INHERITANCE OF CHAFF COLOR, HEAD SHAPE, AND GRAIN TEXTURE IN WHEAT

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The data presented in this thesis are the results obtained from a study of the F2 and F3 generations from a cross between the wheat varieties, Dicklow and Hard Federation. Toward the end of the summer of 1922 this problem was assigned to me by Professor George Stewart. The plants then growing in the field were in the F2 generation, the cross having been made in 1920 by Professor Stewart. The chief purpose of the cross was to improve the grain quality of spring-irrigated wheat by the application of Mendelian principles in such a way as to combine the high-yielding power of Dicklow with the good grain quality of Hard Federation. Before the data obtained in the cross are presented the history, description, and distribution of each parent will be given. This is followed by a brief review of the literature concerning inheritance of three characters in the wheat plant, viz., (1) chaff color, (2) head shape, and (3) grain texture.

**Dicklow**

**History.**—Dicklow wheat is a well-known variety in Utah, Idaho, and parts of Montana and Wyoming. The history of this variety is not definitely known. Aicher(1) states that "all information thus far obtained indicates that it is a selection from the old California Gem or California Club. Mr. James Holly of Utah County, Utah, obtained some California Club wheat from northern California and seeded it on his farm. Excellent results were obtained, and he called the attention of his neighbor, Mr. Richard Low, to his new wheat. Mr. Low obtained some and grew it. He noticed that the wheat contained different types and selected heads of the type he liked best. He grew this selection for several years and the neighbors began clamoring for "Dick" Low's wheat. As the wheat became spread over
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This high yield has been maintained at the Utah Station, it being one of the highest yielding spring wheat varieties. The chief drawback to this variety is the soft, opaque kernel which gives it rather poor bread-making qualities.

**HARD FEDERATION**

**History.**-- Hard Federation is not so well-known in Utah as Dicklow. It originated in Australia as a selection from the Federation variety, which resulted from a cross between Purple-straw and Yandilla. As Hard Federation resembles Federation, it might have been overlooked segregate. The following history is recorded in the AGRICULTURAL GAZETTE of New South Wales (Vol. 25, 1914):

"In consequence of the variations of the ordinary type exhibited by the strain of Federation wheat now being grown at Cowra Experiment Farm, it has been deemed advisable to apply a distinct name to it, and 'Hard Federation' has been selected as the most appropriate. The departure from type was first noted by J.T. Pridham, plant breeder, in 1907 or 1908, one of the plants selected from the stud plants being observed to thresh grain of remarkably hard and flinty appearance. The plant has the distinctive brown head and general appearance of Federation in the field, but the grain was of a class that had never been seen in the variety before. The seed was propagated, and in 1901 the occurrence of white heads was noticed, and from then until 1912 distinctly white heads were common among the brown, but in 1913 there were no white-eared plants, and it is hoped that the seed will now be true to type."

This variety was first introduced into the United States on August 26, 1915 (98). Mr. George Valder, undersecretary and director of the Department of Agriculture, Sidney, New South Wales, Australia, presented the seed of a number of the Australian wheat varieties, one of which was the seed of Hard Federation (S.P.I. No. 41079 and C.I. No. 4733).

**Description.**-- Hard Federation has the spring habit of growth, maturing rather early, with strong, short white stems. The spikes are awnless, oblong, rather dense, and erect. The glubes are glabrous, bronze, short, and wide. The beak, which is the short projection which terminates the keel of the glume, is about 0.5 mm. in length. Awns at the apex are wanting; kernel white, short, hard, and ovate.
Distribution.- According to Clark et al., Hard Federation was first grown at the Sherman County Branch Station, Moro, Oregon, in 1916, and when grown in 5-foot rows gave unusual promise. As a result, increased rows were sown in 1917 and sown to plats in 1918. A small quantity of seed of this variety was sent to Chico, California, for sowing in the fall of 1917. From two years' results (1917 and 1918) the following conclusions are reached by the investigators: Hard Federation (C.I. No. 4733) was the highest yielding variety of spring wheat grown at the Sherman County Branch Station in 1918. It outyielded Federation by only 0.3 bushel, but it outyielded both the Marquis and Early Baart varieties by more than 6 bushels and Pacific Bluestem by more than 7 bushels, per acre. In 1919 Hard Federation again outyielded all other spring varieties except Federation, and it yielded the same, 28.7 bushels. This yield was more than 4 bushels greater than those obtained from Early Baart and Pacific Bluestem and nearly 6 bushels greater than the yield of Marquis. For the two years, 1918 and 1919, Hard Federation had an average yield of 25 bushels per acre, or 5.4 bushels more than Early Baart, 6.1 bushels more than Marquis, and 6.6 bushels more than Pacific Bluestem.

At Chico, California, Hard Federation has not yielded so well. Though yielding the common commercial varieties of that area, it yielded less than White Federation, another of the Australian wheats.

Baking tests of flour made from Hard Federation grown at Moro, Oregon, in 1918 and 1919 show it to be superior to any of the white wheats now grown, also better than Kharkof, a winter wheat, and comparing favorably with Marquis. When grown on California soil, Hard Federation is also a better milling and bread-making wheat than Marquis and Kharkof and holds the same position with the white-kerneled wheats in California as at Moro, Oregon. At the Nephi Dry-farm Substation (Utah) Hard Federation has not maintained the high yield it did at Oregon and California.
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In favorable years the yield has been just slightly under that of the better spring wheat varieties, while in unfavorable years the yield is considerably lower. Under irrigation at Logan, Hard Federation has given fair yields. However, the good milling and bread-making quality possessed by this variety makes it a valuable parent to be crossed on high-yielding varieties in improving the quality of spring-irrigated wheats.

REVIEW OF LITERATURE

Inheritance of Chaff Color.—The inheritance of chaff color in wheat has been reported by many investigators. Spillman (81) was one of the first workers to report inheritance of this nature. In crossing brown- and white-chaffed varieties, brown proved dominant. The F2 segregated into 3 brown to 1 white. In other crosses involving red-, grey-, and white-chaffed parents, the red and the grey was each dominant over white. However, individual plants in the F2 generation exhibited extremes in color, being both darker and lighter than either parent. Biffen (10) in England found red dominant over white in the ratio of 3 red to 1 white. Similar results were obtained by Hayes (39a) of Minnesota and Henkemeyer (45) of Germany. When brown- and white-chaffed wheats were crossed, brown dominated giving a 3:1 ratio in the F2. Crossing spelt on common wheat, red chaff proved dominant, giving a simple Mendelian segregation in the F2 generation (Mayer-Gmelin, 61).

