, which has less carotenoid expression (nonyellow).

Figure 2 represents the results obtained from the Wheatland X BOKY29 crosses. The crosses in which BOKY29 was the female parent gave a higher frequency of individuals in classes having more yellow. The mode for the cross in which BOKY29 was female was class five while the mode for the reciprocal cross was class three. This suggested possible maternal effects of the BOKY29 parent carrying through to the F_2 segregates. A more likely explanation could be environmental influences.

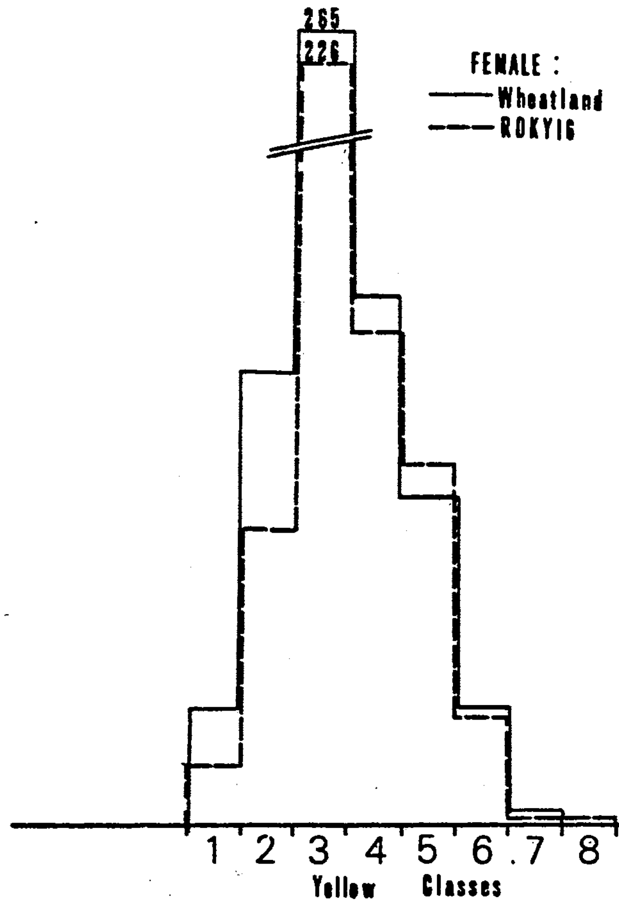

Figure 1. Histogram of Yellow Endosperm Classes for F_2 of Wheatland and ROKY16 Crosses

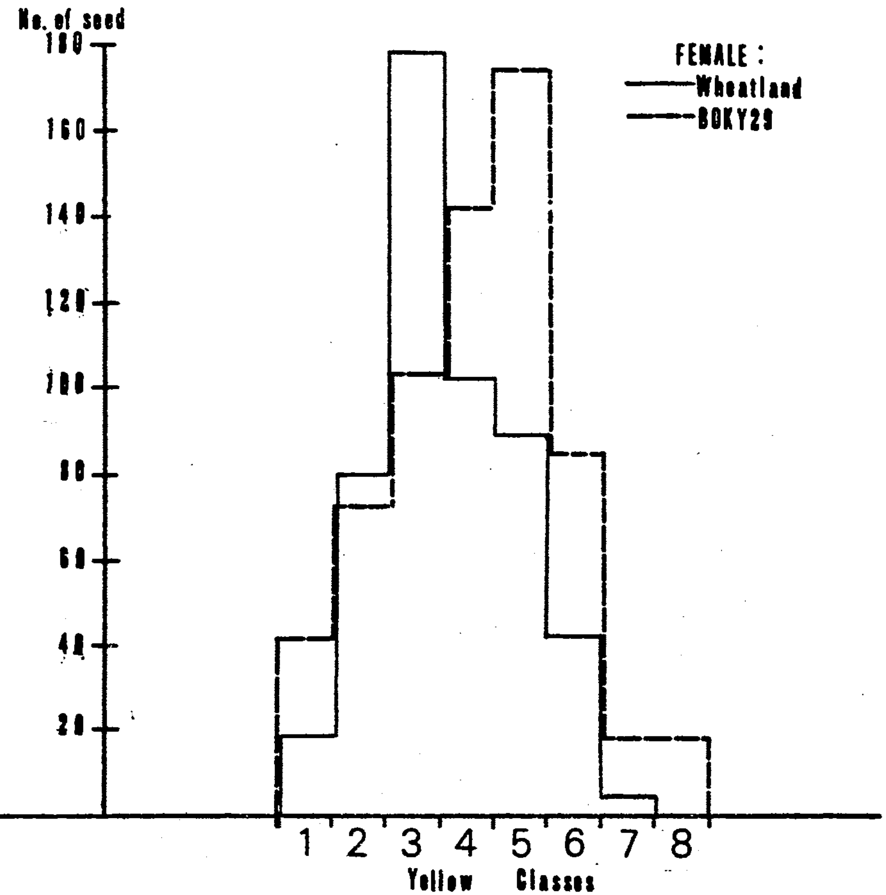

Figure 2. Histogram of Yellow Endosperm Classes for F_2 of Wheatland and BOKY29 Crosses

Two of the F_1 heads for the Wheatland X BOKY29 cross were obtained from the 1968-69 greenhouse and the third head was from the 1969 field. All three of the F_1 heads from the reciprocal cross were obtained from the 1969 field. Yet the one F_1 plant for the Wheatland X BOKY29 cross obtained from the 1969 field planting had a mode of class three.

BOKY29 had a class rating of seven or eight and Wheatland had a class two rating. This would give a midparent value of 4.5. The F_2 segregates from the crosses with these two parents gave a greater number of seeds having a rating lower than the midparent value, just as in the Wheatland X ROKY16 crosses. This again indicated some dominance in the direction of nonyellow.

Considering the results obtained from crosses of Wheatland with both yellow endosperm parents it would appear that Wheatland and the yellow parents differ by more than one gene, and probably more than two genes, for yellow endosperm. There seemed to be a slight expression of dominance in favor of the nonyellow condition. All crosses gave segregates in a class lower than the low parent class. Three of the crosses gave segregates higher than the class of the high parent. This indicated the possibility of Wheatland having some factors for yellow not common to either yellow endosperm parent.

Figures 3 and 4 give the F_2 results obtained from crosses of BOK8 with the two yellow endosperm parents. BOK8 fell in the same yellow endosperm class as Wheatland, class two, and the results obtained from classification of the F_2 endosperm from the BOK8 crosses were very similar to those from Wheatland. The one exception was the BOK8 cross with BOKY29 in which the yellow endosperm line was used as the female parent. This latter cross had a mode of class three while the crosses of BOKY29

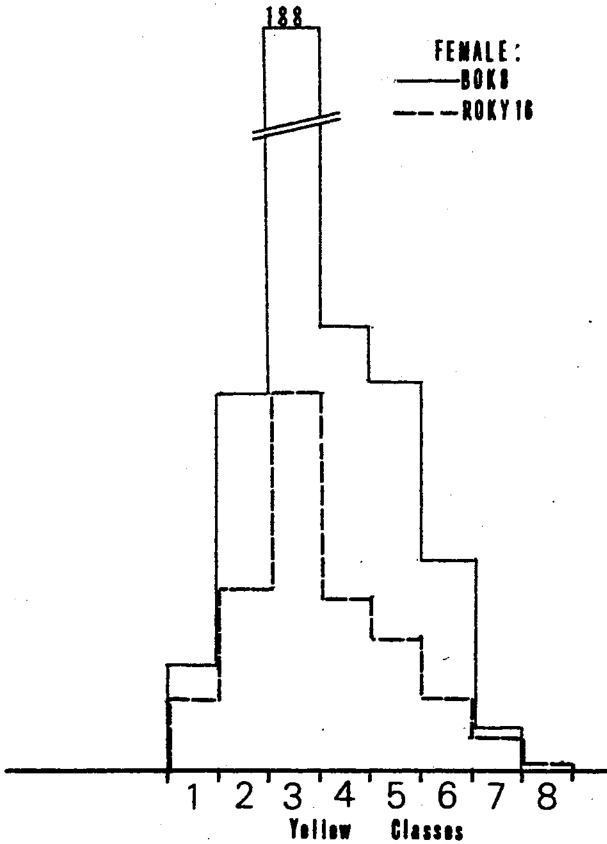

Figure 3. Histogram of Yellow Endosperm Classes for F_2 of BOK8 and ROKY16 Crosses

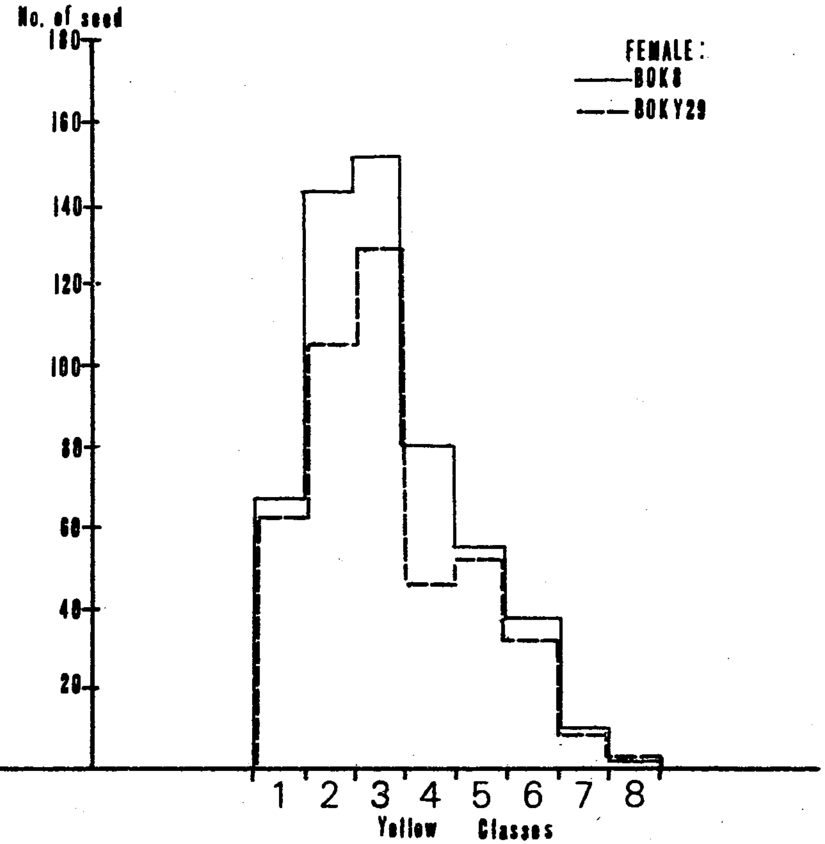

Figure 4. Histogram of Yellow Endosperm Classes for F_2 of BOK8 and BOKY29 Crosses

with Wheatland had a mode of five. One difference was that all crosses involving BOK8 and BOKY29 (F_1 plants) were grown in the 1968-69 greenhouse. A much larger number of class one segregates were obtained from the BOK8 and BOKY29 crosses than from the BOKY29 crosses with Wheatland.

The mode for all types of crosses of BOK8 with the two yellow endosperm parents was class three. This again agreed with three of the four crosses of Wheatland with the yellow endosperm lines. The difference between frequencies of class two segregates and class three segregates was not as great for the BOK8 and BOKY29 cross as that noted for the other normal X yellow endosperm crosses. The same slight tendency of dominance toward nonyellow was indicated in the BOK8 crosses with the yellow endosperm lines as was noted in the Wheatland crosses. The gene action for the expression of yellow endosperm seemed to be essentially the same, except possibly for the cross involving the BOKY29 line as the female parent.

Relationship of Yellow and Defective

Crosses were made between the defective endosperm lines and the yellow endosperm lines. Since the yellow endosperm lines have basically normal type endosperms (plump, starchy), the crosses with the defective endosperm lines gave essentially the same results for F_1 and F_2 endosperm information concerning the defective character as found with the normal X defective crosses. The F_1 endosperms showed a reciprocal difference with emasculated defective plants giving intermediate F_1 endosperms when pollinated with ROKY16 or BOKY29 and the reciprocal crosses giving plump (normal) endosperm seeds.

Table XIX gives the results obtained from classification of F_2

TABLE XIX

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF DEFECTIVE X YELLOW ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes				Values	
Female	Male		Plump	Intermediate	Defective	Total	χ^2	P
Expected Ratio - 2:1:1								
Defective X ROKY16		(O)[1]	3335	1625	1668	6628	0.824	.67
		(E)[2]	3314	1657	1657			
Defective X BOKY29		(O)	845	406	376	1627	3.546	.16
		(E)	813.5	406.75	406.75			
Defective(R) X ROKY16		(O)	585	293	254	1132	3.963	.13
		(E)	566	283	283			
Defective(R) X BOKY29		(O)	735	382	328	1445	4.465	.11
		(E)	722.5	361.25	361.25			
ROKY16 X Defective		(O)	623	293	275	1191	3.084	.21
		(E)	595.5	297.75	297.75			
ROKY16 X Defective(R)		(O)	437	208	187	832	3.18	.20
		(E)	416	208	208			
BOKY29 X Defective		(O)	753	343	363	1459	2.031	.41
		(E)	729.5	364.75	364.75			
BOKY29 X Defective(R)		(O)	283	119	111	513	5.752	.06
		(E)	256.5	128.25	128.25			

[1]Observed values.

[2]Expected values.

endosperm types of defective X yellow endosperm crosses relative to defective, intermediate, or plump endosperm. The results were essentially the same as previously reported for the defective X normal endosperm crosses. The chi-square probability values indicated a reasonable fit to the proposed 2:1:1 ratio of plump:intermediate:defective in nearly all cases. The BOKY29 X Defective(R) cross gave a chi-square probability value of .06 which was rather low, but it was comparable to some of the values obtained from the defective X normal crosses.

The defective endosperm type pearled very poorly, but pearled samples of the defective endosperm parents indicated that they had some yellow endosperm. The seeds from any given sample seemed to vary more than would be expected from environmental causes, especially for the Defective(R) line. The two defective endosperm lines were rated as class four to five for yellow endosperm. F_1 endosperms from crosses of defective and yellow endosperm parents expressed yellow pigmentation.

For F_2 seed classifications of yellow endosperm from the defective X yellow endosperm crosses, only the plump seeds were pearled, since the mutant type kernels pearled poorly. The results for the F_2 endosperm classifications for defective X yellow endosperm crosses are given in Figures 5 - 8.

