INHERITANCE OF LIPOXIDASE ACTIVITY AND STEM SOLIDNESS IN STEWART X GOLDEN BALL DURUM WHEAT

by

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ABSTRACT

Lipoxidase activity of seeds was determined manometrically on single plants of the durum varieties Stewart and Golden Ball, their F1, F2 and first backcrosses, and on bulk samples of the parents and F2 progenies grown in rows. The plants of the same populations were also examined for stem solidness by scoring cross sections of culms. Powers' partitioning method was employed in analyzing the data.

For each character, environmental and genetic variability followed the arithmetic scale, environmental variances were small in relation to genetic variances, heritability estimates were high, and the frequency distributions indicated either one or two isodirectional gene pairs. Partial phenotypic dominance of higher lipoxidase activity and stem solidness was evident.

Stewart and Golden Ball were differentiated by one major and one minor factor pair for each character. The genes for high lipoxidase activity and for stem solidness are carried by Golden Ball, their alleles by Stewart. The major factor for lipoxidase activity showed no or slight genic dominance of higher activity, while the minor factor revealed a great amount of genic dominance in the same direction. The major gene was found to have approximately 4 1/2 times the effect of the minor gene. Both appeared to be less effective when alone and in single dose. Major and minor factors for stem solidness exhibited partial genic dominance of solidness. The major gene had approximately 8 times the effect of

the minor gene. No interallelic interactions were apparent. Progeny tests confirmed the results of the partitioning study.

Lipoxidase activity and stem solidness were not associated, the two major factors segregated independently, and the correlation based on all individual plant data was close to zero. Approximately 10 percent of the F2 plants had low lipoxidase activity combined with a high degree of stem solidness. From their progenies, segregants should be recovered with all factors for low lipoxidase and for stem solidness in the homozygous condition.

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INTRODUCTION

Durum wheat is grown in Canada mostly for export to Europe where it is processed into macaroni and related products. The European consumer, by tradition, prefers a bright yellow macaroni. This color must be derived from the wheat itself since artificial coloring of macaroni is unlawful. Most commercial durum wheats contain a sufficient amount of carotenoid pigments in the endosperm to produce the desirable yellow color. However, some varieties like Golden Ball lose much of the pigment during dough mixing. The cause of this pigment destruction was not known until recently when it was discovered that the enzyme lipoxidase is the oxidizing agent. Lipoxidase activity is high in Golden Ball while it is low in good quality durums like Stewart.

The variety Golden Ball is very valuable from an agronomic point of view. Its stem solidness confers resistance to the wheat stem sawfly, a destructive pest in the Western Prairies, and it is resistant to stem rust race 15 B which caused the great epidemics of the years 1953, 1954 and 1955. While in common wheat much information on the genetics of stem solidness and other characters has been accumulated through aneuploid methods, inheritance studies in tetraploid wheats still depend on factorial analysis.

This investigation was undertaken to evaluate the inheritance of lipoxidase activity and stem solidness in the durum cross Stewart x Golden Ball. Powers' partitioning method of genetic analysis was employed. It appears to be the first report on the genetics of lipoxidase activity in wheat.

LITERATURE REVIEW

Lipoxidase Activity

One of the most important factors of macaroni-making quality is macaroni color. A clear bright yellow is desired by European consumers. The yellow color comes from the yellow carotenoid pigments which are present in the wheat endosperm. Markley and Bailey (1935) found xanthophyll to be the principal component with carotene present only in minor quantities. Irvine and Anderson (1949), by chromatographic analysis of semolinas from good and poor quality durums, identified two pigments, xanthophyll and taraxanthin. Xanthophyll was somewhat more abundant than taraxanthin.

Soon after quality testing of durum wheats began, about 25 years ago, it was noted that a high pigment content of semolina was no guarantee of the yellow color appearing in the finished macaroni product. Certain semolinas bleach out during processing while others retain their color (Fifield et al., 1937). The variety Golden Ball, for instance, has a high pigment content yet produces a pale whitish macaroni (Irvine, 1955).

Irvine and Winkler (1950) studied in detail the destruction of the xanthophyll pigments during macaroni processing. The greatest losses occurred during dough mixing. Increasing temperature and oxygen concentration hastened the rate of destruction. But when mixing was stopped, or oxygen was replaced by nitrogen, pigment destruction ceased. This suggested an oxidation reaction catalyzed by the enzyme lipoxidase. In fact, when soybean lipoxidase was added to semolina of Mindum, a high quality durum, the same type of pigment destruction

was obtained as in Golden Ball.

Sumner and Sumner (1940) demonstrated that the oxidation of carotene is dependent upon the presence of unsaturated fats which are peroxidized by lipoxidase. Sumner (1942), however, showed that carotene oxidation is neither brought about by the intervention of the enzyme nor by the action of the fat peroxides. The peroxidation of unsaturated fat actually must be in progress if oxidation of carotene is to occur. It appears that during the production of the fat peroxide an unstable intermediate is formed which is the oxidizing agent of the carotene.

According to Irvine and Winkler (1950), two alternate pathways are possible for the initial reaction to follow: either the enzyme combines first with oxygen or first with the unsaturated fat. When stored semolina is used for macaroni processing, the reaction appears to follow the first path. Irvine and Winkler postulated that combination of lipoxidase and oxygen has already occurred to some extent in the unwetted semolina. When water is added the cells rupture and the lipoxidase-oxygen complex comes in contact with the unsaturated fat. The intermediate fat peroxide formed during the peroxidation then oxidizes the pigment. Mixing exposes new surfaces of the dough to oxygen thus enabling a recombination of enzyme with oxygen and substrate. The second path is followed when dough is prepared from freshly milled semolina. Here the enzyme first comes in contact with the unsaturated fat during imbibition, mixing then exposes the lipoxidase-fat complex to oxygen.