Fultz Mediterranean (white chaff) when crossed on Harvest King (red chaff) gave red dominant, the F2 segregating into a 3:1 ratio. However, when Turkey Red was crossed with Harvest King the F1 generation was all red, the not as red as the red parent. The F2 gave 1 red, 2 intermediate, to 1 white. Reciprocal crosses gave similar results. When Black Winter Emmer, having a black or purplish black chaff, was crossed on Fultz Mediterranean the F1 gave an intermediate inher-

Inheritance, being more of a mulatto black. The segregation in the F2 was somewhat varied. Plants appeared with red and brown chaff which was not visible in either parent. Considering those colored, regardless of the color and those without color they approached a 3:1 ratio (54). Incomplete dominance is also reported by the Howards (50) of India. In five different crosses of red- and white-chaffed varieties the F1 was intermediate in color. The F2 gave 3 red to 1 white. After brown had proved dominant over yellowish-white in the F1, Tschermak (88) failed to obtain a clear-cut segregation in the F2.

Variations from the normal 3:1 ratios are few. Mortensen (65) after a study of three crosses -- Sevier x New Zealand, Sevier x Dicklow, and Sevier x Little Club -- reports a ratio of 9 red to 7 white in the F2 generation. Sevier was the red-chaffed parent in each case. Separating the F2 generation into dark bronze, medium bronze, light bronze, and white from a white-bronze cross Beach (7) reports a 9:3:3:1 ratio.

In crossing durum on common wheat Love and Craig (59) report a 15:1 ratio for red and white. In this cross two plants characteristic of the wild type appeared in the F2 segregates. Seed from these two plants was sown and the one plant produced progeny that segregated into an approximate 3:1 ratio for red and white. Nilsson-Ehle (68) obtained similar results when certain brown- and white-chaffed crosses were made. The F2 segregated into 15 brown to 1 white. He explains his results on the assumption that brown color is the result of two similar independent factors.

Inheritance of Head Shape. -- Carman (16) is one of the first men to report inheritance of head shape. Crosses between common wheat and rye gave heads 7 inches long, others scarcely two inches long, and some with compound spikelets in the F2 generation. The work of Spillman, reported by Hurst (51), is of interest. The work
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was done before the rediscovery of Mendel's paper. Some 97 successful crosses were made involving *T. compactum* and *T. vulgare* parents. The F₁'s were intermediate and the F₂'s approached a 1:2:1 ratio. Similar intermediate inheritance was obtained by Rimpau(73) from crossing lax and moderately lax heads. The F₂ varied within the respective parental ranges. Crossing clubbed and lax varieties of winter and spring wheat gave a clubbed head intermediate in length in the F₁. The F₂ segregated into 1 clubbed, 2 clubbed intermediate in length to 1 long head. Homozygous intermediates did not appear in the F₃, thus indicating that the intermediate was the hybrid and resegregates(34). Incomplete dominance occurred when Devon wheat, which has a lax head, was crossed on Hedgehog, a clubbed wheat. Crossing long and compact sorts on a short head Wilson(92) reports an F₁ slightly longer than the shorter parent; the F₂ gave a 3:1 ratio. He further stated that it would be possible again to separate the short group into very short and medium long, the latter being the hybrid. Similar results were obtained by Boshnakian(2a) when lax and dense head types were crossed; the F₁ was dense tho not as dense as the parent. The F₂ gave a 3:1 ratio. He concluded that only one factor is involved in the production of density. A study of three crosses reported by Mortensen(65) indicates an intermediate in the F₁. The parents varied from clubbed to lax. The F₂'s were classified into clubbed compact, medium club, long compact, and long loose. Calculations from the number of plants in each group gave a close approach to a 9:3:3:1 ratio.

Thus far, simple Mendelian segregations have been considered wherein the dominance was incomplete. The classification of the material has been based only on the visible appearances of the head with no definite measurements of either parent or offspring. Biffen(9) and Parker(70a) attempted measurements
on head type in an effort to determine the nature of inheritance. Biffen(9) made crosses between Square Heads Master and Red King. The internode length of the former averaged 3.2 and that of the latter 4.6 mm. The F1 gave an average internode length of 4.8 mm, which was more lax than the lax parent. The F2's were divided into two classes: (1) those with an average internode length less than 4.6 mm, and (2) those with an average internode length more than 4.6 mm. On this basis the distribution approached very closely to a 3:1 ratio for dense and lax. Many of the plants gave more lax heads than the lax parent, but none appeared more dense than the dense parent. In another cross involving Rivet and Polish wheat the internode lengths were 3.6 and 6.6 mm, respectively, the F1 giving an intermediate length of 5.8 mm. The F2 ranged from 3.1 to 6.8 mm in average internode length. Grouping them into three classes (two like parents and an intermediate) suggested a 1:2:1 ratio. Parker(70a) made crosses between club and moderately lax sorts. The lax parents were of hybrid origin, tho having bred true for several generations. An attempt was made to separate the F2 material from the one cross by visible appearances into two types. This separation proved rather unsatisfactory. It was found that plants could not be divided into definite groups as was first that, but they formed rather a continuous series varying from very lax to very dense. The grouping when later checked in the F3 generation gave a close approach to a 3:1 ratio.

As a result of the lack of satisfaction encountered with the F2 material of the first cross he decided to submit the material from the other cross to accurate measurements by finding the internode length of the main tillering spike of each plant. The parents consisted of a clubbed and moderately lax-headed type. Internode length of the club was from 1.9 to 2.5 mm, while that for the moderately lax was from 3.9 to 5.1 mm. Measurements of the F1 internode length
were not obtained. However, from photographs and data obtained it was apparently an intermediate. The internode length of the F$_2$ ranged between 1.5 and 5.7 mm. Types appeared even more lax and dense than either parent. Judging from the offspring of the F$_2$ plants it was decided to consider the break between homozygous and heterozygous types at about 3.7 mm in length. From this point of division the ratio of dense to lax was 2.6:1.0, indicating a simple Mendelian ratio. Parker(70a) goes on to state that this seems to indicate the mode of inheritance of the two main divisions but does not account for the extreme lax and dense heads. He further states that environment probably influences the internode length to a greater or less extent. Considerable evidence is given to substantiate this belief. He finally concludes that internode length is not a fine enough measurement in determining density.