Figure 5 gives the results obtained from the Defective X ROKY16 crosses. The mode for the cross in which the Defective line was the female parent was class four while the reciprocal cross gave a mode of class five. One should note that both of these values were greater than the normal endosperm (Wheatland, BOK8) crosses with ROKY16. This clearly indicated the Defective line had more carotenoid pigments than Wheatland or BOK8. One should also note that segregates were obtained

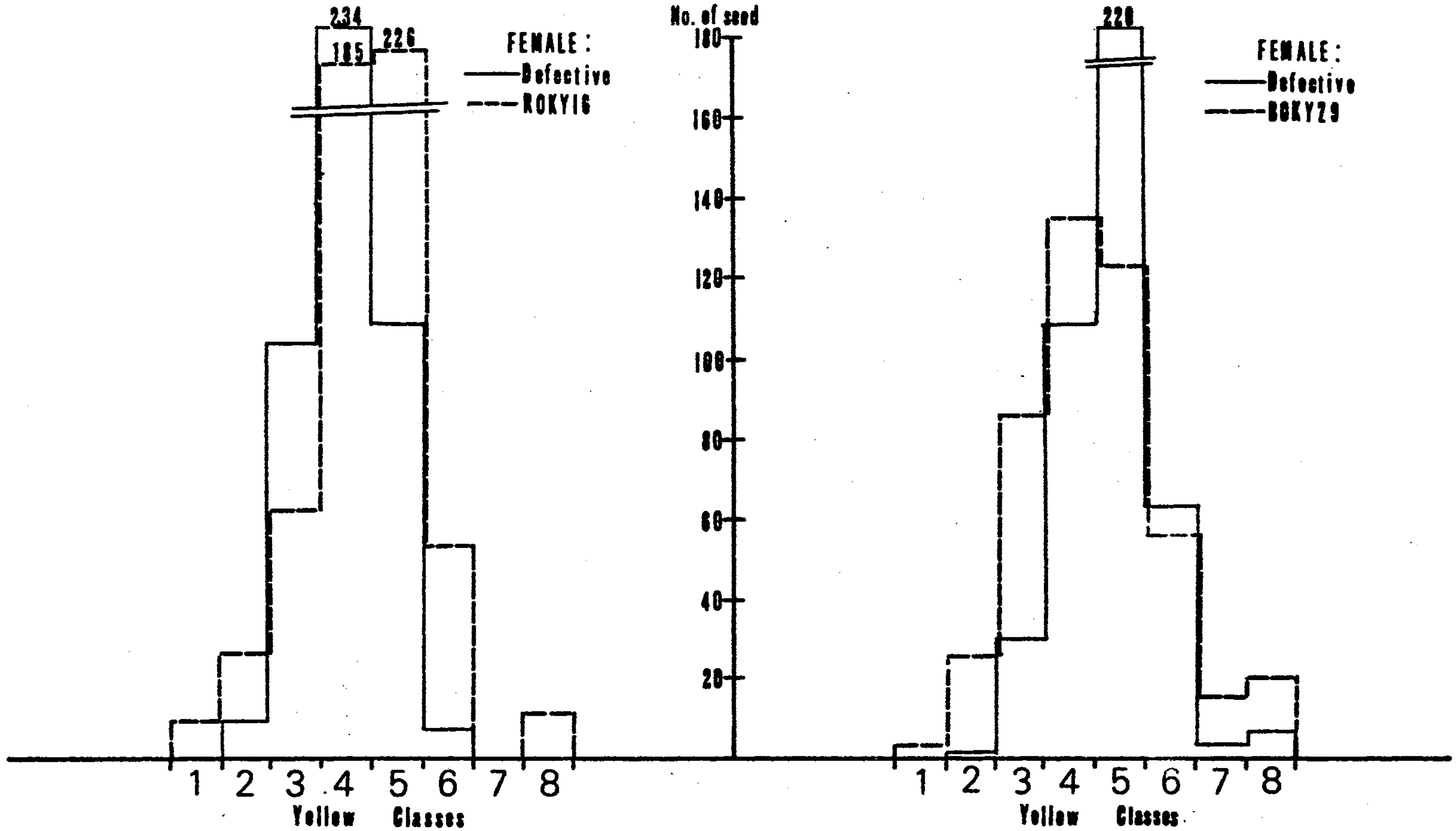

Figure 5. Histogram of Yellow Endosperm Classes for F_2 of Defective and ROKY16 Crosses

Figure 6. Histogram of Yellow Endosperm Classes for F_2 of Defective and BOKY29 Crosses

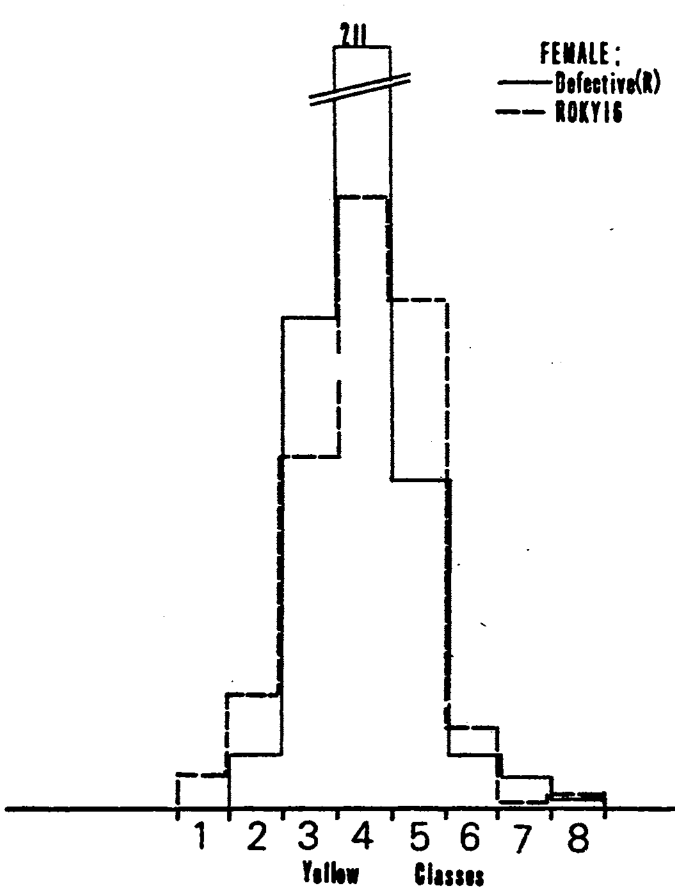

Figure 7. Histogram of Yellow Endosperm Classes for F_2 of Defective(R) and ROKY16 Crosses

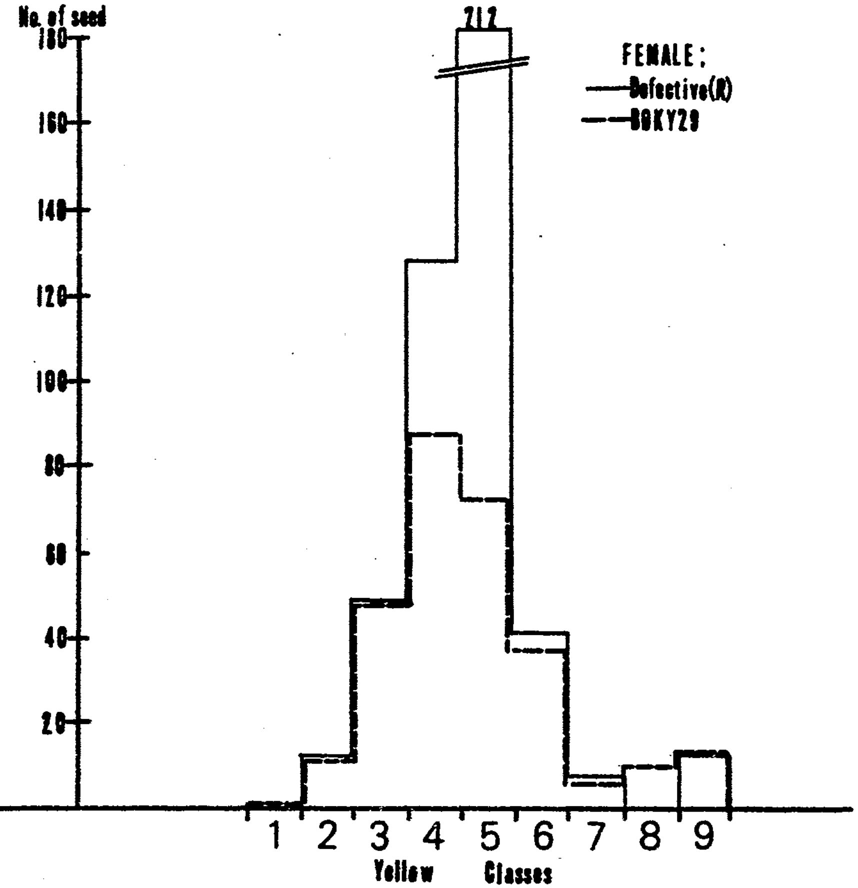

Figure 8. Histogram of Yellow Endosperm Classes for F_2 of Defective(R) and BOKY29 Crosses

both above and below the parental values distributed over the full range of classes. This indicated that the parental lines had some different factors for yellow endosperm. Since the Defective parent was classified as a class four or five and the modes were four and five there is still evidence of some dominance in the direction of nonyellow.

Figure 6 shows the results obtained from the Defective X BOKY29 crosses. The results were essentially the same as for the ROKY16 crosses except that the two modes were switched. When the Defective parent was the female a mode of class 5 was obtained, and a class four mode was obtained for the reciprocal cross.

Figures 7 and 8 give the results for the Defective(R) crosses with ROKY16 and BOKY29, respectively. These results were very similar to the results obtained from the Defective crosses with the yellow endosperm lines. There were two main differences noted. The mode of the ROKY16 X Defective(R) cross was a class four compared to a class five for the ROKY16 X Defective. The second difference indicated was that the BOKY29 X Defective(R) cross gave some segregates which rated higher than the highest class established. It is possible that some of the segregates noted as class eight for the BOKY29 X Defective cross should have actually been rated higher.

The defective X yellow endosperm crosses gave distributions similar to those obtained from the normal X yellow endosperm crosses. The main differences between these two types of crosses was that the crosses involved with the defective endosperm lines gave a more peaked distribution of individuals and a higher mode. These results might have been expected since the defective lines rated higher (class four to five) than the normal endosperm lines (class two). In both types of crosses segregates were obtained out of the range set by the parental class values and some dominance was indicated in the direction of nonyellow.

Relationship of Yellow and Sugary

Crosses were made between the sugary endosperm lines and the two yellow endosperm lines. The results obtained from these crosses concerning plump or normal vs sugary endosperm were essentially the same as the results from the sugary X normal endosperm crosses. The F_1 endosperm was plump for reciprocal crosses with all of the lines. The xenia response of seed from sugary plants pollinated with one of the yellow endosperm parents was noted, as expected.

The results obtained from F_2 endosperm classifications of the sugary X yellow endosperm crosses are given in Table XX. The chi-square probability values indicated an excellent fit to the 3:1 ratio of plump (normal) to sugary. All probability values except one were above .50. This further substantiated the results obtained from the simple recessive mode of inheritance for the sugary endosperm character.

The same procedure for classification of seed for the expression of yellow endosperm was followed as described for the defective X yellow endosperm crosses. Only a sample of the plump kernels from segregating heads were pearled and classified for the presence of carotenoid pigments since the sugary endosperm types also pearled very poorly.

A sample of seed was pearled from each of the sugary endosperm parents to estimate the amount of carotenoid pigments present. Evaluation of these kernels for this character was very difficult since they were rather translucent, high in sugars, and low in starch. The estimated class for the three lines was class one or two. The F_1 endosperms

TABLE XX

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF SUGARY X YELLOW ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes			Values	
Female	Male		Plump	Sugary	Total	χ^2	P
Expected Ratio - 3:1							
Sugary(R)	X ROKY16	(O)[1]	283	97	380	0.056	.86
		(E)[2]	285	95			
Sugary(R)	X BOKY29	(O)	712	246	958	0.235	.65
		(E)	718.5	239.5			
Sugary(W)	X ROKY16	(O)	5952	2000	7952	0.096	.79
		(E)	5964	1988			
Sugary(W)	X BOKY29	(O)	30	12	42	0.285	.62
		(E)	31.5	10.5			
Sugary(F)	X ROKY16	(O)	602	197	799	0.051	.86
		(E)	599.25	199.75			
Sugary(F)	X BOKY29	(O)	1502	495	1997	0.048	.87
		(E)	1497	499.25			
ROKY16	X Sugary(R)	(O)	692	230	922	0.001	.90+
		(E)	691.5	230.5			
ROKY16	X Sugary(W)	(O)	836	290	1126	0.343	.60
		(E)	844.5	281.5			
ROKY16	X Sugary(F)	(O)	1374	460	1834	0.007	.90+
		(E)	1375.5	458.5			
BOKY29	X Sugary(R)	(O)	295	92	387	0.311	.64
		(E)	290.25	96.75			
BOKY29	X Sugary(W)	(O)	415	154	569	1.295	.25
		(E)	426.75	142.25			
BOKY29	X Sugary(F)	(O)	1577	534	2111	0.099	.76
		(E)	1583.25	527.75			

[1]Observed values.

[2]Expected values.

from the crosses of the three sugary lines with the yellow endosperm parent showed only a slight expression of yellow endosperm (class two or three). There was a slight reciprocal difference between F_1 endosperms for crosses in which the yellow endosperm line was used as the seed parent compared to when it was used as the pollen parent. When the yellow endosperm line was used as the seed parent the resulting seeds gave a greater expression of yellow.

Figures 9 through 14 give the results obtained from classifications of the F_2 endosperm of the sugary X yellow crosses for presence of carotenoid pigments. Overall the results obtained were very comparable to the results obtained from the normal X yellow endosperm crosses. The mode for all crosses of sugary X yellow endosperm was class three. This was the same value as noted for all but one of the normal X yellow crosses. The relative distributions were also similar. There was some indication of a lower frequency of class seven and eight segregates. Only one of the sugary X yellow endosperm crosses (BOKY29 X Sugary(F)) gave any class eight segregates. There were no reciprocal differences as noted for the Wheatland X BOKY29 crosses. The Sugary(W) X ROKY16 crosses and reciprocals gave only five classes of segregates, thus not as much variability as noted for the other crosses.

The overall results of the sugary X yellow endosperm crosses indicated that the three sugary lines had a comparable amount of carotenoid pigments. They probably rated a class one or two and would be rather low in carotenoids if chemically analyzed. The expression of yellow endosperm based upon the F_2 data indicated that they were similar to Wheatland and BOK8 in cartenoid content or somewhat lower. If they actually did fall in class one, the expression of dominance was not as

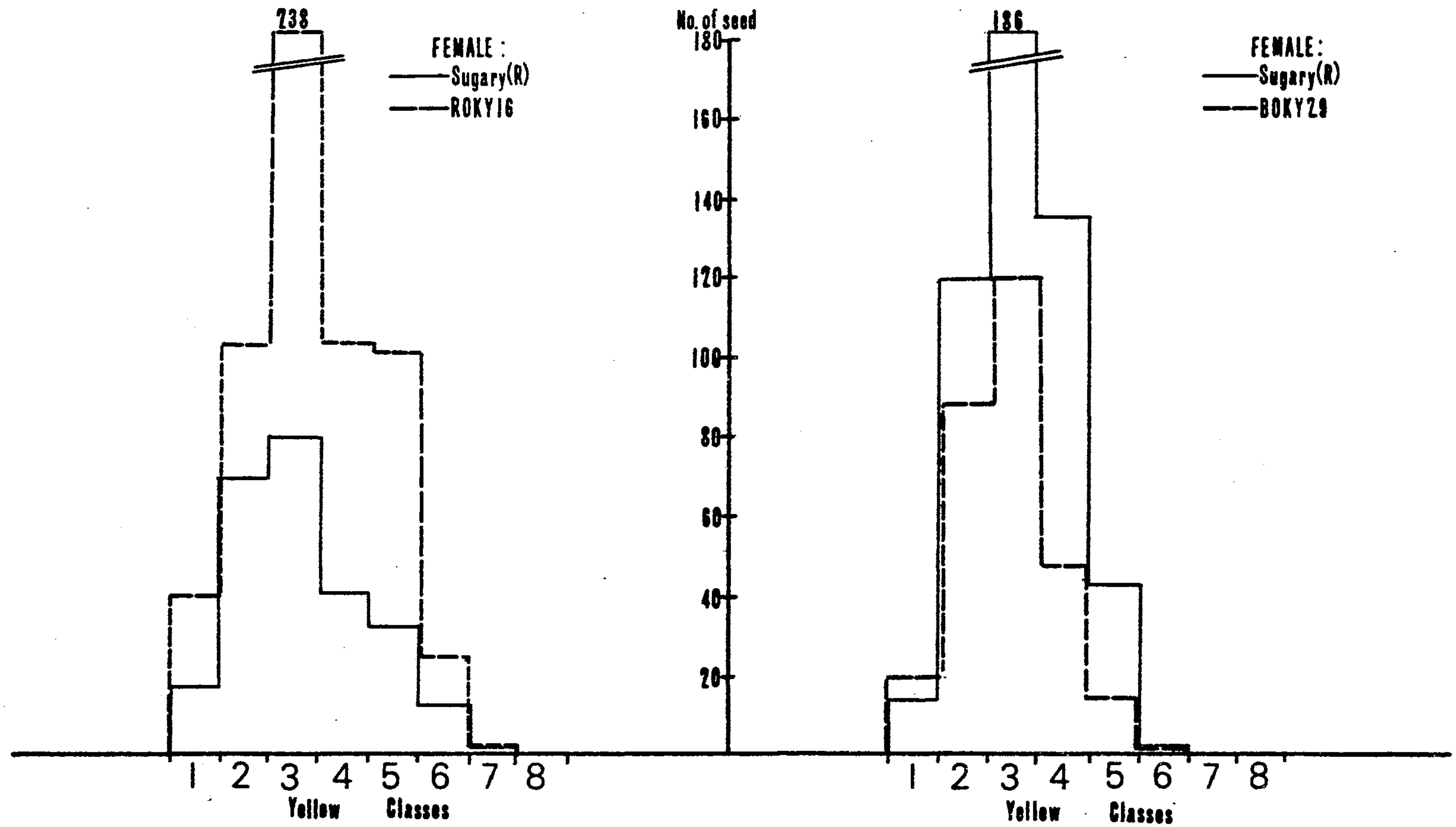

Figure 9. Histogram of Yellow Endosperm Classes for F_2 of Sugary(R) and ROKY16 Crosses