Balls et al. (1943) reported that from a number of unsaturated fatty acids tested only linoleic, linolenic, and arachidonic acids

formed peroxides when oxidized by lipoxidase.

The presence of lipoxidase activity in wheat germ was first demonstrated by Sumner (1943), and in commercial flour by Miller and Kummerow (1948). Irvine and Anderson (1953a) tested aqueous extracts of durum wheat and semolina for lipoxidase activity using a linoleic acid emulsion. The uptake of oxygen closely paralleled the loss of pigment during dough mixing. This correspondence gave proof of the presence of lipoxidase in significant amounts in durum wheats to account for the rate of pigment destruction observed.

A study of the kinetics of wheat lipoxidase was undertaken by Irvine and Anderson (1953a), and oxygen uptake was measured at various levels of pH, oxygen, enzyme, substrate and temperature. This provided the basis for the development of a routine manometric method to determine lipoxidase activity in semolina and ground wheat.

Irvine and Anderson (1953b) by using this method of measurement investigated the varietal and environmental variation in lipoxidase activity. Seven varieties, ranging from the best quality durum (Nugget) to the poorest (Golden Ball), were grown at seven locations in the durum-growing areas of Western Canada in 1952. Semolina lipoxidase activity varied fourfold among varieties while it was little influenced by environment (the variance due to stations was barely significant at the 5 percent level). Semolina pigment, macaroni pigment and macaroni color also varied considerably more with variety than with environment. The data revealed two principal factors concerned in macaroni color: semolina pigment content and lipoxidase activity.

A better prediction of macaroni color could, therefore, be

expected when durum samples were not only tested for pigment but for lipoxidase as well. Irvine and Anderson (1953b) analyzed 138 different semolinas for both pigment content and lipoxidase activity. Macaroni was also processed and pigment content of the ground macaroni determined. A multiple regression equation was calculated relating macaroni pigment to both semolina pigment and lipoxidase activity. Macaroni pigment was predicted from the other two measurements. Experimental and predicted macaroni pigment values were highly correlated with $r = 0.95$, and a standard error of estimate of 0.35 p.p.m.

From 93 samples included in the semolina study, pigment content and lipoxidase activity were also determined on ground wheat and macaroni pigment related to the wheat data. The correlation between experimental macaroni pigment values and calculated values using wheat pigment and wheat lipoxidase was found to be somewhat lower than that for the semolina regression, with $r = 0.91$ and a standard error of estimate of 0.48 p.p.m.

Later, Irvine and Anderson (1955) tested a wider variety of wheat samples which necessitated a revision of the prediction equation. The correlation coefficient for the new equation was found to be higher than previously, $r = 0.944$, while the standard error remained the same. The error of 0.48 p.p.m. is sufficiently low to make the wheat prediction test of great value to the plant breeder. Only eight grams of wheat are required for the pigment determination and 10 grams for the lipoxidase assay. Its great advantage over the semolina test lies in the fact that milling of semolina is not necessary.

Stem Solidness

Stem solidness was studied in tetraploid wheat crosses by Engledow and Hutchinson (1925), Putnam (1942), and Hemstad (1961). Engledow and Hutchinson (1925) described the degree of solidness in the top internode of several wheat species and their hybrids. The stem of Triticum polonicum has a small cavity approximately three inches below the spike but is completely solid at the base of the first internode. The T. turgidum variety Rivet, on the other hand, is solid in the upper part and partly hollow at the base. All F2 plants of this cross had a small lumen at the top but differed in solidness at the base. Of the 522 plants examined, 393 were more or less solid and 129 were "hollow" (less solid than Rivet) indicating a 3:1 ratio. The transgressive segregation toward hollowness, however, suggested the operation of at least two factors. When T. polonicum was crossed with the T. durum variety Kubanka (less solid than Rivet) and with two other durums (less solid than Kubanka) similar segregations were obtained, though the intermediate types were difficult to classify. The cross Rivet x T. aestivum variety Chinese (hollow) also fitted a ratio of 3 solid and intermediate to 1 hollow. Here transgressive segregation occurred toward complete solidness.

Putnam (1942) crossed the solid-stemmed durum variety Golden Ball with the hollow-stemmed durums Pentad, Kahla and Pelissier, and with the hollow T. turgidum variety Alaska. Whole culms were studied in either longitudinal or cross sections. Stem solidness of the F1 plants - examined in Golden Ball x Pelissier - was intermediate but

closer toward the solid parent. In all crosses, the F2's segregated in a ratio of 3 solid + intermediate : 1 hollow. Some plants classified as intermediate proved in progeny tests to be homozygous for solidness. There was no error in the classification of the hollow segregates.

Hemstad (1961) classified the F2 of the durum cross Tremez Preto (solid) x Mindum (hollow) for solidness. The 2nd, 3rd and 4th internodes were cut diagonally and scored from 1 (hollow) to 5 (solid). The sum of the scores represented the solidness index of a plant. Approximately 1/4 of the F2 plants were as solid as Tremez Preto, 1/4 were as hollow as Mindum, and 1/2 were intermediate.

In crosses between tetraploid and hexaploid wheats, most investigators found hollowness to be dominant over solidness. Biffen (1905) was probably the first who reported dominance of hollowness. The hybrids from the cross T. turgidum "Rivet" with hollow T. aestivum had thick, hollow stems and the F2 plants were separated into 170 hollow and 56 solid types. Kajanus (1918) also found a ratio of 3 hollow to 1 solid in one of his T. turgidum x T. aestivum crosses. In another cross, however, the hollow class was not large enough to fit this ratio.