Interesting results were obtained by Nilsson-Ehle which are reported by Newman(65a). In crosses between compact and squarehead(mid-dense) wheats, he obtained compact forms in the F$_1$, and the F$_2$ segregated into compact, mid-dense, and lax. He explains his results on the assumption that compactum carries an "inhibiting" factor which is absent in the other parents used in the cross. He believes this factor is largely responsible for the extreme shortness of the internode of this type. In the absence of this factor, compactum would become one of the common open-headed wheats of the country. When compactum is crossed with a square-headed sort, the behavior is similar to the crossing of an open-headed sort with squarehead, or some such sort with average density. Some have found that when crossing open-headed on squareheads the open are dominant. The F$_2$ generation will be characterized by a majority of open heads. By crossing compactum on squarehead, the long open type prevails instead of the squareheads. This is explained by supposing the main factor difference to be as follows:
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Compactum -- C C L\textsuperscript{1} L\textsuperscript{1} L\textsuperscript{2} L\textsuperscript{2}  
Squarehead --- c c l\textsuperscript{1} l\textsuperscript{1} l\textsuperscript{2} l\textsuperscript{2}

The C factor was considered to inhibit the expression of the lengthening factors L\textsuperscript{1} and L\textsuperscript{2} which resulted in short internodes whenever C was present. If a checker board is constructed to show the possible combinations, it will be seen that there are 64 possibilities. Classifying the individuals gives 48 compact, 15 lax, and 1 squarehead. This accounts for the limited number of squareheads found by Nilsson-Ehle.

Mayer-Gmelin\cite{61} suggests that Nilsson-Ehle's explanation will probably account for the relatively few squareheads that appeared in the F\textsubscript{2} 's from a Compact x Squarehead, but does not account for the appearance of more compact individuals in the segregates than either parent. Mayer-Gmelin\cite{61} found that when Essex, one of the common wheats with compact heads, was crossed on spelt with a lax head the F\textsubscript{1} was intermediate in head length. The F\textsubscript{2} gave plants some of which were similar to the F\textsubscript{1}, others as long as the spelt, and still others actually more compact than the Essex parent. In another cross wherein both parents were lax, individuals appeared in the F\textsubscript{2} with compact heads. Contrary to the belief of Nilsson-Ehle that C is purely inhibiting and negative and the only action it exerts is to prevent the other factors from showing their effect, Mayer-Gmelin suggests that the factor C seems to exert a direct determinative, positive action. Results of this nature have been satisfactorily explained by the multiple factor hypothesis. The number of factors involved cannot accurately be determined. Nilsson-Ehle states that in addition to the main factor differences there are other minor factors which influence spike density and account for a wide range of homozygous forms\cite{40}. 
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Others have encountered difficulty in working out the inheritance of a squareheadedness. Rumker(71) found that when squareheaded types were crossed on vulgare of rather lax-head type, the F2 population was characterized by varied amounts of squareheads which varied in degree. Kajanus(53) found lax heads dominant over squareheads, tho when true compact is crossed on lax heads the compact is dominant. Crossing long and short heads and open and compact heads the mode of inheritance was rather irregular. It was not always possible to make very accurate classification on the F2 individuals. Crossing Fultz Mediterranean(dense head) on Black Winter Emmer(mid-dense head) the F2 generation was rather varied. Some of the heads possessed long, loose, jointed rachises; some close and compact; some clubbed; other intermediate. Some forms appeared with branching spikelets, others resembled spelt, others wheat, and some emmer. Certain forms of heads are always self-sterile, thus preventing further propagation(54).

It appears from the literature reviewed that many investigators report a simple Mendelian inheritance when true compact and lax parents are crossed. The compact type is dominant, but is not always completely so, being more often an intermediate. Occasionally when two lax-headed varieties are crossed rather compact types appear in the F2 generation. When one parent is of the square-headed sort often complicated inheritance results. Boshnakian(5) points out that squareheadedness is the result of growth factors, and he failed to obtain any definite ratios in crosses involving a squareheaded parent.

Possibly the greatest factor contributing to the conflicting results obtained by the various investigators is the lack of standardization in the use of terms. For example, "squareheadedness" as used by one investigator might be entirely different in the mind of another. Until terms are standardized results are not comparable but only suggestive.
Inheritance of Grain Texture.— Experiments have shown that Turkey wheat, the most famous variety grown in the United States today, when taken out of the wheat belt and grown under more humid conditions loses its quality as a bread-making wheat. Turkey is not the only variety that deteriorates; others have done likewise. Is it not possible to produce a strain or variety of wheat that will maintain its quality under the most adverse conditions? If one were to draw conclusions from literature written on the causes of wheat deterioration he would surely feel doomed to be content with the situation as it is now. However, when one reads of the results accomplished by plant breeders, is it not possible to produce varieties with superior qualities under the most adverse conditions? A review of the literature on this subject might give some light on the nature of grain-texture inheritance.

Bryan and Pressley(13) report that in a cross between Turkey and Sonora, the F2 segregated into a 1:2:1 ratio. The two types of texture segregated sharply in the F2 and have maintained their identity, suggesting a fair indication of a single-factor difference in the two degrees of texture. Similar results have been obtained by the Howards(50). Crosses involving varieties (one of which was soft and opaque, the other hard and translucent) gave intermediate inheritance in the F1. The F2 segregated into 1 soft, 2 semi-translucent, and 1 translucent. Nitrogen determinations were made on some of the F2 plants. There seemed to be no relation between translucency and high nitrogen content — both characters seem to be inherited separately. Results obtained from crossing Turkey and Jenkins led Nightingale et al.(66) to conclude that the horny endosperm of Turkey is transmitted as a unit character, the segregation taking place in the F2 generation. Other crosses involving hard- and soft-grained varieties have given simple 3:1 ratios for hard and soft in the F2(7,65).
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To show what can be accomplished by persistent work and because of the extreme importance of this character, the work of Biffen and Humphries(11) and Freeman(29) will be given in some detail.