Figure 10. Histogram of Yellow Endosperm Classes for F_2 of Sugary(R) and BOKY29 Crosses

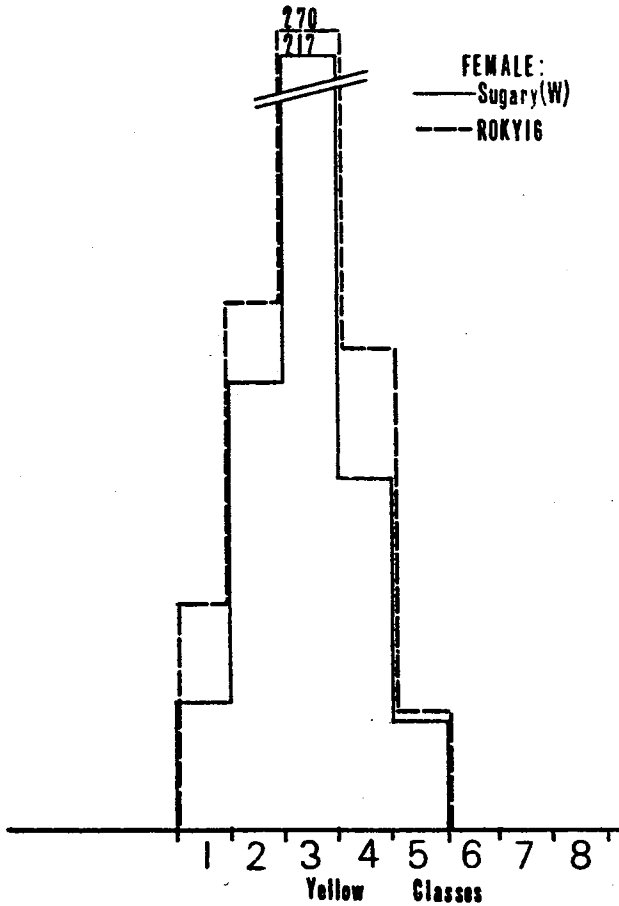

Figure 11. Histogram of Yellow Endosperm Classes for F_2 of Sugary(W) and ROKY16 Crosses

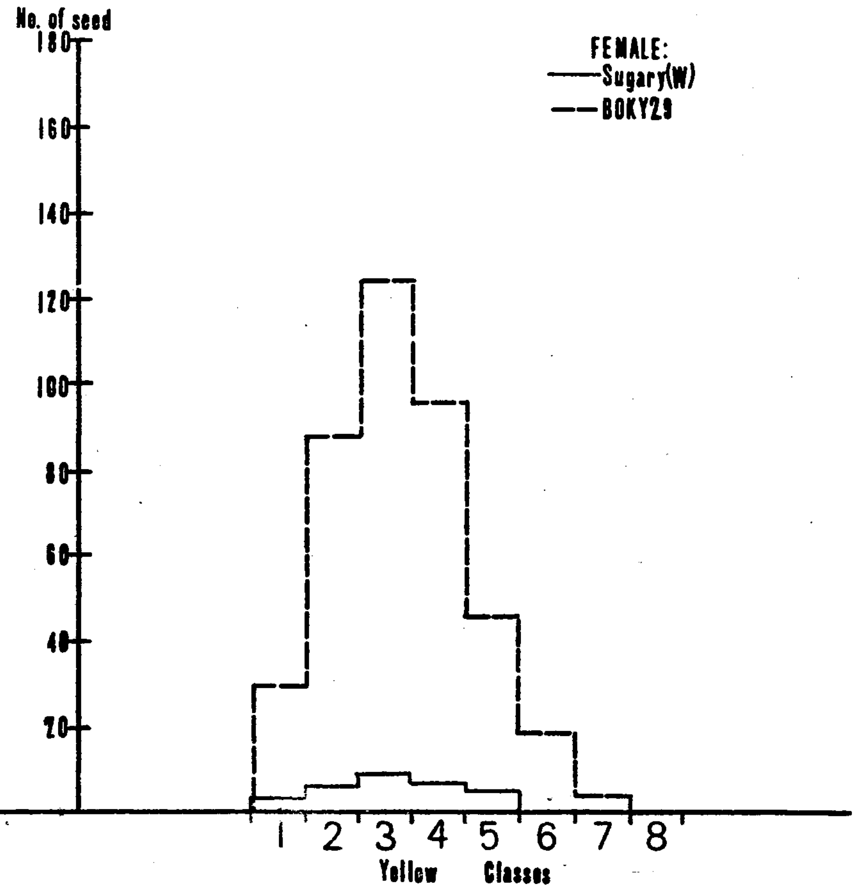

Figure 12. Histogram of Yellow Endosperm Classes for F_2 of Sugary(W) and BOKY29 Crosses

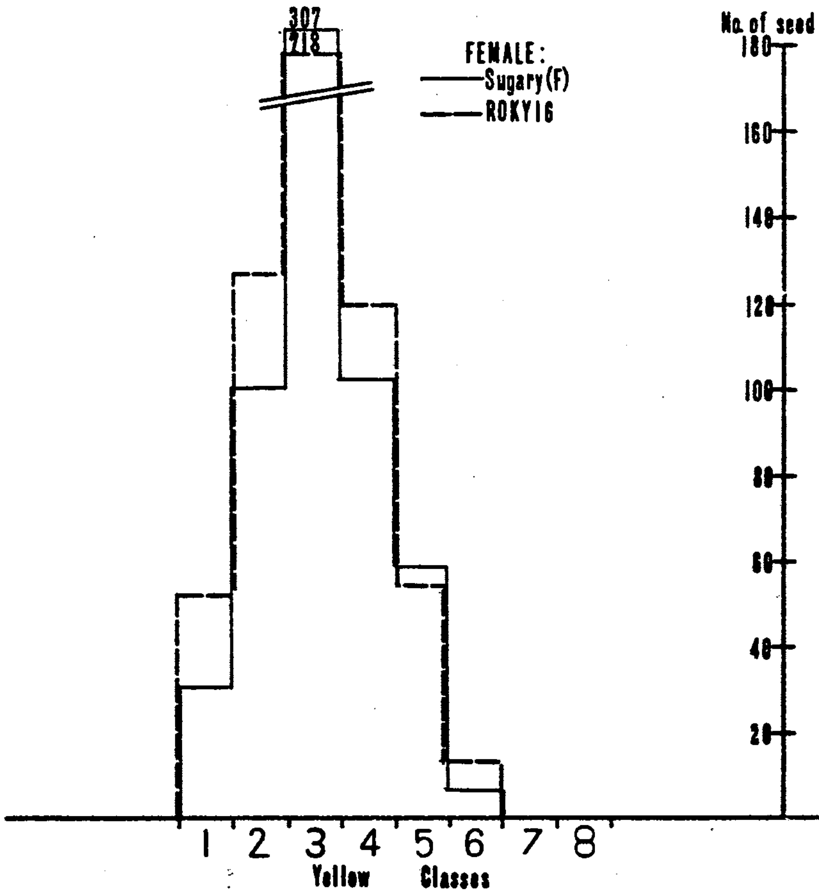

Figure 13. Histogram of Yellow Endosperm Classes for F_2 of Sugary(F) and ROKY16 Crosses

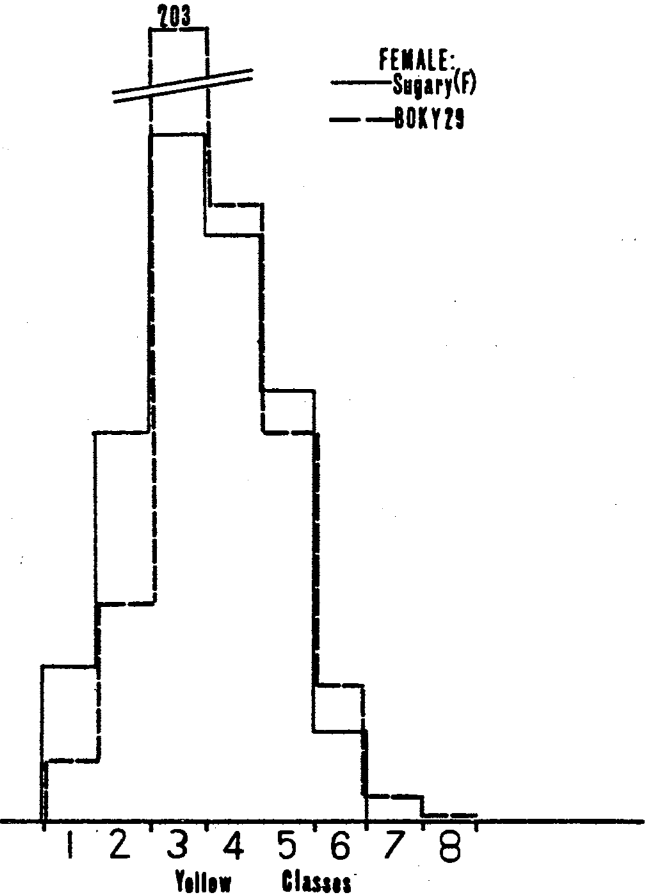

Figure 14. Histogram of Yellow Endosperm Classes for F_2 of Sugary(F) and BOKY29 Crosses

evident as noted for previous crosses. Similarly segregates outside the range of the parents were not as prevalent as those found in the previous results. The genotype for expression of yellow endosperm may not be the same among the three sugary lines, but their contribution to yellow endosperm in crosses was very similar.

Relationship of Yellow and Dent

The crosses of dent X yellow gave the same reaction as the dent X normal crosses for the dent endosperm character. The F_1 endosperm was plump (normal) from all crosses.

Table XXI gives the results obtained from the classification of F_2 endosperm types of dent X yellow endosperm crosses. The calculations indicated a good fit to the 3:1 expected ratio of plump(normal):dent endosperm seeds in the F_2. The chi-square probability values actually indicated an overall better fit of the data to the hypothesized ratio than the results from the dent X normal endosperm crosses. The probability values ranged from .22 to .76. This gave further support to the simple recessive mode of inheritance for the dent endosperm character.

Seeds of the two dent lines cracked very badly when pearled. Only a few whole kernels were obtained from any pearled sample of either dent line. The few which were observed from each line indicated that the endosperm was very white and extremely low or lacking in carotenoid pigments. They were classified as class one on the scale which was used.

The F_1 endosperms from dent X yellow crosses showed a slight amount of carotenoid pigments. There was some xenia effect on seed of dent females and dilution of the yellow endosperm of ROKY16 or BOKY29 when

TABLE XXI

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF DENT X YELLOW ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross Female	Male		Number of Seed in Classes Plump	Dent	Total	Values X^2	P
Expected Ratio - 3:1							
Dent(W)	X ROKY16	(O)[1]	302	112	414	0.931	.34
		(E)[2]	310.5	103.5			
Dent(W)	X BOKY29	(O)	344	123	467	0.447	.52
		(E)	350.25	116.75			
Dent(R)	X ROKY16	(O)	519	178	697	0.108	.76
		(E)	522.75	174.25			
Dent(R)	X BOKY29	(O)	525	175	700	0.711	.41
		(E)	512	188			
ROKY16	X Dent(W)	(O)	773	279	1052	1.30	.24
		(E)	789	263			
ROKY16	X Dent(R)	(O)	629	220	849	0.331	.60
		(E)	636.75	212.25			
BOKY29	X Dent(W)	(O)	908	328	1236	1.557	.22
		(E)	927	309			
BOKY29	X Dent(R)	(O)	762	271	1033	0.839	.35
		(E)	774.75	258.25			

[1]Observed values.

[2]Expected values.

pollinated with one of the dent endosperm lines.

The results of F_2 endosperm classifications are given in Figures 15 through 18. In general the results followed the results of the normal X yellow endosperm crosses even closer than the sugary X yellow endosperm crosses. The mode for six of the crosses was class three

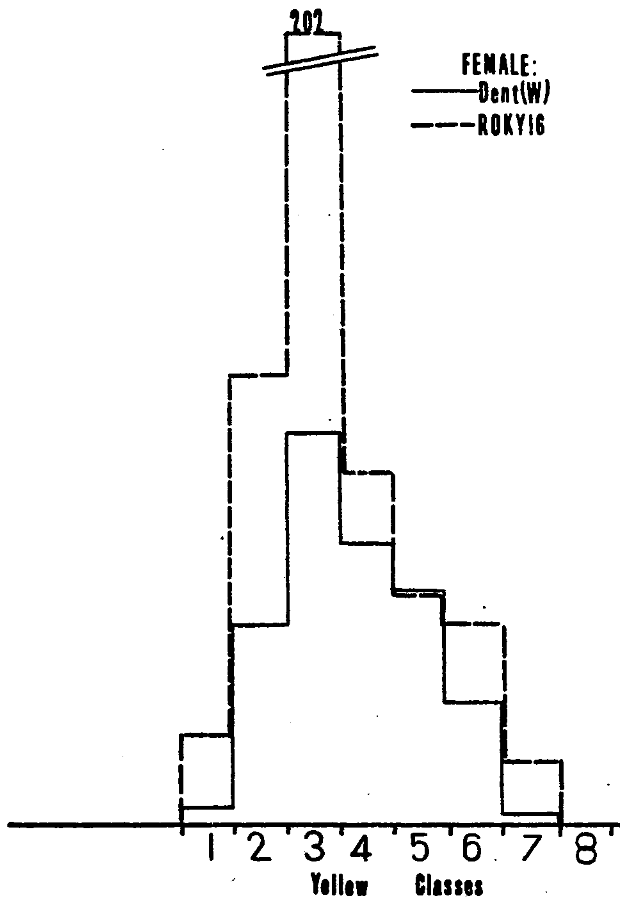

Figure 15. Histogram of Yellow Endosperm Classes for F_2 of Dent(W) and ROKY16 Crosses