Kihara (1924) studied the relationship between chromosome number and stem solidness in a cross between a solid T. durum and a hollow T. aestivum. F2 plants with more than 35 chromosomes were all hollow. Plants with less than 35 chromosomes (whose progenies tended to revert to the 28 chromosome condition) were either hollow, intermediate or solid. Segregation in the offspring of a number of intermediate plants suggested a single gene difference.

Thompson et al. (1935) examined 28-chromosome segregants from

crosses between hollow T. aestivum and solid T. durum, T. dicoccum and T. persicum species. Many plants had small cavities suggesting that a factor for hollow stem is present in the A or B genome. However, no 28 chromosome hybrid was obtained with the hollow, thin-walled stem of T. aestivum. The authors concluded that at least one additional factor must be present in the D genome to produce the hollowness characteristic of T. aestivum.

Matsumura (1936a, 1936b), in the F2 of a T. polonicum x T. spelta cross, found all 28-chromosome plants to be either pithy or with very small cavities. Evidence from trisomics indicated that a gene or genes on one of the D chromosomes inhibited pith production.

Yamashita (1937) made an extensive study of the genetics of stem solidness using crosses between diploid, tetraploid and hexaploid wheats. The solidness of the culms was evaluated by means of cross sections. In the backcross of T. durum-T. aestivum to T. durum the proportion of hollow-stemmed plants increased with the number of univalents (D chromosomes). In some lines of the backcross T. polonicum-T. spelta to T. polonicum the 29-chromosome plants had hollow stems while those with 28 chromosomes were solid. This confirmed Matsumura's result that a single D chromosome carried the main factor for hollowness. In the last mentioned backcross there also occurred 28-chromosome lines in which all plants were hollow indicating that the B genome of T. spelta also carries a gene for hollow stem. Other lines of similar origin segregated in 3 solid : 1 hollow. Solid plants with small cavities were found in greater proportion in the segregating lines than in the homozygous solid lines. This was attributed to incomplete dominance of solidness.

The following factors were postulated by Yamashita (1937):

O_D, principal gene for hollowness in the D genome;

m_A and m_B, factors for hollow stem in the A and B genomes, respectively;

M_B, gene for solidness in the B genome, allelic and incompletely dominant to m_B;

C , factor for pith in the lower internodes, carried by the A genome and complementary to M_B.

O_D is epistatic to M_B which is epistatic to m_A. The alleles at the M_B locus form a series with "more solid" dominant to "less solid".

Matsumura (1947), in his T. polinicum x T. spelta cross, compared the different 29-chromosome plants with 28-chromosome plants and found chromosome e (Sears' XX = 2D*) to carry O_D.

Platt et al. (1941) studied stem solidness in common wheat crosses between the solid varieties S-615 and S-633 and hollow Renown and Thatcher. The F1 plants were partially hollow. From each F2 plant the main culm was classified as either hollow, intermediate or solid. A ratio of 63 hollow and intermediate : 1 solid was indicated in all crosses. Plants that were solid or that approached the solid condition were tested in F3. The fit to a postulated ratio of 10 hollow to 53 intermediate and segregating to 1 solid was satisfactory. Solidness was thought to be controlled by three factor pairs with full solidness being expressed only in plants having these factors in a recessive condition. It was suggested that the genes are cumulative in nature and that four or more dominant genes would produce hollow plants.

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* See Sears (1958) and Okamoto (1962) for new system of numbering chromosomes.

McNeal (1956) made a statistical analysis treating stem solidness as a quantitative character in the cross Thatcher x Rescue. Rescue - derived from Apex x S-615 - was the first solid-stemmed bread wheat licensed for commercial production in Canada. For each plant a solidness index was calculated from six cross sections rated from 1 (hollow) to 5 (solid). Three cuts were made in the top internode, and one in the center of each lower internode. Frequency distributions, means and variances were obtained from the parents, F1, F2, and the first backcross to either parent. The genetic analysis was based on Powers' partitioning method (Powers et al., 1950, Powers, 1951). Thatcher and Rescue were differentiated by one major factor pair and from two to four minor modifying factors. The major gene had 2 1/2 times the effect of the minor genes. The data indicated slight phenotypic dominance of solidness and small amounts of partial genic dominance of solidness for major and minor factors.

McNeal et al. (1957) crossed four solid-stemmed wheats from Portugal with Rescue and compared the solidness distributions of the parental and F2 populations. No major differences were noted indicating that each of the Portuguese wheats possessed the same major gene(s) for stem solidness as Rescue. Small differences and the occurrence of plants in F2 that were less solid than either parent suggested segregation of minor modifying factors.

Larson (1959a) and Larson and MacDonald (1959), by aneuploid methods, evaluated the chromosomes affecting stem solidness in the varieties Chinese Spring and S-615. The solidness index was de-

termined from seven cross sections, three from the top internode and one from the center of each lower internode, rated from 1 hollow to 5 solid. Monosomics or nullisomics of the 21 Chinese chromosome lines were crossed with S-615. In the first study (Larson, 1959a), F2 lines from monosomic F1 plants were compared with normal F2 lines for solidness. Analysis of variance showed that several monosomic lines differed significantly from normal.

Presumably, when a monosomic line is more solid than the normal F2 population its critical chromosome inhibits pith development, and when it is less solid its critical chromosome promotes solidness. Four monosomic F2 lines, 2A, 2D, 6D and 7D, were more solid than normal indicating that these chromosomes carry pith inhibitors in Chinese and - with the exception of 2A - in S-615 also. While the normal F2 segregated for four factors monosomic line 2A gave only a trihybrid ratio. The effect of chromosome 2B was inconclusive. Larson suggested that the genes for hollowness postulated by Yamashita may be in homoeologous group 2. Monosomic line 4B was less solid than the normal F2 in 1948 but not in 1949. The trihybrid ratio obtained in 1948 indicated that chromosome 4B may have a gene for solidness in Chinese. Since no genes for solid stem were revealed in S-615 by this analysis with Chinese as the monosomic parent it was concluded that such genes were probably recessive. They could then only be detected in monosomic S-615 lines.