Farmers, millers, and plant breeders of England had long felt the need of improving the bread-making qualities of English wheats and thus keep the money at home that is spent for importing hard wheats from the United States and Canada to mix with the local weak-quality varieties. Finally a committee (known as the Home-Grown Wheat Committee) was appointed to investigate the situation. A large number of varieties were imported from various hard-grain producing sections. Among other varieties was the variety Fife from Canada. When tried in trial plots it was the only variety which retained its strength when grown under English conditions. It chief drawback was that it did not yield nearly as well as local varieties. This resulted in the crossing of Fife and local high-yielding strains.

In certain of the crosses the strong (meaning the ability to make good bread) parent proved completely dominant over the soft. In other crosses the dominance was not complete, the $F_1$ being intermediate. Likewise, certain of the $F_2$ generations gave clear-cut segregations into hard and soft, while others gave hard and soft as extremes with all gradations between. Some of the kernels that appeared hard had a few starchy flecks. Still others that appeared soft had a few flecks of glutinous patches. These flecked kernels proved to be heterzygous in the $F_3$, while the extremes of hard and soft were homozygous and bred true. Many of these hard homozygous strains were sown in plots the following year. Baking tests were made of these strains, and it was evident that some possessed the good bread-making quality of Fife, the strong parent. From this they concluded that strength and lack of strength segregate in the $F_2$ generation in a similar manner to morphological characters(11).
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Biffen and Humphries\(^{(1)}\) report another cross between \textit{Triticum polonicum} (Polish wheat) and \textit{Triticum turgidum} (Rivet wheat). The purpose was to study the nature of nitrogen inheritance as found in wheat and find out if total nitrogen is an index to the bread-making quality of the wheat. In general, it has been shown that total nitrogen is usually higher in strong wheat than in weak. However, a strong wheat grown under adverse conditions may actually contain less nitrogen than a weak wheat grown under favorable conditions. If the total nitrogen is an index to strength it would eliminate the growing of large quantities of large number of varieties for baking tests. Polish wheat has an unusually high nitrogen content; the grain is brittle, translucent, and white. Rivet wheat is a typical starchy, soft, mellow, red-kerneled wheat low in nitrogen. The average nitrogen content is 2.2 and 1.6 per cent, respectively. In the F\(_1\) generation the grain was uniformly brittle, translucent, and red. Nitrogen determinations were not made of the F\(_1\) plants because they were grown at such wide intervals. From the appearance of the grain they judged it to be high in nitrogen. Segregation for translucent and starchy occurred in the F\(_2\) and approached a simple Mendelian ratio, but the segregation was not clear-cut. Plants appeared which were rather intermediate. This was rather unexpected as the parents had retained their respective texture under similar conditions.

From nitrogen determinations made on these F\(_2\) plants, it was evident that nitrogen contents of from 1.3 to 1.6 or from 2.2 to 2.6 marked with approximate accuracy the pure low or high plants. The heterozygotes were intermediate in nitrogen content and could be distinguished to a rather accurate degree by analysis. They concluded that segregation of the different nitrogen percentages will take place in the F\(_2\), it being possible to isolate them in the F\(_3\). Some of the homozygous strains grown under rather preliminary tests have given promising yields. They are confident of producing strong high-yielding wheats for English conditions by hybrid-
Freeman (29) crossed macaroni wheat with high gluten content on Sonora, a good yielder but with a low gluten content. The aim of the cross was to produce a high milling wheat for the warm climate of Arizona. The F1's were intermediate in texture. Classification of the F2 population was difficult because of various gradations in grain texture -- from a hard translucent kernel similar to the macaroni parent to a soft opaque texture of the soft parent. A classification was attempted into hard, soft, and intermediate. The F3 generation bore out the classification to a reasonable degree, that is, hard-grain plants in the F2 gave only hard and intermediate in the F3, while plants selected with soft grain from the F2 gave soft and intermediate in the F3. Intermediates selected from the F2 gave all classes in the F3. From the ratios obtained in this cross, Freeman suggests an explanation by the appearance of two factors controlling the relative proportions of gluten and starch in the endosperm of the wheat cross studied. The factors show incomplete dominance over their absence and appear to be accumulative in their effect.

In this cross Freeman classified the grain into three types: (1) true hard kernels, (2) true soft kernels, and (3) yellow berry or spotted kernels. True hard kernels are distinguished by the translucent character of the kernel. According to Freeman (29) it is due to the ratio between gluten and starch. When this ratio is high the cell contents are cemented together solidly as the grain dries out in ripening. This gives them a hard, glassy, semi-transparent texture. When the gluten is sufficiently low the cells on drying out at ripening time are not entirely cemented together and air fills in the uncemented cells giving the soft, starchy, opaque appearance. Thin cross-sections of wheat kernels were prepared by cutting and further ground with a hone. When examined under the microscope the spots in the yellow-berry kernels were made up of flakes, whereas
those of the true soft wheats are diffused. Yellow-berry spots are very sensitive to environmental conditions, while true soft is not so sensitive. Freeman concludes that the genetic factors governing the appearance of yellow berry are apparently distinct from those governing true softness. The yellow berry is very sensitive to environmental influences, yet controlled experiments indicate that genetic factors, for a greater or less degree of sensitiveness, are inherited as definitely as other factors governing qualitative characters.

From a review of the literature it appears that grain texture as reported by many investigators is a simple Mendelian character. Certain investigators report hard to be dominant; others report soft to be dominant; whereas others report an intermediate inheritance in the F1. When species crosses are made it often complicates the inheritance as found by Freeman (29). The evidence indicates the possibility of producing strains by hybridization that will retain their strength under rather adverse environmental conditions. We might conclude by stating the words of Biffen: "Mendel's law of inheritance applies to morphological, histological, and constitutional characters, and one can probably recognize as many pairs of characters as there are minute differences between the varieties experimented with".

**PLAN OF THE EXPERIMENT**

As previously stated, the cross was made by Professor Stewart in the summer of 1920. The data concerning the cross up to the F2 generation were furnished by him.

It is known that wheat belongs to a group of plants which are normally self-fertilized except in rare cases. The cross is made at about the time the ovaries are sufficiently mature and before the anthers have broken. All but the outer florets of eight or ten of the central spikelets are removed. The
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upper and lower spikelets are cut off with shears. The central floret of each spikelet is removed by grasping it near the top with forceps and pulling downward. The forceps are then carefully pushed between the lemma and palea and the flower opened. The three stamens are then removed, care being taken not to break open the anthers lest self-fertilization result. When all the stamens are removed pollen from the other parent is secured and shaken on the stigmas in each floret. They should be obtained from anthers that have turned yellow but not broken. Usually a single anther is placed in a floret that has just dehisced or is just ready to. When many crosses are to be made time may often be saved by small portions of pollen on the stigma. After all the emasculated florets are pollinated, the head is wrapped up with a leaf from the wheat plant and labeled. When the grain is mature the heads are broken off and reserved until the next planting season.