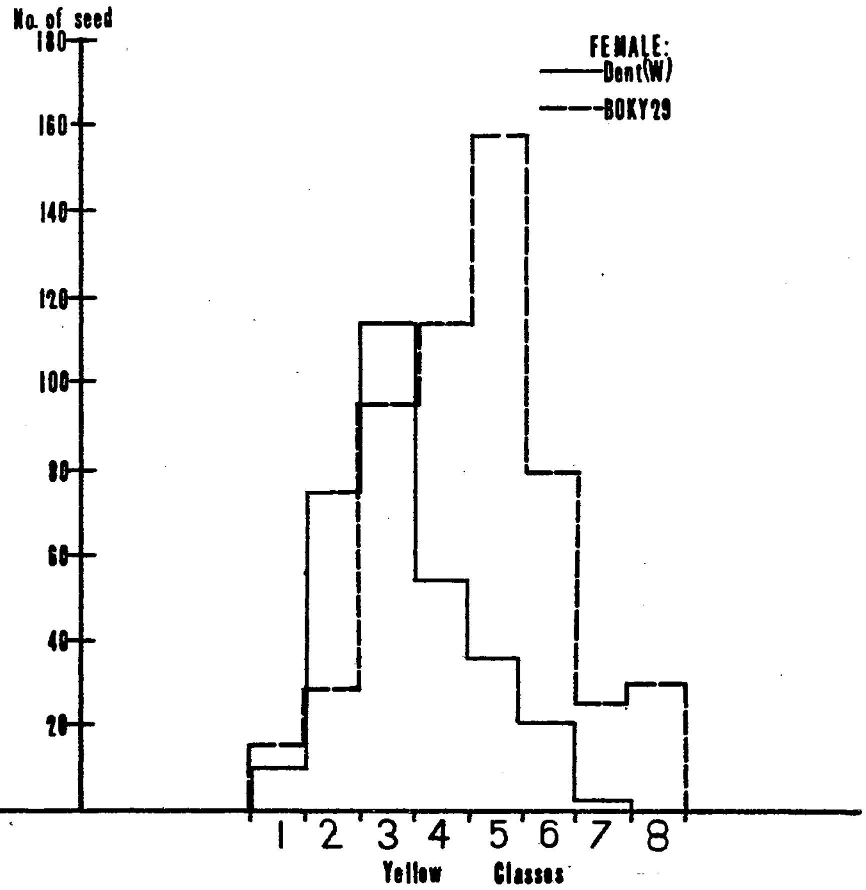

Figure 16. Histogram of Yellow Endosperm Classes for F_2 of Dent(W) and BOKY29 Crosses

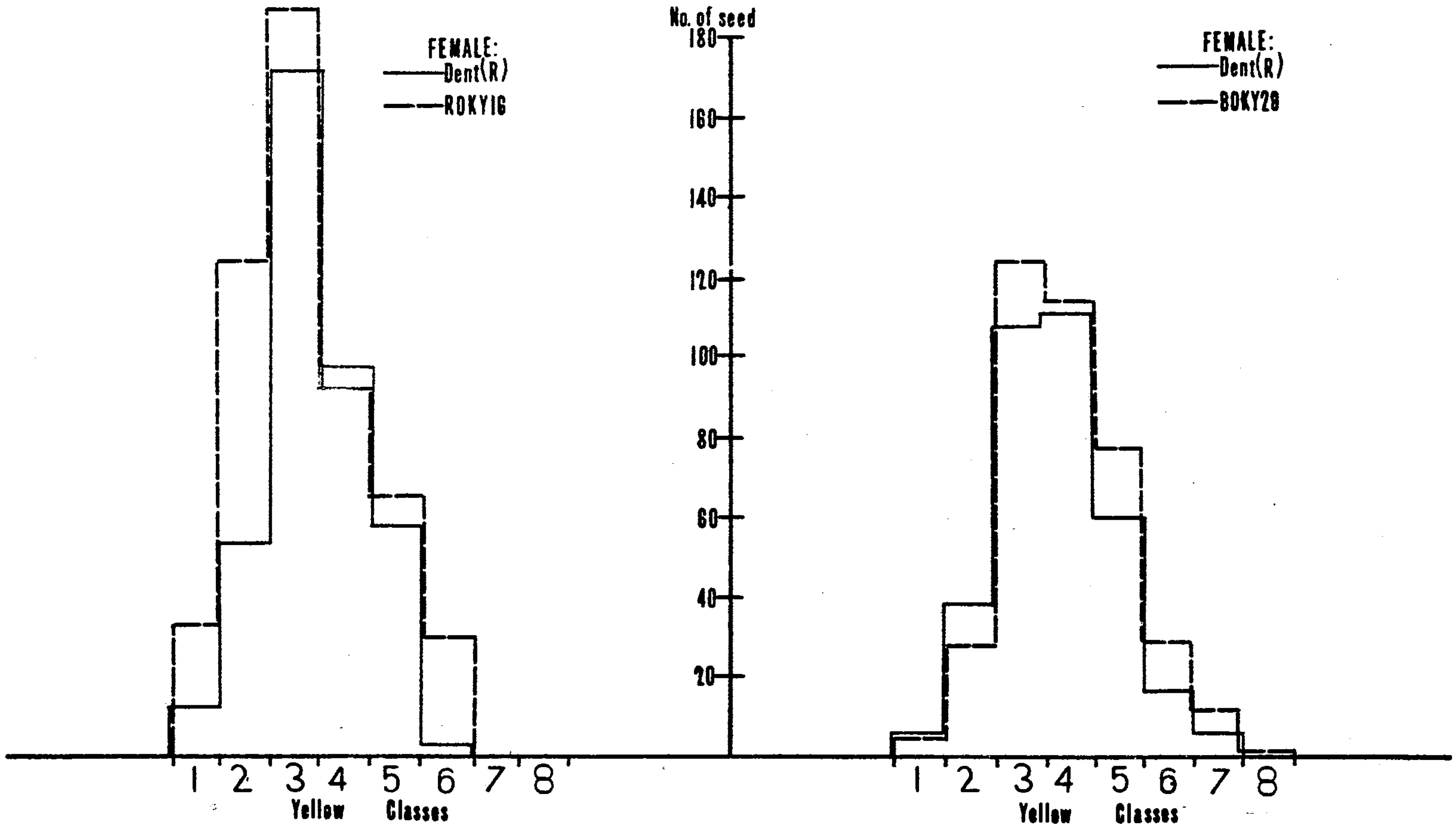

Figure 17. Histogram of Yellow Endosperm Classes for F_2 of Dent(R) and ROKY16 Crosses

Figure 18. Histogram of Yellow Endosperm Classes for F_2 of Dent(R) and BOKY29 Crosses

which was the most frequent class in all but one of the normal X yellow endosperm crosses.

Figures 15 and 16 show the results from the crosses of Dent(W) with ROKY16 and BOKY29, respectively. These results were very similar to those obtained from the Wheatland crosses with the two yellow endosperm parents, especially the Dent(W) X BOKY29 crosses. The difference in the mode for the reciprocal crosses (classes five and three, respectively) was the same noted for the Wheatland crosses. The BOKY29 X Dent(W) cross gave a mode of class five and a much higher frequency in the classes with higher carotenoid expression. There was no great difference indicated in the reciprocal crosses with ROKY16.

In the crosses of Dent(R) with the two yellow endosperm parents the Dent(R) X ROKY16 crosses (Figure 17) gave a much higher apex in the F_2 distribution than the BOKY29 crosses with Dent(R) (Figure 18). These same results were noted for BOK8 in the same respective crosses. One difference in this comparison was that the BOK8 crosses with BOKY29 gave a mode of class three while the Dent(R) X BOKY29 crosses gave a mode of class four. Another difference was that the Dent(R) crosses with ROKY16 gave no segregates in classes seven and eight while the same BOK8 crosses gave such segregates. Overall the crosses with BOK8 and Dent(R) gave very similar results.

It would appear that the dent endosperm lines compared very favorably with Wheatland and BOK8 in carotenoid pigments. The segregation obtained in the F_2 was very similar in the two types of crosses. Their genotype for carotenoid expression does not appear to be exactly the same since the dent parental lines rated a class one and the normal endosperm types rated a class two. The dent lines also showed fewer class seven and eight segregates, except for the BOKY29 X Dent(W) cross, than the normal endosperm types gave. While the dent and normal endosperm types gave very similar results they may not contain exactly the same genotype for expression of yellow endosperm.

Relationship of Yellow and Waxy

The last type of cross examined in the study was the waxy X yellow endosperm crosses. The seed of all parents involved in these crosses were plump in appearance, but the Dwarf Redlan parent gave a red or waxy reaction to iodine solution while the yellow endosperm lines gave a blue or starchy reaction to the iodine test. F_1 endosperms resulting from reciprocal crosses gave a starchy reaction to iodine.

Table XXII gives the results from classifications of F_2 endosperm types of waxy X yellow endosperm crosses for the waxy or starchy character. All four crosses gave a reasonable to good fit to the expected 3:1 ratio of starchy:waxy. These results agreed with those obtained from the waxy X normal crosses and supported the simple recessive mode of inheritance for the waxy character. The results in no way helped to explain the unusual results obtained for the waxy character in the dent and sugary crosses with waxy.

Pearled samples of seed from the Dwarf Redlan parent were classified into category one for yellow endosperm in the standards. When Dwarf Redlan was pollinated with one of the yellow endosperm parents, the F_1 endosperms showed xenia for yellow endosperm and were rated in class three. The reciprocal cross diluted the expression of pigments for both yellow endosperm lines.

Since the starchy and waxy endosperm types were plump, normal

TABLE XXII

CLASSIFICATION OF F_2 ENDOSPERM TYPES OF WAXY X YELLOW ENDOSPERM CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross			Number of Seed in Classes			Values	
Female	Male		Blue	Red	Total	χ^2	P
Expected Ratio - 3:1							
D. Redlan	X ROKY16	(O)[1]	405	123	528	0.819	.32
		(E)[2]	396	132			
D. Redlan	X BOKY29	(O)	246	69	315	1.609	.22
		(E)	236.25	78.75			
ROKY16	X D. Redlan	(O)	391	134	525	0.077	.82
		(E)	393.75	131.25			
BOKY29	X D. Redlan	(O)	374	125	499	0.001	.90+
		(E)	374.25	124.75			

[1]Observed values.

[2]Expected values.

appearing seeds, good pearled samples were obtained from both types. Figures 19 through 22 give the classifications of both starchy (blue) and waxy (red) endosperm types from F_2 endosperm of waxy X yellow endosperm crosses. In general the distribution of carotenoid pigments seemed to be about the same in both the waxy and the starchy endosperm segregates. There was some tendency for higher frequencies of class one (nonyellow) segregates among the waxy types. This was noted in the BOKY29 X Dwarf Redlan and ROKY16 X Dwarf Redlan crosses.

The mode was not the same in all F_2 samples. Crosses with ROKY16 gave a mode of class three in all cases, but this was not true with the BOKY29 crosses. The Dwarf Redlan X BOKY29 cross had a mode of class

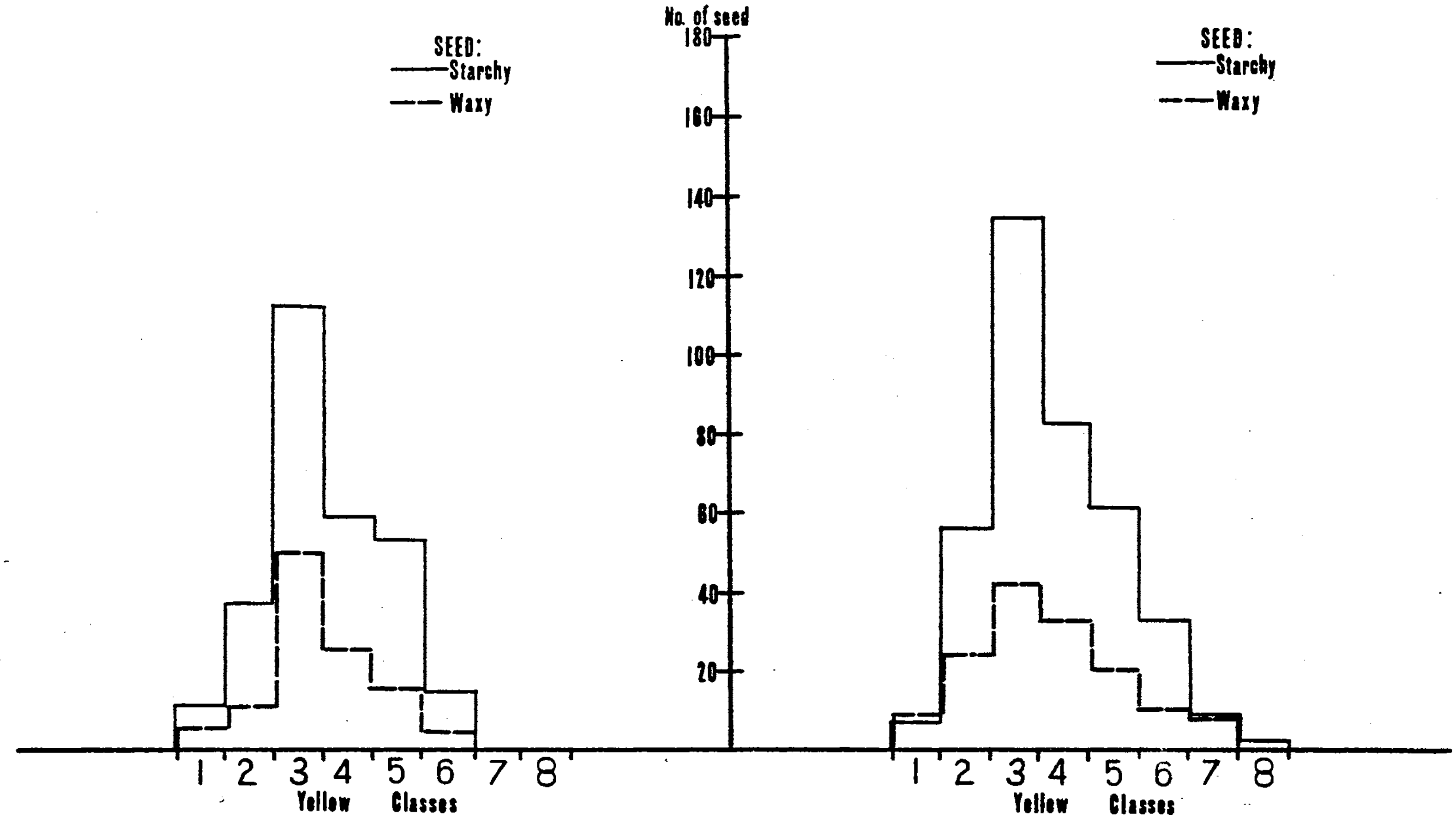

Figure 19. Histogram of Yellow Endosperm Classes for F_2 of Dwarf Redlan X ROKY16

Figure 20. Histogram of Yellow Endosperm Classes for F_2 of ROKY16 X Dwarf Redlan