Larson and MacDonald (1959) produced the monosomic lines in S-615 by backcrossing the Chinese x S-615 hybrids to S-615 for seven generations always using monosomics as the female parent. Monosomic plants from the final backcross were selfed. The monosomic progenies

were compared with the progenies of derived normals, parents and other checks in a lattice design. Stem solidness indices were obtained from the seven standard cross sections and from an extra cut 1-2 cm. below the top of each lower internode. Analysis of variance was made on two sets of data: on standard cuts, and on special cuts plus top internode readings. The monosomic lines 2D, 6D and 7D were more solid than the normal lines in both top and lower internodes. These chromosomes thus appear to possess genes for hollow stem in S-615, confirming the results of the first study. The monosomic lines 3B and 3D had culms less solid in the top internode, and those of homoeologous group 5 (5A, 5B and 5D) were less solid in the four bottom internodes. Presumably, these are then the chromosomes with the stem solidness factors in S-615. It was suggested that Yamashita's gene C for pith in the lower internodes is probably located on chromosome 5A.

Larson and MacDonald (1962) also developed monosomic lines in Rescue and tested these and other derived aneuploids for stem solidness. Rescue differs in pith distribution from its solid-stemmed parent S-615 in that the lower parts of the top internode are less solid while the upper parts of all internodes are more solid. Fewer chromosomes influenced solidness in Rescue than in S-615. Pith development at the base of the first internode was inhibited by chromosomes 3B, 6A and 6D. Chromosome 5A, on the other hand, made the culm solid, especially in the lower internodes. The short arm of 5A was found to carry the factor(s) producing pith in the lower internodes, while the long arm seems to have a gene or genes tending to increase solidness in the center and lower parts of the top internode.

Chromosomes 1A and 1D probably also carry solidness factors since their nullisomics were less solid than normal. The absence in Rescue of the genes for solid top internode on 3B and 3D, and of the pith inhibitor on 7D which tends to make all internodes hollow near the top, were thought to account for the main differences in solidness between Rescue and S-615.

Arnason (1938) and Platt and Larson (1944) had been unsuccessful in transferring the solid stem character of tetraploid wheats to hollow hexaploids. Larson (1959b) made another attempt to transfer the Golden Ball type of solidness, this time using a solid common wheat, namely Rescue. Golden Ball is more solid in the first internode than Rescue, a characteristic difference between solid tetraploids and hexaploids. An increase in solidness of the top internode over that of Rescue was attained in two T. aestivum-like F4 plants. However, the complete solidness of Golden Ball was not obtained. Since chromosome 3B in S-615 carries a gene for solidness in the top internode, it was suggested that Golden Ball has a stronger allele.

Larson (1959c) selected six plants from one of the two F4 lines for further study. F5 plants with a high solid stem index had fewer chromosomes (38 - 40) than those with a lower index (39 - 42). Solidness was also associated with squarehead and dense spike. Squarehead and dense spike were associated with one another and both with low chromosome number. Since Chinese monosomic 3D is squarehead and dense and the nullisomic is very dense, it was suggestive that chromosome 3D might be the lost chromosome. When 40-chromosome plants were crossed with telo-3D the hybrids had 20 pairs plus one telocentric indicating that the lacking pair was chromosome 3D. It

was concluded that a gene or genes on chromosome 3D of Rescue prevented the transfer of the Golden Ball solidness to hexaploid offspring. As the gene on chromosome 3D of S-615 makes the first internode solid, the hollow factor on 3D in Rescue must have come from Apex.

McNeal (1961) also was not able to transfer completely the stem solidness and sawfly resistance of Golden Ball to common wheat (Rescue x N 1315). After several years of selection, T. aestivum-like segregants were obtained with solidness values as high or higher than Rescue and nearly equal to that of Golden Ball in the lower internodes, but not in the two top internodes. All selections were less resistant to sawfly cutting, however. Two selections and Rescue were crossed with each other and the parental and F2 distributions for solidness compared. No major differences were found indicating that the genes for solid stem transferred from Golden Ball act like those of Rescue in the T. aestivum background. The fact that the Golden Ball solidness of the two top internodes was not recovered confirms Larson's findings that a factor or factors in Rescue inhibit complete solidness in the top internode.

Platt (1941) studied the effect of environment on stem solidness. Golden Ball, S-615 and S-633 were grown at many different stations in Canada for three years. Golden Ball was essentially solid at all locations, while the common wheats varied in degree of solidness from locality to locality and from year to year. Light was found to be the most important factor affecting stem solidness. Long hours of sunshine and high temperatures during stem elongation favored the expression of solidness. Wider spacings between plants also increased solidness. When plants of S-615 were lightly shaded during early

morning and late afternoon stems were completely hollow. Full shading of Golden Ball, on the other hand, reduced solidness only slightly. S-615 and S-633 were essentially hollow in the greenhouse.

Holmes et al. (1960) reported that shading of Rescue in the field between the 4-leaf stage and heading reduced the solidness of the three bottom internodes. The lowest (5th) internode was already affected by shading from the 2-leaf stage onward. The second top internode was less solid when shaded from boot-stage to heading.

Roberts and Tyrrell (1961) tested for three years five hollow and solid common wheats, including Rescue, and the durums Golden Ball and Melanopus under shaded cages in the field, at a light intensity 50-60% of the full outdoor intensity. The solid-stemmed bread wheats were lower in solidness and had less resistance to the sawfly than their unshaded checks. The durum wheats, on the other hand, were not affected.