At the time of planting the grain was planted in rows two feet apart, with the kernels about a foot and a half apart in the row. This gave each plant ample room for tillering, with a maximum production of seed for sowing the next season. Planting was done on the college farm east of the windbreak.

When the grain was mature it was harvested and taken to the laboratory. This material constituted the F1 generation. Detailed notes were not obtained on this generation. Thus the texture of the grain in the F1 generation is not known. However, the chaff was bronze similar to the Hard Federation parent. The heads were rather dense and slightly enlarged (clubbed) at the apex. This enlargement at the apex is characteristic of the Dicklow parent. Later, the heads were threshed and saved for the next season's planting. The threshing was done by placing the heads in a small sack and beating the grain out. The chaff was removed by placing the contents of the sack into a sieve and holding it over an electric fan; the chaff being lighter than the grain, the two were readily separated.
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At planting time the seed from the F₁ plants were sown in rows about two and a half feet apart with 3 or 4 inches between kernels. Just before harvest the plants which now constitute the F₂ generation were turned over to me, as previously stated. Counts were made of the total number of plants in the field to see if there was any indication of sterility. An attempt was also made to study the height of plants, but the soil was too heterogeneous to permit such a study.

After heading when counts were being made, it was noticed that a rather large number of dwarf plants occurred. They appeared like bunches of grass -- some sending up a few spindly culms, while others failed to head out at all. Many of the spikes produced kernels, though many were shrunken and immature; others failed to produce seed at all. Some of the plants had red chaff, others white, and some could not be determined for color because of immaturity. Because of this immaturity an accurate classification of these dwarf plants was impossible.

All the F₂ plants were harvested by pulling up the entire plant. These were grouped into various classes for genetic data. Out of these groups plants were selected for the next season's planting.

EXPERIMENTAL RESULTS

From the description of the parents the chief distinguishing differences are chaff color, head shape, and grain texture. Before a discussion as to the mode of inheritance of these characters a consideration will be given to the dwarf plants that appeared in the F₂ and F₃ generations. Both parents are tall and the appearance of dwarf plants (ranging in height from 10 to 16 inches) was rather unexpected.
Fig. 1. Showing the parents. Hard Federation on the left and Dicklow on the right with dwarf plants between.
Counts were made of the total number of plants growing in the field. Only the tall plants were harvested and counted. By subtracting the number of tall plants harvested from the total field count it was possible to obtain the approximate number of dwarf plants. Table 1 shows the relationship between tall and dwarf plants.

Table 1. The number of tall and dwarf plants that appeared in the F2 generation

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Tall Plants</th>
<th>Dwarf Plants</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>5514</td>
<td>4170</td>
<td>1344</td>
<td>3.02 : 0.98</td>
</tr>
<tr>
<td>Theoretical</td>
<td>4136</td>
<td>1378</td>
<td>3.0 : 1.0</td>
</tr>
</tbody>
</table>

From a study of the above table a close approach to a 3:1 ratio for tall and dwarf plants is evident. With the little data at hand it is impossible to formulate any explanation for the appearance of these dwarf plants. Are they accidental and just happen to approach a 3:1 ratio? Or do they follow certain definite laws?

The data obtained from the F3 generation seem to substantiate the latter view. Certain tall plants selected from the F2 generation again segregated into tall and dwarf in the F3 generation. Counts were made of each. Table 2 gives the tall and dwarf plants appearing in the F3 segregates.

Table 2. The number of tall and dwarf plants that appeared in the F3 generation

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Tall Plants</th>
<th>Dwarf Plants</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1433</td>
<td>1125</td>
<td>308</td>
<td>3.1 : 0.9</td>
</tr>
<tr>
<td>Theoretical</td>
<td>1076</td>
<td>359</td>
<td>3.0 : 1.0</td>
</tr>
</tbody>
</table>

The Inheritance of Chaff Color, Head Shape, and Grain Texture in Wheat. -- 20.
The results of the F\textsuperscript{3} generation as presented in the above table seem to affirm the data obtained in the F\textsuperscript{2} generation. Unfortunately, seed from the dwarf plants was not planted, so the behavior in later generations is not known. Other crosses involving the Federation wheats have given similar results, suggesting that it plays no small part in producing dwarf plants. A more detailed investigation of these dwarf plants is necessary before any plausible explanation is possible.

From an economic point of view the inheritance of head shape and chaff color is possibly of little importance, but from a scientific point of view it is of great importance. A knowledge of the inheritance of these characters might suggest the nature of inheritance in other more economically important characters. Grain texture, however, is of vital importance both from an economic and genetic point of view. Economically, it is of importance to the farmer, the miller, and the consumer; genetically, it is of interest and importance to the plant breeder.

**Inheritance of Chaff Color.** Chaff color is one of the major characters in the classification of wheat. Usually a mature plant will develop the color characteristic of the variety, though under adverse conditions, such as drought, the color may be modified to a certain extent. The parents reported in this cross are characterized one by bronze and the other by white chaff. Bronze refers to sort of a reddish-brown color. White refers really to a yellowish-white.

Grouping the F\textsuperscript{2} and F\textsuperscript{3} generations in respect to color resulted in two groups: (1) all plants displaying any tinge of reddish-brown made up the group designated as bronze, (2) all plants lacking this color formed the group designated as white. The number in each group is given in Table 3.
The Inheritance of Chaff Color, Head Shape, and Grain Texture in Wheat. --22.

Table 3. Number of plants with bronze and white chaff in the F₂ generation

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Total Bronze</th>
<th>Total White</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>4173</td>
<td>3076</td>
<td>1097</td>
<td>2.95:1.05</td>
</tr>
<tr>
<td>Theoretical</td>
<td>3130</td>
<td>1043</td>
<td>3.0:1.0</td>
</tr>
</tbody>
</table>

An approach to a simple Mendelian ratio is shown by the above table. Probably only a single factor difference for color is involved.