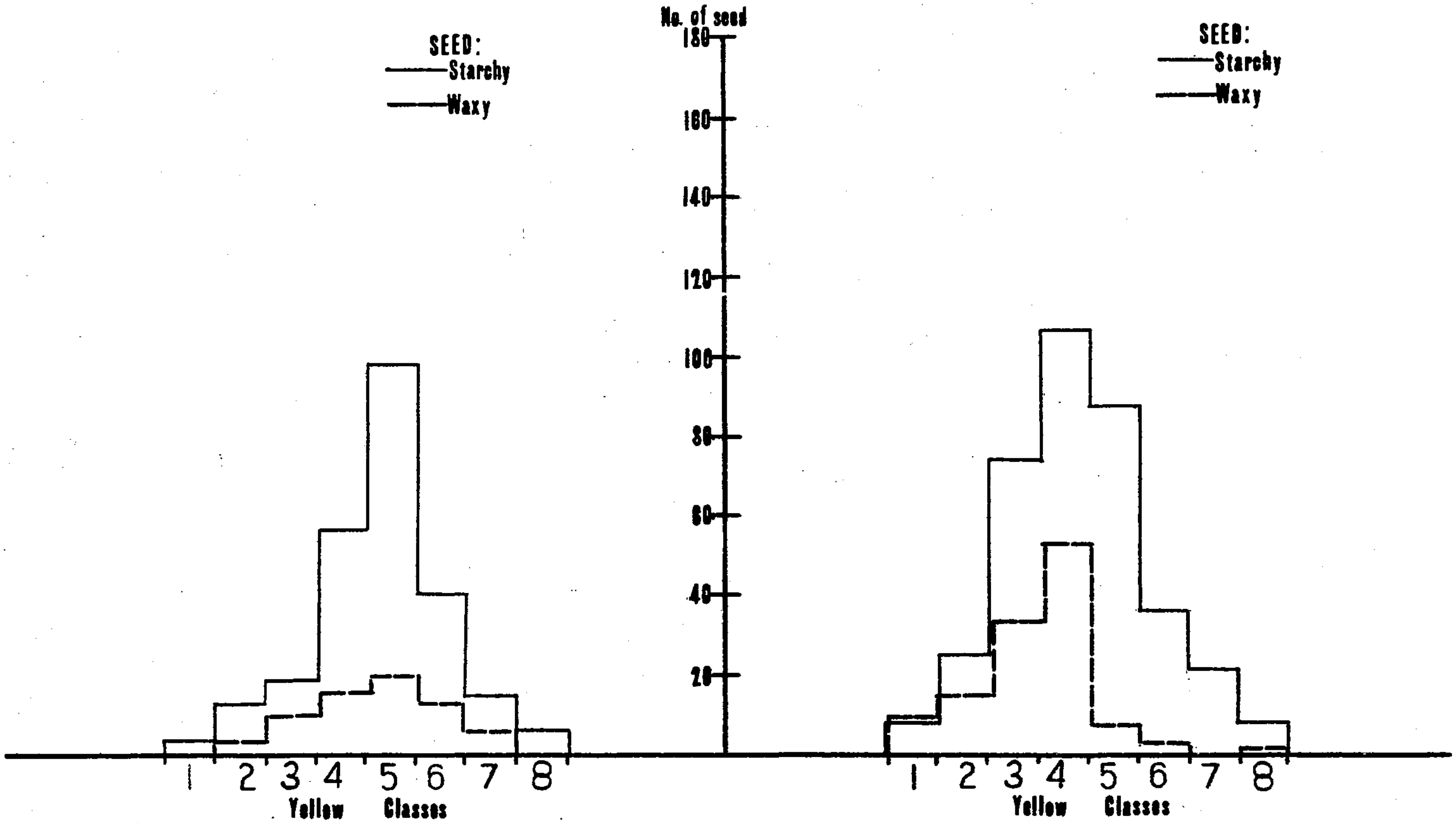

Figure 21. Histogram of Yellow Endosperm Classes for F_2 of Dwarf Redlan X BOKY29

Figure 22. Histogram of Yellow Endosperm Classes for F_2 of BOKY29 X Dwarf Redlan

five for both starchy and waxy endosperm types, but the reciprocal cross gave a mode of class four for both endosperm types. These results showed some expression in the F_2 of the higher carotenoid content from the BOKY29 parent. Such results were not as evident in other yellow endosperm crosses.

One possible reason for the greater frequencies in the higher yellow classes in the Dwarf Redlan X BOKY29 cross was that the seeds were obtained from the 1969-70 greenhouse and some of them were not fully developed. This condition seemed to intensify the expression of yellow endosperm. The reciprocal cross seeds also came from the greenhouse, but they were fully developed.

The overall results from the crosses of waxy and yellow endosperm types did not indicate linkage relationships. The distribution of yellow endosperm was very similar in both starchy and waxy types with only a slight tendency toward less yellow expression in waxy types.

The overall results from the crosses with the two yellow endosperm lines indicated that more than one and possibly several genes were involved in the expression of yellow or nonyellow endosperm. Since the yellow endosperm parents used in this study were not as yellow as the original yellow introduction from Africa, there are probably even more factors involved in the expression of yellow endosperm than indicated in this study.

The classifications of F_2 endosperms indicated a slight amount of dominance toward nonyellow. F_1 and F_2 endosperm classifications indicated that dominance was not complete.

Since only the plump seeds were classified for yellow endosperm. little information was available to evaluate linkage relationships.

The only cross in which all endosperm categories were classified was the cross with waxy (Dwarf Redlan). These crosses gave no real indication of linkage of the locus controlling the waxy endosperm character with loci controlling yellow.

It is known that there is considerable variation in the expression of yellow endosperm in sorghum. It has also been established that environmental factors influence the expression of carotenoid pigments. To gain more conclusive evidence on the inheritance of yellow endosperm in sorghum one would need a better range of yellow endosperm parents in which unbiased samples could be taken. It would be best to have lines as nearly alike as possible in all characteristics except for yellow endosperm (i.e. grain color, carbohydrate type of endosperm, maturity, etc.). The classifications should be supported with chemical tests.

Possible Roles of Mutant Genes in Control of Carbohydrate Synthesis

Previous discussion indicated some of the possible roles of mutant genes of corn on controlling carbohydrate synthesis of the endosperm (14,15,16). The mutant genes studied in this research problem could function similarly in sorghum. The <u>su</u> gene in sorghum could cause a block or partial block in the conversion of sucrose and other sugars into starch and other carbohydrates. This gene could also retard the conversion of WSP[1] to starch. The <u>Wx</u> gene must be necessary for synthesis of amylose. The <u>wxwxwx</u> condition must exist in sorghum for the grain to develop 100% amylopectin.

The dent (<u>dt</u>) and defective (<u>d</u>) genes must function somewhat

[1]Water-soluble-polysaccarides.

differently than the su and wx genes. Both the dt and d genes could have a quantitative effect on the amount of some given enzyme being produced. If they caused a reduction in the amount of a given enzyme being produced this could reduce the amount of endosperm produced by the seed of the mutant genotype. The defective gene (d) produces a more dramatic effect than the dent (dt) gene in this respect. They could affect the same enzyme but in two different ways to account for the expression of the respective mutant traits.

Overall these four endosperm mutant genes have considerable possibility for studying the control of carbohydrate synthesis in endosperm formation of sorghums. It would be desirable to isolate more endosperm mutants and determine their inheritance and relationship to these mutants. Such a study would need to be approached from a chemical as well as a genetic standpoint.

Table XXIII gives a summary of the inheritance of the four mutant endosperm types involved in this study.

TABLE XXIII

SUMMARY OF GENOTYPE AND INHERITANCE OF MUTANT ENDOSPERM TYPES

Mutant	Genotype	Inheritance	F_2 Ratio
Defective	ddd	partial recessive	2:1:1
Sugary	sususu	simple recessive	3:1
Dent	dtdtdt	simple recessive	3:1
Waxy[1]	wxwxwx	simple recessive	3:1
Yellow	- - -	quantitative	

[1]Modifier genes may alter this inheritance.

CHAPTER V

SUMMARY AND CONCLUSIONS

A study was conducted to determine the inheritance and genetic relationship of six endosperm types in sorghum. The six types were designated as normal, defective, sugary, dent, waxy, and yellow. Two selected lines for each of the normal, defective, dent, and yellow endosperm types were used. Three sugary endosperm lines and one waxy endosperm line were utilized.

All possible crosses among the various endosperm types were made, excluding crosses of the same endosperm type. F_1 and F_2 endosperm types were classified. The F_2 data for all crosses were analyzed. On the basis of these data the nature of inheritance was determined when possible for each endosperm type. All classifications were based upon visual observation of the seed and its endosperm, considering the phenotype of the parental types involved.

The results indicated that three of the endosperm types, sugary, dent, and waxy, were inherited as independent simple recessives. The defective endosperm type appeared to be controlled by an independent partial recessive (incomplete dominance). The expression of yellow endosperm appeared to be conditioned by more than one and possibly several factors with some evidence of dominance toward nonyellow. The normal allele(s) for each of the endosperm types involved were present in the normal endosperm lines used.

No linkage was indicated between any of the traits studied. Some unexplained gene action was noted in the waxy X dent and waxy X sugary crosses. It was also determined that the Sugary(F) line must be a double homozygous recessive for both waxy and sugary with sugary being epistatic to waxy.

Reciprocal cross differences were noted for the F_1 endosperm from crosses involving the defective and the yellow endosperm types. The F_2 segregates showed reciprocal differences in a few of the crosses involving yellow endosperm. This was not evident for the other types of crosses.

All genotypes involved in the study affected the quantity and/or quality of carbohydrate stored in the endosperm of the sorghum kernel. Factors affecting the carotenoid pigment expression were also involved.

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APPENDIX A

Description of Lines

I. Defective endosperm type: This mutant type was first found in an F_2 field hybrid progeny of Durra C.I. No. 696 in 1945 by Sieglinger (26). The grain had a very collapsed or degenerate endosperm. The original line resulting from this selection plus one additional line obtained from a cross with Ryer Milo were used.

A. Defective Endosperm -1-2-1-1 was the original line selected. It was a grain type about 40 inches tall with red grain and awns. It began blooming about 52 days after planting. (100 seed wt. $\bar{x}$ = 1.97 gms.).

B. Defective(R) was another line with defective endosperm. This line was homozygous for defective endosperm but showed some segregation for height and maturity. The predominant type was about 50 inches tall and bloomed four or five days later than the regular Defective. The line produced healthier, more viable seeds than the original defective endosperm selection did. (100 seed wt. $\bar{x}$ = 2.40 gms.).

II. Sugary endosperm type: The sugary, shrunken, or dimpled endosperm type had been noted by several workers. The seeds were usually about 25% smaller than normal seeds and contained at least twice as much sugar. Three lines were used of this type.

A. Kasha Kasha X 10-2-2-1-1-1 or Sugary(R) was a line with red grain and plants about 54 inches tall. The heads were oval and compact and bloomed about two days later than Defective. The seed ranged from slightly dimpled to shriveled depending on the environment. (100 seed wt. $\bar{x}$ = 2.40 gms.).

B. Sugary(W) or Sugary White came from the cross Sterile Tan Redlan X Large Shrunken Seed. It was short (33 inches) and had tan plant color with white grain. It took about 50 days to bloom and frequently showed some male sterility. (100 seed wt. $\overline{x}$ = 2.32 gms.).

C. Sugary(F) or Sugary Forage was a Kasha Kasha type from shrunken Sorgo X Tan Sumac. It was a tall forage type (70 inches) with small wrinkled brown grain and a tan juicy stalk. (100 seed wt. $\overline{x}$ = 1.42 gms.).

III. Dent endosperm type: This mutant endosperm type was also located by Sieglinger (personal communication) in his breeding material at the Perkins Experiment Station. This endosperm type apparently was derived from Scented Sorghum, an introduction from India.

A. Dent(W) was a selection from the complicated pedigree -- AWD1-Scented, F_7 X ATR-Cy Red-Kau-5-1 X India 13- Cy11- Korgi-4. It had white grain, purple plant color, awns, and was about 47 inches tall. It bloomed about five or six days later than Defective. This line was often sterile in the greenhouse during the winter. (100 seed wt. $\overline{x}$ = 2.33 gms.).

B. Dent(R) was a selection with red grain from a pedigree very similar to the Dent(W) line. It had purple plant color, awns, and kernels which were more frequently hollow than dented, and showed some segregation for sterility. It was about 42 inches tall and bloomed about the same time as Defective. (100 seed wt. $\overline{x}$ = 2.90 gms.).

IV. Waxy endosperm type: The line used for this endosperm type was Dwarf Redlan or BOK3. This line has been released by the Oklahoma Agricultural Experiment Station and has a male sterile counterpart (AOK3). It had red grain color, purple plant color, no awns, and bloomed in about 53 days under field conditions. The endosperm was soapy in appearance and gave a red reaction to the iodine test. The plants were about 39 inches tall. (100 seed wt. $\overline{x}$ = 2.91 gms.).

V. Yellow endosperm type: This endosperm type has been incorporated into many adapted cultivated types in the United States at the present time. The original source of yellow endosperm was from some nonadapted material introduced from Africa. When seed of this type were pearled they showed a distinct yellow (carotinoid pigments) coloration not evident in cultivated sorghums previously.

A. ROKY16 came from a cross of Cytoplasmic male-sterile No. 11 X Resistant Dwarf Yellow Milo 332-Short Kaura. It was released by the Oklahoma Agricultural Experiment Station in 1966 as a restorer type. The plants of this line had tan plant color, red grain color, awns, long and slightly conical heads, and yellow endosperm. It was about 41 inches tall and bloomed in 52 days in the field. (100 seed wt. $\overline{x}$ = 3.15 gms.).

B. BOKY29 was an experimental line from the sorghum breeding program of Oklahoma State University with a pedigree of Redlan-Kaura X Dwarf Hydro-Rice. This line had white grain color, purple plant color, very small awns, semi-kafir type heads, and bloomed in 54 days. The plants were about 38 inches tall. The grain had a normal starchy type endosperm with yellow pigmentation. The line had a male sterile counterpart.

(100 seed wt. $\bar{x}$ = 2.68 gms.).

VI. Normal Endosperm type: This referred to the common plump starchy endosperm type which has an outer corneous or horny layer and an inner floury portion. This endosperm type gave a starchy or blue reaction to the iodine test indicating that about 25% amylose was present.

A. Wheatland was a line released by the Oklahoma Agricultural Station and developed by Mr. Sieglinger at Woodward, Oklahoma. This line had red grain color, purple plant color, no awns, and was about 32 inches tall. It bloomed in about 54 days. The seeds were large and plump with a normal endosperm (starchy). (100 seed wt. $\bar{x}$ = 3.89 gms.).

B. BOK8 was the other normal endosperm line used. It had been released by the Oklahoma Agricultural Experiment Station and came from the pedigree -- Dwarf Kafir X Sedan Red Kafir-8-2. This line also came from a selection made by Mr. Sieglinger at Woodward, Oklahoma. BOK8 was an early kafir type with red grain color, red plant color, no awns, and grew to a height of 34 inches. It bloomed in about 50 days. The seeds were medium-sized and plump with a normal starchy endosperm. The male sterile line of this was also used. (100 seed wt. $\bar{x}$ = 2.76 gms.).