MATERIALS AND METHODS

Source of Materials

The durum variety Stewart was produced in North Dakota from the cross Mindum durum x Vernal emmer backcrossed twice to Mindum (Bayles and Clark, 1954). Golden Ball had been introduced from South Africa by the U. S. Department of Agriculture in 1918, according to Dollery and Owen (1950). Seed of the two varieties was obtained from the Department of Plant Science, University of Manitoba.

Reciprocal crosses between Stewart and Golden Ball were made in the field in 1956. Part of the F1 was grown in a growth cabinet the following winter and backcrossed to either parent. For spring planting in 1957 the following populations were available:

Stewart (S), progenies from plants used for crossing;

Golden Ball (B), " " " " " " ;

F1, (S·B) and (B·S);

F2, progenies from single F1 plants, 3 progenies from (S·B) and 3 progenies from (B·S);

First backcross to Stewart (B1): (S·B)S, S(S·B), (B·S)S and S(B·S);

First backcross to Golden Ball (B2): (S·B)B, B(S·B), (B·S)B, and B(B·S).

Experiments

The statistical design was a randomized complete block with three replications. Each replicate consisted of one row each of the parents, F1, the two backcrosses, and six F2 lines, with the 11 rows randomized within each replication. Rows and plants within rows were spaced 1 1/2 feet apart. The seeds were hand-planted, 13

seeds per row. Several rows of parental material encircled the experiment to eliminate any border effect. A small part of each population was sown nearby to have transplants available should seeds in the experiment fail to germinate or seedlings become attacked by wireworms. Thirty-six sites were replanted three weeks after sowing.

A separate nursery consisted of 116 F3 lines from the same cross made by Dr. Jenkins in 1955. The F2 plants had been harvested in 1956. The progenies were planted in 1-row plots together with the parental varieties which were interspersed at 8 row intervals. The rows were 18 1/2 feet in length, spaced one foot apart and contained from 100 to 130 plants.

In 1958, progenies from the B1, B2 and F2 plants of the randomized block experiment were sown in 2-row plots with one row of Golden Ball and one row of Stewart every fifth plot. The 18 1/2 foot rows were spaced one foot apart and contained from 60 to 80 plants.

Classification

The plants from the 1957 randomized block experiment were pulled and taken to the field house. After each plant was classified for stem solidness and spike characters, one or two representative heads were saved and the rest threshed by hand. The seeds were cleaned and divided into two parts: one part for sowing the progeny plus some reserve, the other for determining lipoxidase activity. It should be emphasized that the plants of the respective generations were scored for stem solidness, whereas their seeds (next generation) were tested for lipoxidase activity. The F2 plants harvested in 1956 had been handled similarly except that lipoxidase activity was determined on F3 lines (F4 seeds) grown in 1957.

In the 1957 block experiment there should have been 39 plants each of the parents, F1 and the backcrosses, and 234 plants of F2 available for classification. This was not necessarily realized, however, since not all transplants survived, some plants had insufficient seed to allow for both quality and progeny testing, and others could not be correctly classified for stem solidness because their culms were severely damaged.

The F3 lines in 1957 and the progenies of the backcrosses and F2 in 1958 were cut with the sickle and threshed by machine. The 1957 lines were tested for lipoxidase and those of 1958 were classified for stem solidness.

Lipoxidase Assay

Irvine and Anderson (1953a, 1953b) developed a manometric assay for lipoxidase in wheat which was used in this study. The writer made the determinations in the Grain Research Laboratory in Winnipeg. The F3 lines grown in 1957 were tested the following winter while the single plant material of 1957 was evaluated one year later.

Preparation of substrate

A stable emulsion of linoleic acid was prepared as follows: To 10 ml. of 60% linoleic acid were added 2 ml. of Triton X-100, a surface active agent which has no effect on the lipoxidase system. Distilled water was added drop by drop, with mechanical stirring, until the emulsion became foamy and stiff or inverted. It was then diluted to 250 ml. with distilled water and beaten at high speed in a Waring Blendor for three minutes. The resulting emulsion was stored in a refrigerator, where it remained stable for a month or longer. A new emulsion was made every three weeks and tested against the old one.

Preparation of 0.067 Molar phosphate buffer

9.1 g. of KH_2PO_4 and 9.5 g. of Na_2HPO_4 were each dissolved in one liter of distilled water. Then 700 ml. of the first solution were mixed with 300 ml. of the second and the pH tested with a pH meter. If the pH was higher than 6.5 some more KH_2PO_4 was added, if it was lower, Na_2HPO_4 was added until the meter showed exactly a pH of 6.5.

Enzyme extract

Five grams of wheat were ground with 2.5 g. of sand and 10 ml.

of distilled water in a mechanical mortar for five minutes. Irvine and Anderson used twice the amount of wheat, sand and water, and ground for three minutes. No differences in lipoxidase activity were found between the two methods. The mass was transferred to a 50 ml. round-bottomed plastic tube and centrifuged at top speed in a clinical centrifuge for 10 minutes. The supernatant - enzyme extract - was then decanted into a glass vial.

Method

Lipoxidase activity was determined by the direct manometric method of Warburg which measures the uptake of oxygen by a mixture of enzyme and substrate in a buffered solution.

The following amounts were pipetted into a conventional 50 ml. Warburg flask: 1.0 ml. of substrate and 2.6 ml. of phosphate buffer into the main compartment, and 0.4 ml. of enzyme extract into the sidearm. Irvine and Anderson employed 15 ml. flasks with 1.0 ml. of substrate, 2.0 ml. of phosphate buffer, and 0.8 ml. of enzyme extract.

The water bath of the Warburg apparatus was maintained at 30°C. Shaking speed was 120 oscillations per minute at an amplitude of 4 cm. During the first 10 to 15 minutes of shaking the stopcocks were left open and the manometers were set. Shaking was stopped to close the stopcocks, resumed, and then the contents of the sidearm were tipped into the main compartment, rinsing the sidearm twice. The stop watch was started at the moment of tipping the first flask. The flasks were tipped at 30 second intervals, and each manometer was read after five minutes reaction time.