Theoretically, provided the grouping was accurate, the 1097 plants in the white group are recessive for color and should breed true for white in the F₃ generation. One-third of the 3076 in the group are homozygous for color and should breed true in the F₃; the other two-thirds are heterozygous and will again segregate. The data obtained in the F₃ generation verify this expectation to a rather accurate degree.

Because of the extreme rate in which wheat propagates itself by the production of seed, it is practically impossible to grow all the progeny of the F₂ generation in separate rows. Consequently, only 279 plants were selected for replanting. The grain from each plant was seeded separately in rows 15 feet long with a 2-foot space between rows.

As expected, many of the rows showed segregation for color in the F₃ generation. Twenty-two of these rows were again classified into bronze and white. This classification is presented in Table 4.

Table 4. Number of plants with bronze and white chaff in the F₃ segregate

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Bronze</th>
<th>White</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>3461</td>
<td>2530</td>
<td>931</td>
<td>2.9:1.1</td>
</tr>
<tr>
<td>Theoretical</td>
<td>2596</td>
<td>865</td>
<td>3.0:1.0</td>
</tr>
</tbody>
</table>
From a study of the above table the distribution in each group shows a close approach to a 3:1 ratio. This is in agreement with the results obtained from a classification of the F₂ generation. Chaff color is quite a stable character, and a mature plant grown under average conditions will usually express this character, provided the hereditary qualities are present. Thus a separation for color was rather easy, and when checked by the F₃ generation proved quite accurate. Only three plants selected as white turned out to be bronze. Those selected as bronze gave almost exactly one-third bronze and two-thirds re-segregated.

In conclusion it appears that the inheritance of chaff color, as determined, is in agreement with results obtained by most investigators.

**Inheritance of Head Shape.** — The head is the entire inflorescence on one culm. It is more often spoken of in literature as the spike, and occasionally it is designated as the ear. Possibly no other character in wheat varieties is quite so variable as that of head shape. This does not refer to the influence of environment (though that plays an important part) but to the characteristic head types of different varieties. The parents in this cross differ in head shape. Hard Federation has an oblong rather dense head, while Dicklow possesses a head that is rather compact and enlarged at the apex which is spoken of as a clavate head.

The F₂ plants were grouped into two classes — one designated as clubbed (which was not a true club, but only enlarged at the apex and included various degrees of density), and a second class which included all others and designated as long loose. This again, is a misleading term as the true differentiation was the clavate character and not the degree of density, and not the degree of density, as is suggestive by the term "long loose". The distribution obtained in each group from this classification is given in Table 5.
The Inheritance of Chaff Color, Head Shape, and Grain Texture in Wheat. -- 24.

Table 5. Distribution of plants with clubbed and long, loose heads in the F2 generation

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Heads</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Clubbed</td>
<td>Long, loose</td>
</tr>
<tr>
<td>4173</td>
<td>3413</td>
<td>760</td>
</tr>
<tr>
<td>Theoretical</td>
<td>3130</td>
<td>1043</td>
</tr>
</tbody>
</table>

The data in the above table include all the plants in the F2 generation which originally came from 17 cross-fertilized flowers using the same parents in all cases. The table shows a wide variation from the expected ratio. A study was made of the progeny of each original cross with the thought that possibly a slight variation in the parents might complicate the results expressed on the total basis; or that certain original crosses tended to produce a higher per cent of plants with the clavate head character than others. By comparing the progeny in the F2 and F3 generations that originally came from the same cross it might give some light on the question. The data from the F3 generation were obtained only from those rows segregating for this character. This relationship is given in Table 6.

Table 6. Showing the relationship between the ratio of clubbed to long, loose obtained in the F2 generation to the per cent of clubbed obtained in the F3 generation from each original cross

<table>
<thead>
<tr>
<th>Cross No.</th>
<th>Ratio of Clubbed to Long Loose in F2</th>
<th>Per cent of Clavate in F3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5.2:1</td>
<td>15.9</td>
</tr>
<tr>
<td>4</td>
<td>2.9:1</td>
<td>29.0</td>
</tr>
<tr>
<td>5</td>
<td>8.7:1</td>
<td>45.6</td>
</tr>
<tr>
<td>6</td>
<td>3.1:1</td>
<td>0.0</td>
</tr>
<tr>
<td>7</td>
<td>2.1:1</td>
<td>0.0</td>
</tr>
<tr>
<td>8</td>
<td>4.9:1</td>
<td>30.0</td>
</tr>
<tr>
<td>9</td>
<td>5.8:1</td>
<td>4.5</td>
</tr>
<tr>
<td>10</td>
<td>4.3:1</td>
<td>24.1</td>
</tr>
<tr>
<td>13</td>
<td>9.0:1</td>
<td>24.8</td>
</tr>
<tr>
<td>14</td>
<td>5.6:1</td>
<td>22.4</td>
</tr>
<tr>
<td>15</td>
<td>7.3:1</td>
<td>34.7</td>
</tr>
<tr>
<td>16</td>
<td>4.0:1</td>
<td>9.0</td>
</tr>
</tbody>
</table>
The Inheritance of Chaff Color, Head Shape, and Grain Texture in Wheat. --25.

The above table seems to indicate that whenever there was a wide ratio between clubbed and long loose in the F2, clubbed plants appeared in the F3. However, they do not always appear in proportion to the width of the ratio, that is, when the progeny of a cross gives a high ratio of clubbed to long loose in the F2, a proportionately high ratio does not necessarily follow between the two characters in the F3 generation. From the little data obtained it appears that the environment, as pointed out by Boshnakian(5), plays a very important part in the modification of this character. This is also borne out by field observations. Rows that appeared to be breeding true for an oblong and rather dense head type gave one or two distinctly clavate heads at the end of the row where it had an advantage because of extra feeding area, as between each belt of rows there was a 3-foot alleyway. Heads on these same plants exhibited a great variation in respect to this character, some not so fully mature often lacking the character entirely. The Dicklow variety when growing under favorable conditions develops a large majority of the heads with this clavate character, but while growing under adverse conditions few clavate heads appear. (See Picture on next page.)

From an examination of the F3 generation and results obtained in the F2, it was decided to classify the heads into three groups: (1) Those that displayed the clavate character constituted one group and were designated as long compact clavate; (2) those that were long and compact but not clavate were designated as long compact; and (3) the others which were long and loose constituted the other group. These terms are more descriptive of the true head type in each group. The results obtained on the long compact clavate group have been presented in connection with the F2 data, so it will not be necessary to re-consider them here. However, it might be stated that no definite segregations took place in the F3 generation in regard to this character. Some rows displayed quite a large number of plants of this type, others only a few.
The long compact and long loose head characters are more stable, and definite segregation seems to take place. The following table shows the distribution in each of the groups obtained from a classification of the $F_3$ generation.