APPENDIX B

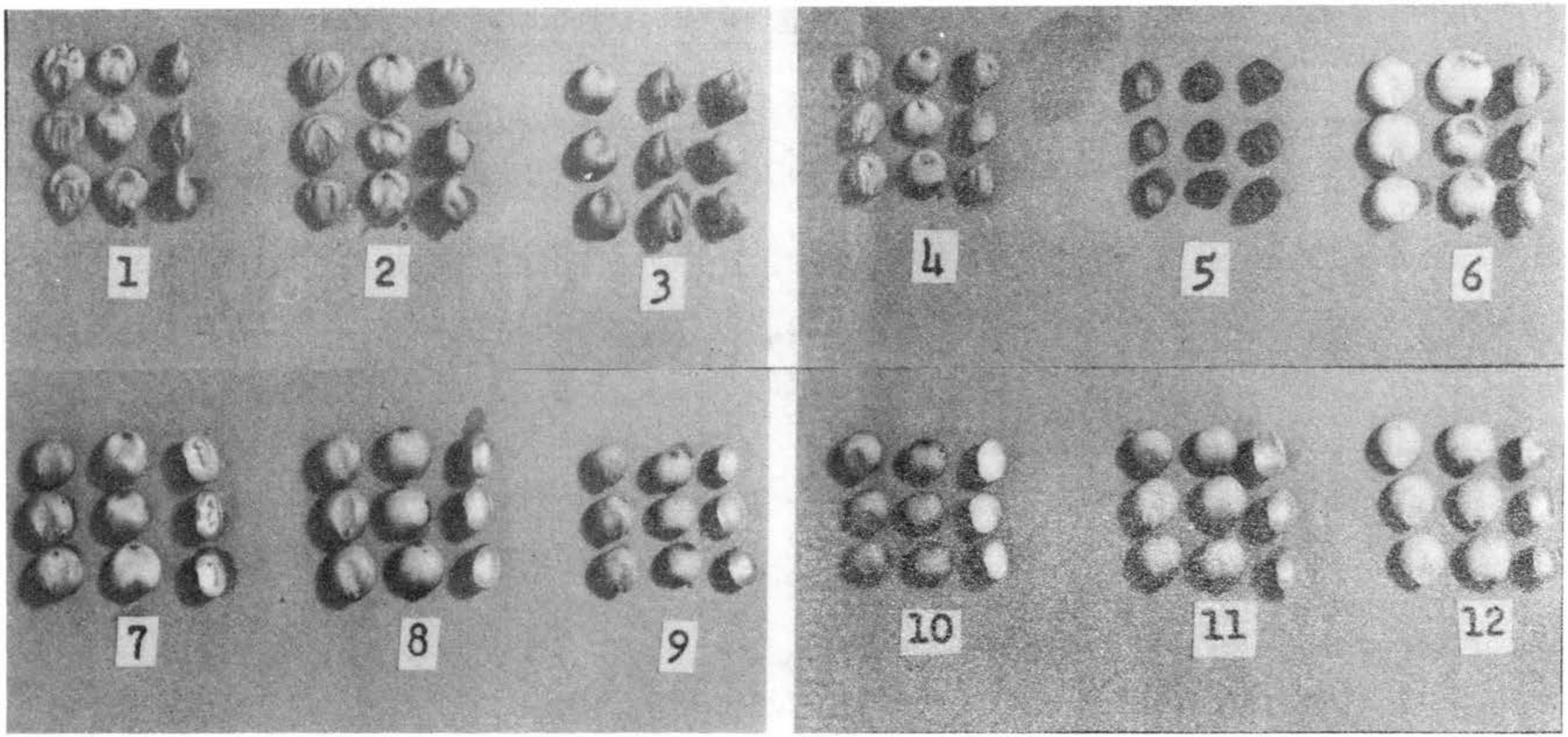

Figure 23. Typical Kernels of Endosperm Types Studied. 1) Defective; 2) Defective(R); 3) Sugary(R); 4) Sugary(W); 5) Sugary(F); 6) Dent(W); 7) Dent(R); 8) Wheatland; 9) BOK8; 10) Dwarf Redlan; 11) ROKY16; 12) BOKY29.

APPENDIX C

TABLE XXIV

CLASSIFICATION OF F_2 ENDOSPERM TYPES FROM ALL CROSSES WITH CHI-SQUARE AND PROBABILITY VALUES

Cross (Female X Male)		Number of Seed in Classes: Plump		Intermediate		Defective		Total	Values: χ^2	P
Defective X Wheatland	(O)[2]	508		230		225		963	2.97	.24
E.R.[1] 2:1:1	(E)[3]	481.50		240.75		240.75				
	(O)	768		389		342		1499	4.44	.12
	(E)	749.50		374.75		374.75				
	(O)	758		341		337		1436	4.48	.12
	(E)	718		359		359				
Defective X BOK8	(O)	710		345		335		1390	0.792	.70
E.R. 2:1:1	(E)	695		347.5		347.5				
	(O)	561		270		238		1069	4.542	.11
	(E)	534.5		267.25		267.25				
	(O)	596		326		299		1221	1.883	.41
	(E)	610.5		305.25		305.25				
		Blue	Red	Blue	Red	Blue	Red			
Defective X D. Redlan	(O)	145	39	64	22	68	25	363	1.952	.85
E.R. 6:2:3:1:3:1	(E)	136.14	45.38	68.07	22.69	68.07	22.69			
	(O)	139	48	66	18	75	21	367	2.01	.85
	(E)	137.64	45.88	68.82	22.94	68.82	22.94			
	(O)	110	34	49	19	45	13	270	2.592	.77
	(E)	101.28	33.76	50.64	16.88	50.64	16.88			

TABLE XXIV (Continued)

Cross			Number of Seed in Classes			Total	Values	
Female	Male						χ^2	P
			Plump	Sugary Intermediate	Sugary Defective Defective			
Defective X Sugary(R)		(O)	74	76	43	193	0.788	.68
E.R. 6:6:4		(E)	72.38	72.38	48.25			
		(O)	168	173	108	449	0.289	.85
		(E)	168.36	168.36	112.24			
		(O)	169	155	100	424	1.070	.62
		(E)	159	159	106			
Defective X Sugary(W)		(O)	125	114	83	322	0.604	.73
E.R. 6:6:4		(E)	120.78	120.78	80.52			
		(O)	139	142	107	388	1.405	.48
		(E)	145.50	145.50	97			
		(O)	158	172	105	435	0.773	.70
		(E)	163.14	163.14	108.76			
Defective X Sugary(F)		(O)	231	210	139	580	1.345	.49
E.R. 6:6:4		(E)	217.5	217.5	145.0			
		(O)	235	221	159	615	0.582	.74
		(E)	230.64	230.64	153.76			
		(O)	226	228	172	626	2.055	.35
		(E)	234.78	234.78	156.52			
			Plump	Dent Intermediate	Defective Dent Defective			
Defective X Dent(W)		(O)	139	136	99	374	0.464	.81
E.R. 6:6:4		(E)	140.28	140.28	93.52			

TABLE XXIV (Continued)

Cross			Number of Seed in Classes			Total	Values	
Female	Male						χ^2	P
		(O)	155	171	105	431	0.886	.65
		(E)	161.64	161.64	107.76			
		(O)	148	136	100	384	0.722	.71
		(E)	144	144	96			
Defective X Dent(R)		(O)	165	167	97	429	0.830	.68
E.R. 6:6:4		(E)	160.86	160.86	107.24			
		(O)	128	125	77	330	0.526	.78
		(E)	123.78	123.78	82.52			
		(O)	180	198	140	518	1.969	.37
		(E)	194.28	194.28	129.52			
			Plump	Intermediate	Defective			
Defective X ROKY16		(O)	901	431	449	1781	0.612	.73
E.R. 2:1:1		(E)	890.5	445.25	445.25			
		(O)	1430	728	738	2896	0.517	.78
		(E)	1448	724	724			
		(O)	1004	466	481	1951	1.896	.38
		(E)	975.5	487.75	487.75			
Defective X BOKY29		(O)	301	140	136	577	1.139	.59
E.R. 2:1:1		(E)	288.5	144.25	144.25			
•		(O)	280	137	128	545	0.71	.72
		(E)	272.5	136.25	136.25			
		(O)	264	129	112	505	2.192	.34
		(E)	252.5	126.25	126.25			
Defective(R) X Wheatland		(O)	463	220	204	887	2.296	.32
E.R. 2:1:1		(E)	443.5	221.75	221.75			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes						Total	Values: χ^2	P
	(O)	205		117		92		414	3.062	.21
	(E)	207		103.5		103.5				
	(O)	615		333		337		1285	2.379	.28
	(E)	642.5		321.25		321.25				
Defective(R) X BOK8	(O)	647		295		296		1238	2.536	.27
E.R. 2:1:1	(E)	619		309.5		309.5				
	(O)	161		82		75		318	0.258	.87
	(E)	159		79.5		79.5				
	(O)	175		90		81		346	0.515	.78
	(E)	173		86.5		86.5				
		Blue	Red	Blue	Red	Blue	Red			
Defective(R) X D. Redlan	(O)	149	58	71	20	67	22	387	3.401	.64
E.R. 6:2:3:1:3:1	(E)	145.14	48.38	72.57	24.19	72.57	24.19			
	(O)	144	50	78	21	76	22	391	2.095	.84
	(E)	146.64	48.88	73.32	24.44	73.32	24.44			
	(O)	211	76	101	34	95	21	538	6.648	.27
	(E)	201.78	67.26	100.89	33.63	100.89	33.63			
		Plump		Sugary Intermediate		Sugary Defective Defective				
Defective(R) X Sugary(R)	(O)	126		126		74		326	0.920	.63
E.R. 6:6:4	(E)	122.28		122.28		81.52				
	(O)	71		70		56		197	1.241	.55
	(E)	73.86		73.86		49.24				
	(O)	168		175		101		444	1.349	.50
	(E)	166.5		166.5		111				

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes			Total	Values: χ^2	Values: P
Defective(R) X Sugary(W)	(O)	116	115	64	295	1.59	.44
E.R. 6:6:4	(E)	110.64	110.64	73.76			
	(O)	209	208	123	540	1.425	.48
	(E)	202.5	202.5	135			
	(O)	152	138	89	379	1.155	.58
	(E)	142.14	142.14	94.76			
Defective(R) X Sugary(F)	(O)	168	172	126	466	1.078	.61
E.R. 6:6:4	(E)	174.78	174.78	116.52			
	(O)	246	231	160	637	0.476	.81
	(E)	238.86	238.86	159.24			
	(O)	209	213	142	564	0.048	.90+
	(E)	211.5	211.5	141			
		Plump	Dent Intermediate	Defective Dent Defective			
Defective(R) X Dent(W)	(O)	179	185	120	484	0.075	.90+
E.R. 6:6:4	(E)	181.5	181.5	121			
	(O)	185	199	126	510	0.33	.87
	(E)	191.28	191.28	127.52			
	(O)	98	98	71	267	0.362	.86
	(E)	100.14	100.14	66.76			
Defective(R) X Dent(R)	(O)	155	158	114	427	0.685	.72
E.R. 6:6:4	(E)	160.14	160.14	106.76			
	(O)	121	131	80	332	0.545	.78
	(E)	124.5	124.5	83			
	(O)	193	197	112	502	1.978	.36
	(E)	188.28	188.28	125.52			

TABLE XXIV (Continued)

Cross (Female X Male)		Number of Seed in Classes			Total	Values χ^2	Values P
		Plump	Intermediate	Defective			
Defective(R) X ROKY16	(O)	147	76	75	298	0.06	.90+
E.R. 2:1:1	(E)	149	74.5	74.5			
	(O)	211	106	83	400	3.855	.15
	(E)	200	100	100			
	(O)	227	111	96	434	1.959	.37
	(E)	217	108.5	108.5			
Defective(R) X BOKY29	(O)	227	111	98	436	1.519	.47
E.R. 2:1:1	(E)	218	109	109			
	(O)	254	140	118	512	1.922	.36
	(E)	256	128	128			
	(O)	254	131	112	497	1.697	.42
	(E)	248.5	124.25	124.25			
		Plump	Sugary				
Sugary(R) X Wheatland	(O)	156	64		220	1.964	.17
E.R. 3:1	(E)	165	55				
	(O)	52	16		68	.079	.83
	(E)	51	17				
	(O)	77	25		102	.013	.90+
	(E)	76.5	25.5				
Sugary(R) X BOK8	(O)	288	107		395	.919	.32
E.R. 3:1	(E)	296.25	98.75				
	(O)	294	88		382	.785	.38
	(E)	286.5	95.5				

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes			Total	Values: χ^2	Values: P
	(O)	339	112		451	.007	.90+
	(E)	338.75	112.75				
		Plump	Sugary Intermediate	Sugary Defective Defective			
Sugary(R) X Defective	(O)	38	36	22	96	.278	.86
E.R. 6:6:4	(E)	36	36	24			
	(O)	38	46	24	108	1.234	.55
	(E)	40.5	40.5	27			
	(O)	49	48	27	124	.698	.72
	(E)	46.5	46.5	31			
Sugary(R) X Defective(R)	(O)	153	134	77	364	4.24	.13
E.R. 6:6:4	(E)	136.5	136.5	91			
	(O)	107	109	70	286	.061	.90+
	(E)	107.28	107.28	71.52			
	(O)	158	158	88	404	2.415	.29
	(E)	151.5	151.5	101			
		Plump	Sugary				
Sugary(R) X D. Redlan	(O)	187	74		261	1.566	.22
E.R. 9:3:4 (No)	(E)	195.75	65.25				
3:1 (Yes)	(O)	208	75		283	.345	.61
	(E)	212.27	70.75				
	(O)	264	81		345	.427	.52
	(E)	258.75	86.25				

TABLE XXIV (Continued)

Cross Female X Male		Number of Seed in Classes			Total	Values χ^2	P
		Plump	Dent	Sugary Dent / Sugary			
Sugary(R) X Dent(W)	(O)	212	78	108	398	1.509	.48
E.R. 9:3:4	(E)	223.92	74.64	99.52			
	(O)	203	66	78	347	1.243	.53
	(E)	195.21	65.07	86.76			
	(O)	166	56	79	301	.255	.88
	(E)	169.29	56.43	75.24			
Sugary(R) X Dent(R)	(O)	54	25	34	113	3.296	.18
E.R. 9:3:4	(E)	63.54	21.18	28.34			
	(O)	129	41	52	222	.366	.85
	(E)	124.92	41.64	55.52			
	(O)	90	43	49	182	4.07	.14
	(E)	102.42	34.14	45.52			
		Plump	Sugary				
Sugary(R) X ROKY16	(O)	42	12		54	.223	.66
E.R. 3:1	(E)	40.5	13.5				
	(O)	112	37		149	.003	.90+
	(E)	111.75	37.25				
	(O)	129	48		177	.424	.52
	(E)	132.75	44.25				
Sugary(R) X BOKY29	(O)	194	73		267	.78	.39
E.R. 3:1	(E)	200.25	66.75				
	(O)	258	90		348	.137	.73
	(E)	261	87				

TABLE XXIV (Continued)

Cross (Female X Male)		Number of Seed in Classes			Total	Values X^2	Values P
	(O)	260	83		343	.117	.74
	(E)	257.25	85.75				
Sugary(W) X Wheatland	(O)	696	215		911	.952	.33
E.R. 3:1	(E)	624.75	208.25				
	(O)	631	202		833	.251	.66
	(E)	624.75	208.25				
	(O)	275	97		372	.229	.67
	(E)	279	93				
Sugary(W) X BOK8	(O)	51	21		72	.667	.43
E.R. 3:1	(E)	54	18				
	(O)	83	33		116	.736	.40
	(E)	87	29				
	(O)	44	11		55	.733	.40
	(E)	41.25	13.75				
		Plump	Sugary Intermediate	Sugary Defective Defective			
Sugary(W) X Defective	(O)	280	258	202	740	2.955	.22
E.R. 6:6:4	(E)	277.5	277.5	185			
	(O)	407	354	254	1013	3.479	.18
	(E)	379.86	379.86	253.24			
	(O)	573	540	388	1501	1.545	.47
	(E)	562.86	562.86	375.24			
Sugary(W) X Defective(R)	(O)	43	40	23	114	1.25	.55
E.R. 6:6:4	(E)	42.78	42.78	28.52			

TABLE XXIV (Continued)