Lipoxidase activity was calculated as oxygen uptake in micro-

liters per minute during the first five minutes of reaction, per gram of wheat.

Moisture content of seeds

From seed on which lipoxidase activity was being determined random samples were taken for moisture testing. No significant differences in moisture content were found between seeds of single plants and between seeds of lines. The latter material, however, was lower in moisture because it had been dried after threshing. There was a slight decrease in moisture content during storage. All lipoxidase data were converted to a 14 percent moisture basis.

Stem Solidness

The method used by Larson and MacDonald (1959) for rating stem solidness was modified to include three cross sections from each internode. Cuts were made with sharp scissors, in the top internode, 5 cm. below the spike, in the center, and 5 cm. above the base; and in the three lower internodes, 1-2 cm. below the top, in the center, and 1-2 cm. above the base, depending on the length of the internode. Approximately half the culms of a plant (or at least three) were examined.

The cross sections were scored from 1 to 5 according to Larson (1959a): 1, thin-walled, hollow; 2, thick-walled, hollow; 3, intermediate; 4, small lumened; and 5, solid. For each cut the readings were averaged to the nearest whole number, and the 12 indices then totalled to obtain the plant's solidness index. Most culms consisted of four internodes, a fifth internode was ignored.

All plants of the randomized block experiment and the F2 from

1956 were classified by this method. Their progenies, however, were rated from a single cut made with a sickle approximately one foot above ground when the lines were harvested. It was neither feasible nor necessary to examine whole culms of individual plants in progenies. Putnam (1942) reported that one or two cuts through the fourth or fifth internode proved adequate for the purpose of checking F2 classification by breeding behaviour in F3. This was confirmed by the writer in trials on F3 lines in 1957, where individual plants were classified, as well as the progeny as a whole, either from stubble or from the sheaf.

Statistical Analysis

The data on lipoxidase activity and stem solidness were analyzed by the partitioning method of genetic analysis developed by Powers et al. (1950), Powers (1951, 1955) and McNeal (1956). Several other techniques were also employed.

Means, phenotypic variances, and scaling values

Means and phenotypic (total) variances of the parents, F1, F2, B1 and B2 were computed from the individual plant data. Cross combinations within the B1, B2 and F2 populations and families within the latter were tested for homogeneity by analysis of variance.

Theoretical means and scaling values were calculated to determine whether the variability followed the arithmetic or geometric scale. The formulas proposed by Wright (1922), Powers and Lyon (1941), and Powers (1955) were employed in obtaining the theoretical means (Table 1). Scaling tests were made according to Mather (1949) using the formulas in Table 2. The individual plant data were then transformed to frequency distributions.

Table 1. Formulas for computing arithmetic means, their standard errors, and geometric means

Population	Arithmetic mean	Standard error of arithmetic mean	Geometric mean
F1	$\frac{P1 + P2}{2}$	$\sqrt{\frac{s^2_{P1} + s^2_{P2}}{4}}$	$\sqrt{P1 \times P2}$
F2 (1)	$\frac{P1 + 2F1 + P2}{4}$	$\sqrt{\frac{0.5s^2_{P1} + s^2_{F1} + 0.5s^2_{P2}}{4}}$	$\sqrt[4]{P1 \times F1^2 \times P2}$
F2 (2)	$\frac{B1 + B2}{2}$	$\sqrt{\frac{s^2_{B1} + s^2_{B2}}{4}}$	$\sqrt{B1 \times B2}$
B1	$\frac{F1 + P1}{2}$	$\sqrt{\frac{s^2_{F1} + s^2_{P1}}{4}}$	$\sqrt{F1 \times P1}$
B2	$\frac{F1 + P2}{2}$	$\sqrt{\frac{s^2_{F1} + s^2_{P2}}{4}}$	$\sqrt{F1 \times P2}$

P1 = Obtained mean of Stewart
P2 = " " " Golden Ball, etc.
s_{P1} = Standard error of obtained mean of Stewart, etc.

Table 2. Formulas for calculating scaling values and their standard errors

Scaling value	Standard error
$A = 2B1 - F1 - P1$	$s_A = \sqrt{4s^2_{B1} + s^2_{F1} + s^2_{P1}}$
$B = 2B2 - F1 - P2$	$s_B = \sqrt{4s^2_{B2} + s^2_{F1} + s^2_{P2}}$
$C = 4F2 - 2F1 - P1 - P2$	$s_C = \sqrt{16s^2_{F2} + 4s^2_{F1} + s^2_{P1} + s^2_{P2}}$
$A = B = C = 0$	

Environmental and genetic variances

The environmental variances of the segregating populations were estimated from the obtained means and variances of the non-segregating populations by use of the formula $y = mx + b$, where m is the slope of the line, x is the corresponding mean of the predicted variance, and b is the variance for which x equals zero (Powers 1942, McNeal 1956).

The following formulas were employed for predicting the values of m and b:

$$m = \frac{\frac{V_{P2} - V_{P1}}{P2 - P1} + \frac{V_{P2} - V_{F1}}{P2 - F1} + \frac{V_{F1} - V_{P1}}{F1 - P1}}{3}$$

$$b = \frac{V_{P1} + V_{F1} + V_{P2} - m\,(P1 + F1 + P2)}{3}$$

where V_{P1} = Total variance of Stewart, etc.

The environmental variance of a segregating population was derived by substituting its obtained mean for x in the formula $y = mx + b$ and solving for y.

The genetic variance was obtained by subtracting the environmental variance from its corresponding phenotypic variance.