Table 7. Showing the relation of long compact to long loose in the $F_3$ segregates

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Long Compact</th>
<th>Long Loose</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1175</td>
<td>894</td>
<td>281</td>
<td>3.04:0.96</td>
</tr>
<tr>
<td>Theoretical</td>
<td>882</td>
<td>293</td>
<td>3:1</td>
</tr>
</tbody>
</table>
The data presented in the above table were taken only from those segregating for these characters in the F3 generation. It appears from a study of the table that these characters follow Mendelian principles.

In conclusion, the data seem to indicate that the clavate head type is influenced to such a degree by environment that no definite ratios are obtainable. However, a more thorough study of this character in later generations is necessary to substantiate or disprove the conclusions thus far drawn. Long compact and long loose head types appear to be much more stable under varying influences and follow rather closely to a simple Mendelian ratio.

Inheritance of Grain Texture.-- Probably no other character in wheat is influenced by environment to such a degree as grain texture. Attempts have been made to find some easily determined character that is correlated with bread-making quality. As yet this has not been successful, tho in general a good bread wheat is characterized by a hard translucent grain with a rather high percentage of nitrogen and gluten with proper proportions of gliaden and glutenin in the gluten.

Texture, as used in this thesis, refers only to the degree of hardness. This was determined by cutting with a pocket knife or biting several kernels from two or three of the better developed heads on the plant. The hard kernels were relatively hard and translucent, whereas the soft kernels were opaque and starchy.

According to the U.S. grain standards the grain from the Hard Federation parent normally grades as hard white, tho under unfavorable conditions it may grade soft white. Dicklow always grades soft white. The bread-making quality of each parent has been determined. That of Hard Federation is superior to Dicklow, probably greater than the degree of hardness between the two parents.

An attempt was made to classify the F2 generation into two groups -- hard and soft. The segregation was not clear-cut by any means. Various grade-
The Inheritance of Chaff Color, Head Shape, and Grain Texture in Wheat. -- 28.

tions prevailed between very hard and translucent to soft and chalky. The decision as to hard and soft was based possibly more on kernel translucency than on the degree of hardness. In attempting to determine hardness, it is extremely difficult to know just where to draw the line between hard and soft. The grain from the plants just brought in from the seedhouse, where it was stored, to the laboratory was much easier to cut or chew than the same grain after being in the warm laboratory a few days. This was probably due to considerable extent to a difference in moisture content.

Hard kernels seemed to predominate, and from a study of this generation alone one would have concluded that hard was dominant (tho possibly not completely), rather tending toward an intermediate. Fortunately, in hybridization work later generations provide an excellent check on the conclusions drawn from a study of the F2 generation. From a study of the progeny of 279 F2 plants grown in the F3 generation it seems quite evident that the classification of the F2 material was anything but a true classification. The following table gives the nature of inheritance for those planted as hard and soft selected from the F2 generation and checked in the F3 generation.

Table 8. Percentage of those planted as hard and soft, breeding true and re-segregating in the F3 generation

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hard</td>
<td>13.7</td>
<td>79.5</td>
<td>6.8</td>
</tr>
<tr>
<td>Soft</td>
<td>36.8</td>
<td>63.2</td>
<td>--- : 0</td>
</tr>
</tbody>
</table>

A consideration of the data presented in the above table indicates that it was impossible to differentiate between kernels that were hard because of heredity and those that were hard because of environment. Assuming hard to be dominant and
differing from soft by a single factor by the law of chance, we should expect 

per cent

one-third, or 33-1/3\(^3\) of those planted as hard, to be homozygous and breed 
true for hard in the F3 generation. Two-thirds, or 66-2/3 per cent, should 
again segregate in the F3 generation. Comparing these percentages with those 
of the above table, only 13.7 per cent of those planted as hard bred true for 
hard as compared to 33-1/3 per cent as was expected; 79.5 per cent segregated as 
compared to 66-2/3 per cent; 6.8 per cent of all those planted as hard actually 
bred true for soft in the F3 generation.

Let us now consider those planted as soft. In this case, assuming soft 
as dominant, likewise we should expect 33-1/3 per cent to be homozygous and 
breed true in the F3 generation and 66-2/3 per cent to again break up. Compar-
ing this with the percentages given in the table, one observes a very close 
approach to what was expected.

From the data presented in the above table one would not be entirely 
justified in concluding which character was dominant. However, from a study 
of those segregating for hard and soft in the F3 generation the above con-
cclusions seem to be justified. The distribution of plants with hard and soft 
grain is given in Table 9.

Table 9, Distribution of plants with hard and soft grain in the F3 
generation

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Grain</th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Soft</td>
<td>Hard</td>
</tr>
<tr>
<td>4285</td>
<td>3242</td>
<td>1043</td>
</tr>
<tr>
<td>Theoretical</td>
<td>3214</td>
<td>1071</td>
</tr>
</tbody>
</table>

In classifying the hard and soft in the F3 generation, the segregation 
seemed rather clear-cut. The plants of this generation were grown rather thik 
in rows with a 2-foot space between rows and not spaced in the row like those of the 
F2 generation. Soil conditions were also more uniform. This might have some in-
fluence on developing plants more typical of average field conditions. As indicated by the table, the segregation approaches a 3:1 ratio, with soft dominant.

Di- and Tri-hybrid. So far the inheritance of a single character has been considered. One of the principles of Mendel's law is that each character is inherited as a unit; otherwise, normal Mendelian segregation will not occur except as two characters are completely linked when the segregation would be typical of a mono-hybrid. However, linkage was not known in Mendel's day.

Since the mechanism upon which the di-hybrid operates is well-known, it is unnecessary to restate it. It will be recalled that the parents differed in three characters. Thus, we may consider each character separately -- or consider two or even three characters together. A consideration of two characters together is given in Table 10.