Cross: Female	Cross: Male		Number of Seed in Classes			Total	Values: χ^2	Values: P
		(O)	84	67	51	202	1.914	.37
		(E)	75.78	75.78	50.52			
		(O)	38	39	25	102	.027	.90+
		(E)	38.25	38.25	25.5			
			Blue	Red	Sugary			
Sugary(W) X D. Redlan		(O)	26	11	15	52	.829	.68
E.R. 9:3:4		(E)	29.25	9.75	13.0			
		(O)	113	36	51	200	.082	.90+
		(E)	112.5	37.5	50			
		(O)	109	28	44	181	1.581	.45
		(E)	101.79	33.98	45.24			
			Plump	Dent	Sugary Dent Sugary			
Sugary(W) X Dent(W)		(O)	748	273	305	1326	4.514	.12
E.R. 9:3:4		(E)	745.92	248.64	331.52			
		(O)	1047	384	488	1919	2.743	.25
		(E)	1079.46	359.82	479.76			
		(O)	772	284	380	1436	3.618	.15
		(E)	807.75	269.25	359			
Sugary(W) X Dent(R)		(O)	20	10	11	41	1.158	.60
E.R. 9:3:4		(E)	23.04	10.24	10.24			
		(O)	29	11	15	55	.281	.86
		(E)	30.96	10.32	13.76			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes: Plump	Sugary	Total	Values: χ^2	P
Sugary(W) X ROKY16	(O)	1760	597	2357	.136	.74
E.R. 3:1	(E)	1767.75	589.25			
	(O)	1912	660	2572	.499	.49
	(E)	1929	643			
	(O)	2280	743	3023	.289	.62
	(E)	2267.25	755.75			
Sugary(W) X BOKY29	(O)	30	12	42	.285	.62
E.R. 3:1	(E)	31.5	10.5			
Sugary(F) X Wheatland	(O)	831	271	1102	.099	.78
E.R. 3:1	(E)	826.5	275.5			
	(O)	930	307	1237	.021	.90+
	(E)	927.75	309.25			
	(O)	1097	337	1434	1.719	.20
	(E)	1075.5	358.5			
Sugary(F) X BOK8	(O)	462	170	632	1.215	.28
E.R. 3:1	(E)	474	158			
	(O)	798	264	1062	.011	.90+
	(E)	796.5	265.5			
	(O)	1115	394	1509	.992	.32
	(E)	1131.75	377.25			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes: Plump	Sugary Intermediate	Sugary Defective Defective	Total	Values: χ^2	P
Sugary(F) X Defective	(O)	117	122	80	319	.106	.90+
E.R. 6:6:4	(E)	119.64	119.64	79.76			
	(O)	85	96	59	240	.695	.72
	(E)	90	90	60			
	(O)	48	39	28	115	.955	.70
	(E)	43.14	43.14	28.76			
Sugary(F) X Defective(R)	(O)	91	94	57	242	.32	.85
E.R. 6:6:4	(E)	90.78	90.78	60.52			
	(O)	89	73	62	224	2.381	.29
	(E)	84	84	56			
	(O)	119	117	73	309	.33	.85
	(E)	115.85	115.85	77.24			
		Plump (Red)	Sugary				
Sugary(F) X D. Redlan	(O)	285	87		372	.516	.50
E.R. 3:1	(E)	279	93				
	(O)	148	56		204	.667	.42
	(E)	153	51				
	(O)	179	51		230	.98	.32
	(E)	172.5	57.5				

TABLE XXIV (Continued)

Cross: Female Male		Number of Seed in Classes			Total	Values: χ^2	Values: P
		Plump	Sugary Intermediate	Sugary Defective Defective			
Sugary(F) X Dent(W)	(O)	83	23	26	132	3.329	.18
E.R. 9:3:4	(E)	74.25	27.75	33			
	(O)	74	25	34	133	.025	.90+
	(E)	74.79	24.93	33.24			
	(O)	71	22	24	117	1.352	.50
	(E)	65.79	21.93	29.24			
		Plump	Dent	Sugary Dent Defective			
Sugary(F) X Dent(R)	(O)	84	36	33	153	2.64	.26
E.R. 9:3:4	(E)	86.04	28.68	38.24			
	(O)	121	45	53	219	.473	.80
	(E)	123.21	41.07	54.76			
	(O)	102	38	45	185	.391	.83
	(E)	104.04	34.68	46.24			
		Plump	Sugary				
Sugary(F) X ROKY16	(O)	165	49		214	.505	.50
E.R. 3:1	(E)	160.5	53.5				
	(O)	164	57		221	.073	.82
	(E)	165.74	55.25				
	(O)	273	91		364	0	1.00
	(E)	273	91				

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes			Total	Values: χ^2	Values: P
Sugary(F) X BOKY29	(O)	552	182		734	.016	.90
E.R. 3:1	(E)	550.5	183.5				
	(O)	550	190		740	.18	.70
	(E)	555	185				
	(O)	400	123		523	.612	.43
	(E)	392.25	130.75				
		Plump	Dent				
Dent(W) X Wheatland	(O)	193	77		270	2.177	.15
E.R. 3:1	(E)	202.5	67.5				
	(O)	248	96		344	1.551	.22
	(E)	258	86				
	(O)	245	74		319	.553	.48
	(E)	239.25	79.75				
Dent(W) X BOK8	(O)	113	44		157	.767	.38
E.R. 3:1	(E)	117.75	39.25				
	(O)	45	19		64	.751	.40
	(E)	48	16				
	(O)	57	23		80	.60	.44
	(E)	60	20				
		Plump	Intermediate Dent	Defective Dent Defective			
Dent(W) X Defective	(O)	116	128	94	338	1.992	.37
E.R. 6:6:4	(E)	126.78	126.71	84.52			
	(O)	166	143	107	446	1.81	.40
	(E)	156	156	104			

TABLE XXIV (Continued)

Cross Female X Male		Number of Seed in Classes				Total	χ^2	P
	(O)	148	135	83		366	1.67	.42
	(E)	137.16	137.16	91.44				
Dent(W) X Defective(R)	(O)	108	106	90		304	3.456	.18
E.R. 6:6:4	(E)	114	114	76				
	(O)	80	75	55		210	.321	.83
	(E)	78.78	78.78	52.52				
	(O)	91	82	58		231	.468	.80
	(E)	86.64	86.64	47.76				
		Plump		Dent				
		blue	Red	Blue	Red			
Dent(W) X D. Redlan	(O)	23	4	9	2	38	2.075	.58
E_1.R. 9:3:3:1	(E_1)	21.42	7.14	7.14	2.38			
E_2.R. 3:1	(O)	76	10	20	3	107	10.996	.01
	(E_1)	61.29	20.43	20.43	6.81			
	(O)	95	10	40	5	150	1.56	.22
	(E_2)	102.51		37.51				
		Plump	Dent	Sugary Dent Sugary				
Dent(W) X Sugary(R)	(O)	137	46	60		243	.006	.90+
E.R. 9:3:4	(E)	136.71	45.57	60.76				
	(O)	166	68	92		326	3.771	.15
	(E)	183.42	61.14	81.52				
	(O)	134	45	57		236	.093	.90+
	(E)	132.75	44.25	59				

TABLE XXIV (Continued)

Cross (Female × Male)		Number of Seed in Classes			Total	Values χ²	Values P
Dent(W) X Sugary(W)	(O)	66	25	29	120	.344	.86
E.R. 9:3:4	(E)	67.5	22.5	30			
	(O)	45	18	22	85	.459	.81
	(E)	47.79	15.93	21.24			
	(O)	36	12	13	61	.442	.82
	(E)	34.29	11.43	15.24			
Dent(W) X Sugary(F)	(O)	171	85	89	345	9.207	.01
E.R. 9:3:4	(E)	194.04	64.68	86.24			
	(O)	198	93	99	390	7.502	.02
	(E)	219.42	73.14	97.52			
	(O)	356	120	142	618	1.36	.52
	(E)	347.67	115.89	154.52			
		Plump	Dent				
Dent(W) X ROKY16	(O)	158	60		218	.741	.40
E.R. 3:1	(E)	163.5	54.5				
	(O)	88	33		121	.223	.67
	(E)	90.75	30.25				
	(O)	56	19		75	.004	.90+
	(E)	56.25	18.75				
Dent(W) X BOKY29	(O)	145	51		196	.109	.75
E.R. 3:1	(E)	147.0	49				
	(O)	89	38		127	1.64	.21
	(E)	95.25	31.75				
	(O)	110	34		144	.148	.72
	(E)	108	36				

TABLE XXIV (Continued)

Cross Female X Male		Number of Seed in Classes			Total	Values χ^2	P
Dent(R) X Wheatland	(O)	152	43		195	.904	.35
E.R. 3:1	(E)	146.25	48.75				
	(O)	32	15		47	1.199	.28
	(E)	35.25	11.75				
	(O)	58	17		75	.217	.66
	(E)	56.25	18.75				
Dent(R) X BOK8	(O)	146	60		206	1.871	.18
E.R. 3:1	(E)	154.5	51.5				
	(O)	28	11		39	.213	.67
	(E)	29.25	9.75				
		Plump	Intermediate Dent	Defective Dent Defective			
Dent(R) X Defective	(O)	150	148	92	390	.427	.82
E.R. 6:6:4	(E)	146.28	146.28	97.52			
	(O)	134	145	93	372	.434	.81
	(E)	139.5	139.5	93			
	(O)	134	132	83	349	.291	.88
	(E)	130.86	130.86	87.24			
Dent(R) X Defective(R)	(O)	66	73	50	184	.559	.78
E.R. 6:6:4	(E)	70.86	70.86	47.24			
	(O)	57	63	42	162	.37	.83
	(E)	60.78	60.78	40.52			
	(O)	54	60	37	151	.337	.84
	(E)	56.64	56.64	37.76			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes				Total	Values: χ^2	Values: P
		Plump		Dent				
		Blue	Red	Blue	Red			
Dent(R) X D. Redlan	(O)	10	2	3	1	16		
E.R. 9:3:3:1	(O)	33	5	8	1	49		

Cross: Female X Male		Plump	Dent	Sugary Dent / Sugary	Total	Values: χ^2	Values: P
Dent(R) X Sugary(R)	(O)	80	29	38	147	.205	.89
E.R. 9:3:4	(E)	82.71	27.57	36.76			
	(O)	107	42	44	193	1.331	.51
	(E)	108.54	36.18	48.24			
	(O)	139	43	56	238	.461	.82
	(E)	133.92	44.64	59.52			
Dent(R) X Sugary(W)	(O)	161	73	80	314	4.798	.09
E.R. 9:3:4	(E)	176.67	58.89	78.52			
	(O)	157	49	54	260	2.652	.26
	(E)	146.25	48.75	65			
	(O)	160	70	77	307	3.62	.16
	(E)	172.71	57.57	76.76			
Dent(R) X Sugary(F)	(O)	144	61	82	287	4.308	.12
E.R. 9:3:4	(E)	161.46	53.82	71.76			
	(O)	139	105	97	341	42+	0
	(E)	191.79	63.93	85.24			
	(O)	339	170	169	678	19.17	0
	(E)	381.42	127.14	169.52			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes		Total	Values χ^2	Values P
		Plump	Dent			
Dent(R) X ROKY16	(O)	113	40	153	.107	.76
E.R. 3:1	(E)	114.75	38.25			
	(O)	269	94	363	.155	.76
	(E)	272.25	90.75			
	(O)	137	44	181	.045	.87
	(E)	135.75	45.25			
Dent(R) X BOKY29	(O)	243	90	332	.579	.46
E.R. 3:1	(E)	249	83			
	(O)	269	99	368	.711	.41
	(E)	276	92			
		Blue	Red			
D. Redlan X Wheatland	(O)	147	48	195	.015	.90+
E.R. 3:1	(E)	146.25	48.75			
	(O)	106	32	138	.241	.65
	(E)	103.5	34.5			
	(O)	166	47	213	.979	.33
	(E)	159.75	53.25			
D. Redlan X BOK8	(O)	164	47	211	.836	.37
E.R. 3:1	(E)	158.25	52.75			
	(O)	174	52	226	.477	.51
	(E)	169.5	56.5			
	(O)	117	39	156	0	1.0
	(E)	117	39			

TABLE XXIV (Continued)

Cross (Female X Male)		Plump Blue	Plump Red	Intermediate Blue	Intermediate Red	Defective Blue	Defective Red	Total	Values χ^2	Values P
D. Redlan X Defective	(O)	48	19	20	7	20	8	122	1.825	.87
E.R. 6:2:3:1:3:1	(E)	45.8	15.3	22.9	7.6	22.9	7.6			
	(O)	145	43	64	23	73	23	371	1.112	.90+
	(E)	139.1	46.4	69.6	23.2	69.6	23.2			
	(O)	72	25	33	8	34	10	182	1.687	.89
	(E)	68.3	27.8	34.1	11.4	34.1	11.4			
D. Redlan X Defective(R)	(O)	64	21	33	9	38	11	176	1.228	.90+
E.R. 6:2:3:1:3:1	(E)	66	22	33	11	33	11			
	(O)	122	50	60	21	62	20	335	1.856	.87
	(E)	125.6	41.9	62.8	20.9	62.8	20.9			
	(O)	75	21	36	8	36	9	185	2.416	.80
	(E)	69.4	23.1	34.7	11.6	34.7	11.6			

Cross		Plump Blue	Plump Red	Sugary	Total	χ^2	P
D. Redlan X Sugary(R)	(O)	106	5	39	150		
E_1.R. 9:3:4	(E_1)	84.42	28.14	37.5		24.6	0
E_2.R. 3:1	(E_2)	112.5		37.5		.08	.90+
	(O)	56	8	19	83		
	(E_1)	46.7	15.6	20.75		7.708	.03
	(E_2)	62.25		20.75		.196	.90+
	(O)	674		214	888	.384	.84
	(E_2)	666.0		222.0			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes			Total	Values: χ²	Values: P
D. Redlan X Sugary(W)	(O)	69	23	29	121	.069	.90+
E.R. 9:3:4	(E)	68.04	22.68	30.24			
	(O)	73	25	28	125	.545	.78
	(E)	70.29	23.43	31.24			
	(O)	204	69	86	359	.221	.89
	(E)	201	67.32	89.76			
D. Redlan X Sugary(F)	(O)		456	137	593	1.132	.30
E.R. 3:1	(E)		444.75	148.25			
	(O)		244	87	331	.291	.62
	(E)		248.25	82.75			
	(O)		360	125	485	.155	.72
			363.75	121.25			

Cross: Female X Male		Plump: Blue	Plump: Red	Dent: Blue	Dent: Red	Total	Values: χ²	Values: P
D. Redlan X Dent(W)	(O)	243	32	94	13	384	1.680	.20
E.R. 9:3:3:1 (No)	(E)	288		96				
E.R. 3:1	(O)	306	48	143	15	513	9.374	.002
	(E)	384		128				
	(O)	338	48	133	14	532	1.892	.17
	(E)	399.75		133.25				
D. Redlan X Dent(R)	(O)	88	10	36	4	138	1.169	.30
E.R. 3:1	(E)	103.5		34.5				
	(O)	81	9	31	2	123	.220	.66
	(E)	92.25		30.75				
	(O)	101	13	38	6	158	.684	.42
	(E)	118.5		39.5				

TABLE XXIV (Continued)

Cross (Female X Male)		Number of Seed in Classes			Total	Values X^2	Values P
		Blue	Red				
D. Redlan X ROKY16	(O)	92	37		129	.933	.32
E.R. 3:1	(E)	96.75	32.25				
	(O)	87	26		113	.240	.66
	(E)	84.75	28.25				
	(O)	226	60		286	2.467	.12
	(E)	214.5	71.5				
D. Redlan X BOKY29	(O)	64	17		81	.695	.41
E.R. 3:1	(E)	60.75	20.25				
	(O)	97	26		123	.979	.32
	(E)	92.25	30.75				
	(O)	85	26		111	.147	.71
	(E)	83.25	27.75				
		Plump	Intermediate	Defective			
Wheatland X Defective	(O)	168	88	89	345	.240	.89
E.R. 2:1:1	(E)	172.5	86.25	86.25			
	(O)	133	60	61	254	.574	.76
	(E)	127	63.5	63.5			
	(O)	136	60	67	263	.681	.72
	(E)	131.5	65.75	65.75			
Wheatland X Defective(R)	(O)	189	78	77	344	3.166	.20
E.R. 2:1:1	(E)	172	86	86			
	(O)	149	62	69	280	1.507	.48
	(E)	140	70	70			

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes			Total	Values: χ^2	P
	(O)	169	78	70	317	1.796	.41
	(E)	158.5	79.25	79.25			
		Blue	Red				
Wheatland X D. Redlan	(O)	220	63		283	1.133	.30
E.R. 3:1	(E)	212.25	70.75				
	(O)	233	85		318	.508	.50
	(E)	238.5	79.5				
	(O)	191	55		246	.916	.33
	(E)	184.5	61.5				
		Plump	Sugary				
Wheatland X Sugary(R)	(O)	238	92		330	1.459	.24
E.R. 3:1	(E)	247.5	82.5				
	(O)	135	38		173	.849	.37
	(E)	129.74	43.25				
	(O)	318	118		436	.991	.32
	(E)	327	109				
Wheatland X Sugary(W)	(O)	203	73		276	.31	.62
E.R. 3:1	(E)	207	69				
	(O)	256	83		339	.048	.88
	(E)	254.25	84.75				
	(O)	213	77		290	.372	.56
	(E)	217.5	72.5				
Wheatland X Sugary(F)	(O)	859	305		1164	.893	.34
E.R. 3:1	(E)	873	291				