Estimates of heritability and number of effective factor pairs

Heritability estimates (h^2) were calculated according to Burton (1951), and Mahmud and Kramer (1951). The number of effective gene pairs was estimated from means and variances using the methods proposed by Castle - Wright (1921), Weber (1950), Burton - Wright (1951), and Mather (1949). The formulas are given in Table 3.

Table 3. Formulas used for estimating heritability and number of effective gene pairs from means and variances

Author	Heritability	Number of gene pairs
Burton (1951)	$\frac{V_{F2} - V_{F1}}{V_{F2}}$	
Mahmud & Kramer (1951)	$\frac{V_{F2} - \sqrt{V_{P1} \cdot V_{P2}}}{V_{F2}}$	
Castle - Wright (1921)		$\frac{d^2}{8\ (V_{F2} - V_{F1})}$
Weber (1950)		$\frac{d^2}{8\ (V_{F2} - \sqrt[3]{V_{P1} \cdot V_{P2} \cdot V_{F1}})}$
Burton - Wright (1951)		$\frac{0.25\ (0.75 - h + h^2)\ d^2}{V_{F2} - V_{F1}}$
Mather (1949)		$\frac{d^2}{4\ D}$

$d = P2 - P1$

$h = \frac{F1 - P1}{P2 - P1}$

$D = 2\ (2\ V_{F2} - V_{B1} - V_{B2})$, using genetic variances

Additional estimates of heritability and number of effective factor pairs were obtained by substituting the F2 environmental variance calculated from $y = mx + b$ for V_{F1}, $\sqrt{V_{P1} \cdot V_{P2}}$, and $\sqrt[3]{V_{P1} \cdot V_{P2} \cdot V_{F1}}$ in the respective formulas.

Powers' (1955) method was employed to estimate the number of effective gene pairs from obtained frequency distributions. The distributions expressed in numbers were converted to the percentage basis.

From the lower tail of the curves the following estimates were available: B2/F1, B1/P1, F2/P1, and F2/B1. Starting from end classes the percentage frequency of a class (plus all lower classes) in one population was divided by the percentage frequency of the same class (plus all lower classes) in the other population, and multiplied by 100. A second estimate was obtained from the next higher class, etc.

From the higher tail of the curves the following estimates were available: B1/F1, B2/P2, F2/P2, and F2/B2. Here the percentage frequencies were cumulated from higher to lower classes.

The obtained percentage values were then compared with the theoretical values listed by Powers (1955) to determine the number of factor pairs and whether they were isodirectional or nonisodirectional.

Theoretical frequency distributions

The theoretical frequency distributions were calculated from the means and standard errors of a single determination by use of Pearson's (1930) Table II which gives the area and ordinate of the normal curve in terms of the abscissa (Powers, 1950).

Pearson's "x" value was obtained by subtracting any given class

limit from the mean and dividing the remainder by the standard error. This value was looked up under column heading x in Pearson's Table II to find the corresponding value under column heading 1/2 (1+a).

When the value of x was positive, the corresponding value of 1/2 (1+a) was subtracted from 1.0 and multiplied by 100 to give the percent of the population expected to fall in the class in question plus all lower classes. When the x value was negative, the value of 1/2 (1+a) was immediately multiplied by 100.

From this percentage were now subtracted those of all lower classes to obtain the percentage for the class in question. Multiplication with the total number of individuals in the population, divided by 100, gave the number of plants expected in this class. The obtained and theoretical numbers were then compared by use of the X^2 test.

Theoretical means and frequency distributions of genotypes

The theoretical means of the Aa genotype in B1 and B2 and those of the aa and AA genotypes in F2 were estimated according to Powers (1951) and McNeal (1956).

Let y equal the mean, Z the upper limit of the class considered, s_d the standard error of a single determination, and x stand for Pearson's x value, then $y = Z + s_d x$, if Z is smaller than y, or $y = Z - s_d x$ if Z is greater than y.

The standard error for the Aa genotype was obtained from the variance of the F1. The standard errors of the genotypes aa and AA were estimated using the formula $y = \sqrt{mx + b}$. For the aa genotype, m and b were computed from means and variances of Stewart and F1; for the AA genotype, m and b were calculated from means and

variances of Golden Ball and F1.

Pearson's x value was obtained as follows: From end-classes of the obtained frequency distribution the number of plants falling beyond a selected upper class limit were divided by the number expected for the respective genotype and subtracted from 1.0. The resulting value was looked up in Pearson's Table II under the column heading 1/2 (1+a) and the corresponding x value found in the column of x.

The means of the remaining genotypes - aa in B1, AA in B2, and Aa in F2 - were obtained by subtraction. The product of "number of plants · mean" of the determined genotype was subtracted from that of the population and divided by the number of individuals of the remaining genotype. (See page 27a).

From the theoretical means and standard errors were then constructed theoretical frequency distributions for each genotype. The genotype distributions of a population were combined and compared with the observed distribution. In testing for goodness of fit, a common frequency distribution was used (Powers 1950). X^2 was calculated as $\sum \frac{(\text{Obtained} - \text{Common})^2}{\text{Common}}$ .2.

Obtained frequency distributions of genotypes and their means

The theoretical genotype distributions served as the basis for partitioning the obtained frequency distributions of the segregating populations. When there was no overlapping of theoretical distributions, the number obtained in a given class became the number in that class in the respective genotype. When overlapping occurred, the number for each genotype in the class in question was determined by proportion from the theoretical distributions.

The mean and its standard error were then computed for each

The theoretical genotype means were arrived at in the following sequence: Using the standard error of a single determination of F1, the Aa genotype means of B1 and B2 were calculated. The means of aa B1 and AA B2 were then determined by subtraction. Standard errors for the aa and AA genotypes were estimated and used in computing the means of these genotypes in F2, respectively. Finally, the mean of the remaining Aa F2 genotype was derived by subtraction.

of the obtained genotype distributions of the segregating populations, as well as for the obtained distributions of the parents and F1.