Table 10. Distribution of the F2 generation from a cross wherein the parents differed in two characters, viz., color and head shape

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Clubbed</th>
<th></th>
<th>Long</th>
<th></th>
<th></th>
<th>Ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Red</td>
<td>White</td>
<td>Red</td>
<td>White</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4173</td>
<td>2513</td>
<td>900</td>
<td>563</td>
<td>197</td>
<td></td>
<td>9.6:3.4:2.3:0.8</td>
</tr>
<tr>
<td>Theoretical</td>
<td>2345</td>
<td>783</td>
<td>783</td>
<td>261</td>
<td></td>
<td>9.0:3.0:3.0:1.0</td>
</tr>
</tbody>
</table>

There is a slight approach to the normally expected 9:3:3:1 ratio. From a previous discussion on head shape it was noted that a wide ratio between clubbed and long loose prevailed; consequently, the results presented in the table are expected after knowing the behavior of the clubbed heads.
The Inheritance of Chaff Color, Head Shape, and Grain Texture in Wheat.

Table 11. Number of plants obtained in each group from the F₃ segregates when two characters are considered, viz., long compact, bronze, and white; and long loose, bronze and white.

<table>
<thead>
<tr>
<th>Total Plants</th>
<th>Long Compact</th>
<th>Long Loose</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Bronze : White</td>
<td>Bronze : White</td>
</tr>
<tr>
<td>1175</td>
<td>628 : 266</td>
<td>203 : 78</td>
</tr>
<tr>
<td>Theoretical</td>
<td>657 : 219</td>
<td>219 : 73</td>
</tr>
</tbody>
</table>

Here again, the ratios approach the theoretical expectation of a normal dihybrid cross. The long compact white group contains a few too many for that class which should have fallen in the long compact bronze group theoretically. Except for those few results would have been quite in agreement with the expected.

Theoretically the long whites are recessive and should breed true for the two characters concerned. One-third of the long red should breed true, the other two-thirds re-segregating in the F₃ into a 3:1 ratio for color. Likewise, one-third of the clubbed white breed true and two-thirds break up into a 3:1 ratio for head type; the color which is recessive will be constant. Of the clubbed red plants, one-ninth will be homozygous and breed true; two-ninths will be homozygous for clubbed head but heterozygous for color and will segregate into a 3:1 ratio for color; two-ninths will be homozygous for color and heterozygous for clubbed and will therefore segregate into a 3:1 ratio for clubbed. The remaining four-ninths will be heterozygous for both characters and consequently will segregate into a 9:3:3:1 ratio.

Thus hybridization provides a means of obtaining any combination of characters desired, provided the parents possess the characters. No definite study was made of the F₃ generation to see if the percentages approached the theoretical. However, from an examination of the rows in the field, it was evident the above phenomenon was taking place. Some rows were apparently breeding thus for one character and segregating for others; a few breeding true for all characters but one, which was again
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segregating; and still others breeding true for all characters visible. In fact, it was possible to obtain individuals with any combination of visible character possessed by the parents.

Because of the complications that arose all three characters of the $F_2$ will not be considered together. We shall now turn to a consideration of three characters studied together in the $F_3$ generation. Considering all the rows that segregated for all three characters in the $F_3$ generation it is possible to compare the results with a theoretical expectation for a normal tri-hybrid cross. The following table shows the distribution in each group.

Table 12. The distribution in each group when three characters are involved in a cross, viz., chaff color, head shape, and grain texture

<table>
<thead>
<tr>
<th>Bronze</th>
<th>White</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Plants</td>
<td></td>
</tr>
<tr>
<td>Long Compact</td>
<td>Long Loose</td>
</tr>
<tr>
<td>Total Plants</td>
<td></td>
</tr>
<tr>
<td>Soft : Hard</td>
<td>Soft : Hard</td>
</tr>
<tr>
<td>Soft : Hard</td>
<td>Soft : Hard</td>
</tr>
<tr>
<td>Soft : Hard</td>
<td>Soft : Hard</td>
</tr>
<tr>
<td>Total Plants</td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Bronze</th>
<th>White</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total Plants</td>
<td></td>
</tr>
<tr>
<td>Long Compact</td>
<td>Long Loose</td>
</tr>
<tr>
<td>Total Plants</td>
<td></td>
</tr>
<tr>
<td>Soft : Hard</td>
<td>Soft : Hard</td>
</tr>
<tr>
<td>Soft : Hard</td>
<td>Soft : Hard</td>
</tr>
<tr>
<td>Soft : Hard</td>
<td>Soft : Hard</td>
</tr>
<tr>
<td>Total Plants</td>
<td></td>
</tr>
</tbody>
</table>

Considering only the limited number of plants involved in the above calculation it appears quite evident that each of the three characters considered is a unit character inherited independently of the others. Certain of these plants are homozygous for all characters and breed true in later generations. Others are homozygous for two characters and heterozygous for the others and will thus re-segregate for that character in later generations. Still others are homozygous for one character and heterozygous for two characters and will segregate in the next generation. Certain other plants are heterozygous for all characters and should segregate for all characters into an approximate ratio of $27:9:9:3:3:3:1$.  


Fig. 3. Showing the parents, the F₁, and the classification of the F₃ generation into three head types. "B" indicates bronze chaff and "b" indicates white chaff.

GENERAL CONCLUSIONS

The purpose of the cross was to combine the high-yielding power of Dicklow with the good bread-making qualities of Hard Federation. This has not been definitely accomplished as yet, tho several of the strains that are apparently breeding true look promising. Certain ones possess a grain texture equal, if not superior, to that of Hard Federation. The yield has not yet been determined as this is the first year pure strains occurred. Some single rows this year gave
very promising yields. Several seasons are necessary before any significant data on yield will be available. After next year's harvest sufficient grain will be available for baking tests which will provide a true check as to the ability of the grain to make good bread.

My problem was especially concerned with working out the genetic data. This constituted a study of the F2 and F3 generations. The appearance of dwarf plants in the F2 generation was rather unexpected. The nature of their occurrence seems to follow definite hereditary laws. The inheritance of the clavate character is influenced to such a degree by environment that expected Mendelian ratios were upset. Chaff color, grain texture, and the long compact head type all seem to be unit characters and are inherited independently. Grain texture, tho heritable, was influenced to such a degree by environment that a classification of the F2 material proved inaccurate. A study of the F3 generation served as a check on the F2 generation. This study brought out clearly the misconception concerning the inheritance of hard grain. The study further indicated that chaff color, the long compact head, and grain texture are simple Mendelian characters inherited in a Mendelian fashion.
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