TABLE XXIV (Continued)

Cross (Female X Male)		Number of Seed in Classes								Total	χ^2	P
	(O)	318			118					436	.991	.32
	(E)	327			109							
	(O)	320			123					451	1.242	.28
	(E)	338.25			112.75							
		Plump			Dent							
Wheatland X Dent(W)	(O)	247			78					325	.173	.70
E.R. 3:1	(E)	243.75			81.25							
	(O)	331			111					442	.003	.90+
	(E)	331.5			110.5							
	(O)	301			92					393	.531	.49
	(E)	294.75			98.25							
Wheatland X Dent(R)	(O)	242			94					336	1.587	.22
E.R. 3:1	(E)	252			84							
	(O)	256			87					343	.024	.90+
	(E)	257.25			85.75							
	(O)	307			106					413	.097	.79
	(E)	309.75			103.25							
		1	2	3	4	5	6	7	8			
Wheatland X ROKY16	(O)	8	28	70	41	17	3					
	(O)	6	36	88	33	21	2					
	(O)	6	29	76	36	24	6					
	(O)	7	12	31	13	14	15	2				
Wheatland X BOKY29	(O)	4	18	32	32	34	17	4				
	(O)	9	29	49	28	17	7					
	(O)	6	32	95	40	36	17	1				

TABLE XXIV (Continued)

Cross: Female X Male		Number of Seed in Classes			Total	Values: χ^2	P
		Plump	Intermediate	Defective			
BOK8 X Defective	(O)	209	91	108	408	1.539	.46
E.R. 2:1:1	(E)	204	102	102			
	(O)	196	91	96	383	.343	.84
	(E)	191.5	95.75	95.75			
	(O)	253	116	100	469	4.011	.13
	(E)	234.5	117.25	117.25			
BOK8 X Defective(R)	(O)	46	20	21	87	.311	.85
E.R. 2:1:1	(E)	43.5	21.75	21.75			
	(O)	81	41	32	154	1.467	.48
	(E)	77	38.5	38.5			
	(O)	76	34	34	144	.722	.72
	(E)	72	36	36			
		Blue	Red				
BOK8 X D. Redlan	(O)	99	29		128	.375	.57
E.R. 3:1	(E)	96	32				
	(O)	34	11		45	.007	.90+
	(E)	33.75	11.25				
	(O)	193	70		263	.367	.59
	(E)	197.25	65.75				
		Plump	Sugary				
BOK8 X Sugary(R)	(O)	168	60		228	.211	.67
E.R. 3:1	(E)	171	57				

TABLE XXIV (Continued)

Cross			Number of Seed in Classes		Total	Values	
Female	Male					X^2	P
		(O)	237	79	316	0	1.0
		(E)	237	79			
		(O)	277	86	363	.332	.62
		(E)	272.25	90.75			
BOK8 X Sugary(W)		(O)	269	84	353	.273	.64
E.R. 3:1		(E)	264.75	88.25			
		(O)	217	62	279	1.148	.30
		(E)	209.25	69.25			
		(O)	269	92	361	.045	.86
		(E)	270.75	90.25			
BOK8 X Sugary(F)		(O)	142	39	181	1.212	.28
E.R. 3:1		(E)	135.75	45.25			
		(O)	185	61	246	.005	.90+
		(E)	184.5	61.5			
		(O)	92	25	117	.823	.37
		(E)	87.75	29.25			
			Plump	Dent			
BOK8 X Dent(W)		(O)	111	36	147	.02	.90
E.R. 3:1		(E)	110.25	36.75			
		(O)	79	28	107	.077	.81
		(E)	80.25	26.75			
		(O)	139	59	198	2.431	.13
		(E)	148.5	49.5			
BOK8 X Dent(R)		(O)	296	106	402	.401	.55
E.R. 3:1		(E)	301.5	100.5			

TABLE XXIV (Continued)

Cross (Female X Male)		Number of Seed in Classes								Total	Values χ²	P
	(O)	255			94					349	.696	.42
	(E)	261.75			87.25							
	(O)	315			123					438	2.219	.15
	(E)	328.5			109.5							
		1	2	3	4	5	6	7	8			
BOK8 X ROKY16	(O)	8	30	61	23	24	10					
	(O)	6	27	58	47	43	16	3				
	(O)	12	36	69	39	29	28	8				
BOK8 X BOKY29	(O)	28	60	70	28	15	13	4	1			
	(O)	25	56	43	23	21	8	1	1			
	(O)	14	26	37	29	19	16	6				
ROKY16 X Wheatland	(O)	3	15	58	40	25	6	1				
	(O)	5	24	83	30	29	6	-	1			
	(O)	6	28	85	44	30	12					
ROKY16 X BOK8	(O)	7	13	27	9	10	6	4	2			
	(O)	8	22	30	17	13	7	3				
	(O)	4	11	36	17	10	5	2				
		Plump			Intermediate			Defective				
ROKY16 X Defective	(O)	202			89			84		375	2.278	.29
E.R. 2:1:1	(E)	187.5			93.75			93.75				
	(O)	220			98			86		404	3.921	.13
	(E)	202			101			101				

TABLE XXIV (Continued)

Cross (Female X Male)		Number of Seed in Classes								Total	Values χ²	Values P
	(O)	201			106			105		412	.247	.88
	(E)	206			103			103				
		1	2	3	4	5	6	7	8			
ROKY16 X Defective	(O)	4	8	19	58	62	12	-	1			
	(O)	6	12	20	69	89	13	-	3			
	(O)	-	7	22	58	75	28	-	1			
		Plump			Intermediate			Defective				
ROKY16 X Defective(R)	(O)	157			82			66		305	1.945	.37
E.R. 2:1:1	(E)	152.5			76.25			76.25				
	(O)	122			60			59		241	.046	.90+
	(E)	120.5			60.25			60.25				
	(O)	158			66			62		286	3.258	.18
	(E)	143			71.5			71.5				
		1	2	3	4	5	6	7	8			
ROKY16 X Defective(R)	(O)	6	14	24	35	43	22	1	3			
	(O)	1	7	26	49	28	6					
	(O)	1	6	31	57	47						
		Blue			Red							
ROKY16 X D. Redlan	(O)	125			36					161	.599	.43
E.R. 3:1	(E)	120.75			40.25							
	(O)	140			51					191	.295	.62
	(E)	143.25			47.75							

TABLE XXIV (Continued)

Cross: Female	Male		Number of Seed in Classes								Total	Values: X^2	P
		(O)	126			47					173	.433	.53
		(E)	129.75			43.25							
			1	2	3	4	5	6	7	8			
ROKY16 X D. Redlan		(O) blue	1	19	46	30	21	9	4				
		(O) red	2	10	16	9	8	2	4				
		(O) blue	6	17	39	29	25	10					
		(O) red	6	6	16	12	5	2					
		(O) blue	-	20	48	23	15	14	5	2			
		(O) red	1	8	9	12	7	6	4				
			Plump			Sugary							
ROKY16 X Sugary(R)		(O)	218			76					294	.114	.74
E.R. 3:1		(E)	220.5			73.5							
		(O)	220			73					293	.001	.90+
		(E)	219.75			73.25							
		(O)	254			81					335	.12	.73
		(E)	251.25			83.75							
			1	2	3	4	5	6	7	8			
ROKY16 X Sugary(R)		(O)	8	33	81	38	32	11	2				
		(O)	17	33	89	30	31	6					
		(O)	15	37	68	35	39	8					

TABLE XXIV (Continued)

Cross: Female	Male		Number of Seed in Classes								Total	Values: χ^2	P
			Plump			Sugary							
ROKY16 X Sugary(W)		(O)	251			90					341	.353	.59
E.R. 3:1		(E)	255.75			85.25							
		(O)	280			90					370	.091	.78
		(E)	277.5			92.5							
		(O)	305			110					415	.501	.50
		(E)	311.25			103.75							
			1	2	3	4	5	6	7	8			
ROKY16 X Sugary(W)		(O)	24	41	80	45	23						
		(O)	14	38	95	35	32	15					
		(O)	15	43	95	33	28	13					
			Plump			Sugary							
ROKY16 X Sugary(F)		(O)	430			149					579	.167	.71
E.R. 3:1		(E)	434.25			144.75							
		(O)	447			153					600	.08	.80
		(E)	450			150							
		(O)	497			158					655	.269	.63
		(E)	491.25			163.75							
			1	2	3	4	5	6	7	8			
ROKY16 X Sugary(F)		(O)	15	43	74	42	22	7					
		(O)	16	40	70	43	25	4					
		(O)	34	43	67	34	7	2					

TABLE XXIV (Continued)

Cross (Female)	Cross (Male)		Number of Seed in Classes								Total	Values X^2	Values P
			Plump			Dent							
ROKY16 X Dent(W)		(O)	159			57					216	.223	.66
E.R. 3:1		(E)	162			54							
		(O)	280			94					374	.004	.90+
		(E)	280.5			93.5							
		(O)	334			128					462	1.804	.18
		(E)	346.5			115.5							
			1	2	3	4	5	6	7	8			
ROKY16 X Dent(W)		(O)	7	38	56	25	13	10	4				
		(O)	6	31	81	29	16	16	6				
		(O)	8	35	65	28	24	21	5				
			Plump			Dent							
ROKY16 X Dent(R)		(O)	232			92					324	1.994	.17
E.R. 3:1		(E)	243			81							
		(O)	190			51					241	1.893	.18
		(E)	180.75			60.25							
		(O)	207			77					284	.676	.42
		(E)	213			71							
			1	2	3	4	5	6	7	8			
ROKY16 X Dent(R)		(O)	10	39	69	35	24	15					
		(O)	8	40	60	32	19	5					
		(O)	15	45	57	25	22	11					

TABLE XXIV (Continued)

Cross Female X Male		Number of Seed in Classes 1	2	3	4	5	6	7	8	Total	Values χ^2	P
BOKY29 X Wheatland	(O)	7	23	33	47	49	28	5	9			
	(O)	19	25	38	42	58	29	6	5			
	(O)	15	24	30	51	66	27	7	4			
BOKY29 X BOK8	(O)	10	13	40	17	19	11	-	1			
	(O)	38	56	46	11	16	14	5				
	(O)	15	36	42	17	17	7	5	3			
		Plump			Intermediate			Defective				
BOKY29 X Defective	(O)	255			116			110		481	1.898	.38
E.R. 2:1:1	(E)	240.5			120.25			120.25				
	(O)	262			120			131		513	.707	.72
	(E)	256.5			128.25			128.25				
	(O)	236			107			122		465	1.073	.60
	(E)	232.5			116.25			116.25				
		1	2	3	4	5	6	7	8			
BOKY29 X Defective	(O)		6	27	45	38	15	5	10			
	(O)		10	27	50	54	26	6	5			
	(O)	3	10	33	40	30	15	4	6			
		Plump			Intermediate			Defective				
BOKY29 X Defective(R)	(O)	81			29			29		139	3.805	.14
E.R. 2:1:1	(E)	69.5			34.75			34.75				

TABLE XXIV (Continued)

Cross: Female	Cross: Male		Number of Seed in Classes									Total	Values: X^2	Values: P
		(O)	91			42			37			170	1.142	.59
		(E)	85			42.5			42.5					
		(O)	111			48			45			204	1.676	.42
		(E)	102			51			51					
			1	2	3	4	5	6	7	8	9			
BOKY29 X Defective(R)		(O)	1	2	18	28	16	6	2	5	2			
		(O)	-	3	20	27	18	13	3	3	4			
		(O)	-	8	9	31	37	18	2	2	6			
			Blue			Red								
BOKY29 X D. Redlan		(O)	131			48						179	.315	.62
E.R. 3:1		(E)	134.25			44.75								
		(O)	113			31						144	.925	.33
		(E)	108			36								
		(O)	130			46						176	.121	.74
		(E)	132			44								
			1	2	3	4	5	6	7	8				
BOKY29 X D. Redlan		(O) blue	3	5	18	35	36	14	9	7				
		(O) red	3	7	8	23	5	2						
		(O) blue	1	12	27	28	24	11	8	2				
		(O) red	2	3	13	9	1	2	-	1				
		(O) blue	4	8	29	43	27	11	5	-				
		(O) red	5	5	13	21	2	-	-	-				

TABLE XXIV (Continued)

Cross			Number of Seed in Classes								Total	Values	
Female	Male											χ^2	P
			Plump			Sugary							
BOKY29 X Sugary(R)		(O)	81			28					109	.028	.90+
E.R. 3:1		(E)	81.75			27.25							
		(O)	87			30					117	.025	.90+
		(E)	87.75			29.25							
		(O)	127			34					161	1.293	.25
		(E)	120.75			40.25							
			1	2	3	4	5	6	7	8			
BOKY29 X Sugary(R)		(O)	8	34	27	13	1						
		(O)	6	31	60	24	5						
		(O)	4	22	31	9	8	1					
			Plump			Sugary							
BOKY29 X Sugary(W)		(O)	86			34					120	.711	.41
E.R. 3:1		(E)	90			30							
		(O)	123			48					171	.86	.37
		(E)	128.25			42.75							
		(O)	206			72					278	.12	.74
		(E)	208.5			69.5							
			1	2	3	4	5	6	7	8			
BOKY29 X Sugary(W)		(O)	19	40	55	41	32	13	3				
		(O)	2	11	31	25	8	3	1				
		(O)	7	35	37	28	6	3					

TABLE XXIV (Continued)

Cross: Female	Cross: Male		Number of Seed in Classes								Total	Values: X^2	Values: P
			Plump			Sugary							
BOKY29 X Sugary(F)		(O)	403			137					540	.04	.88
E.R. 3:1		(E)	405			135							
		(O)	634			220					854	.264	.65
		(E)	640.5			213.5							
		(O)	540			177					717	.037	.88
		(E)	537.75			179.25							
			1	2	3	4	5	6	7	8			
BOKY29 X Sugary(F)		(O)	1	11	58	46	35	5	2				
		(O)	6	21	69	54	39	20	5	1			
		(O)	7	18	75	43	17	7	-				
			Plump			Dent							
BOKY29 X Dent(W)		(O)	339			116					455	.059	.86
E.R. 3:1		(E)	341.25			113.75							
		(O)	320			119					439	1.04	.31
		(E)	329.25			109.75							
		(O)	249			93					342	.877	.36
		(E)	256.5			85.5							
			1	2	3	4	5	6	7	8			
BOKY29 X Dent(W)		(O)	5	5	25	39	61	32	9	13			
		(O)	4	12	35	41	54	23	9	5			
		(O)	7	12	35	34	42	24	8	12			

TABLE XXIV (Continued)

Cross			Number of Seed in Classes								Total	Values	
Female	Male											χ^2	P
			Plump			Dent							
BOKY29 X Dent(R)		(O)	416			150					566	.681	.43
E.R. 3:1		(E)	424.5			141.5							
		(O)	243			86					329	.228	.67
		(E)	246.75			82.25							
		(O)	103			35					138	.009	.90+
		(E)	103.5			34.5							
			1	2	3	4	5	6	7	8			
BOKY29 X Dent(R)		(O)	2	12	59	45	39	15	6				
		(O)	2	9	30	38	20	8	4	1			
		(O)	2	7	34	30	18	7	2				

[1]Expected ratio.

[2]Observed values.

[3]Expected values.

VITA

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Doctor of Philosophy

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