Finally, the differences - and their standard errors - between means of genotypes within and between populations were determined.

Predicted gains

Expected genetic gains were calculated by use of the formula ih^2 derived by Dickerson and Hazel (1944), where i = selection differential in F2, and h^2 = heritability.

Association

Association between lipoxidase activity and stem solidness was tested by X^2 for independent segregation and by correlation.

X^2 for B1 was calculated from $\frac{(a - b - c + d)^2}{N}$, and X^2 for F2 from $\frac{(a - 3b - 3c + 9d)^2}{9\ N}$ according to Mather (1957).

The four genotypic groups a, b, c and d were derived from the genotypes for the major factors as follows:

Population	Genotypic group							
	a		b		c		d	
	L[1)]	S[2)]	L	S	L	S	L	S
B 1	Aa	Aa	Aa	aa	aa	Aa	aa	aa
F 2	Aa+AA	Aa+AA	Aa+AA	aa	aa	Aa+AA	aa	aa

1) Lipoxidase activity
2) Stem solidness index

The correlation coefficient, r, was computed from the individual plant data by standard procedure.

RESULTS AND DISCUSSION

Lipoxidase Activity

Frequency distributions of populations

Obtained frequency distributions for lipoxidase activity of all populations and theoretical frequency distributions of parents and F1 with X^2 test for normality are given in Table 4. The non-segregating populations follow the normal probability integral very closely as shown by the high P values. The scale on which the data were taken thus appears to be appropriate for analysis.

The frequency distributions of the segregating populations lie between those of the parents. B1 and F2 populations contain no plants that fall below the frequency distribution of Stewart and the B2 population has no plants beyond the distribution of Golden Ball. Only five individuals in F2 were higher in lipoxidase activity than Golden Ball. The factors differentiating Stewart and Golden Ball in lipoxidase activity appear to be isodirectional.

One major gene pair is indicated by the following: The B1 and B2 populations show an approximate 1:1 ratio with valleys in class 55 and classes 105-110, respectively. The F2 distribution has low points in classes 70-75 and in class 115 giving an approximate 1:2:1 ratio. The number of minor factors involved seems to be very small since in both backcrosses and in F2, plants were recovered which fall in the extreme classes of the parents, the lowest class in F2 being the only exception.

There are no significant differences between the populations of the four cross combinations in each backcross and between the two

Table 4. Frequency distributions for lipoxidase activity, number of plants per population, and goodness of fit test for normality of nonsegregating populations

Lipoxidase activity[1]	Frequency distribution for lipoxidase activity											
	Stewart		B 1	F 1		F 2	B 2	G. Ball	
	O[2]	T[3]	O	O	T	O	O	O	T
25		1							
30	6	3	1						
35	7	9	5			2			
40	14	12	6			6			
45	7	8	5			6			
50	1	2	3			5			
55	1	1	1			12			
60			2			9			
65			2			7			
70			2			5			
75			4		1	5			
80			3	3	2	9	1		
85			3	7	5	9	4		
90			1	3	7	12	3		
95			1	8	7	20	5		
100				7	5	14	4		
105				2	3	9	1		
110				2	1	8	1		
115					1	7	2	1	1
120						9	1	3	3
125						5	4	5	5
130						7	3	9	8
135						8	1	5	7
140						3	2	6	5
145						4	1	2	2
150						4			
155						1			
N	36		39	32		186	33	31	
D.F.	5			6				6	
X^2	2.4028			4.3619				0.8964	
P	0.80-0.70			0.70-0.50				0.99-0.98	

1) Classes are designated by upper limit of class
2) Obtained
3) Theoretical

cross combinations and six progenies in F2 (Table 5).

Means and Variances

Means and variances for lipoxidase activity are presented in Table 6. The obtained means of F1 and F2 are closer to the arithmetic than to the geometric means. No significant differences exist between obtained and theoretical means in B2. The obtained mean of B1, however, is closer to the geometric mean. The scaling values are: $A = -18.24 \pm 6.33$, $B = -7.65 \pm 7.06$, $C = 11.42 \pm 9.36$. Only A, involving B1, is greatly different from zero.

Environmental and genetic variability appear to be primarily following the arithmetic scale. No transformations of the data were therefore attempted.

A small amount of partial phenotypic dominance of higher lipoxidase activity is evident from the obtained F1 mean which is significantly higher than the mid-parent. The obtained F2 mean is slightly lower than the F1 mean.

No significant difference exists between obtained F2 mean and arithmetic calculated from F1 and parental means. However, the arithmetic mean derived from backcross means is significantly lower, Obtained and arithmetic means of B2 are similar, within limits of random sampling, but the obtained B1 mean is significantly lower than its arithmetic mean. These results suggest that there are interallelic interactions of the genes governing lipoxidase activity.

Genetic variances are large in relation to environmental variances. The similar genetic variances of the backcross populations indicate no genic dominance.

Table 5. Analyses of variance of backcross and F2 populations for lipoxidase activity

Variations	D.F.	Variance	F	nec. F	
				5%	1%
B 1					
Cross combinations	3	392.3506	1.10	2.87	4.40
Plants	35	356.2107			
B 2					
Cross combinations	3	173.8923	0.44	2.93	4.54
Plants	29	395.4414			
F 2					
Cross combinations	1	1.4260	0.002	3.90	6.78
Progenies	4	674.2825	0.76	2.42	3.42
Plants	180	882.8815			

Table 6. Means and variances for lipoxidase activity

Population	Mean			Variance	
	Obtained	Theoretical		Environmental	Genetic
		Arithmetric	Geometric		
Stewart	36.81 ± 0.95			32.3742	
B 1	54.77 ± 3.03	63.89 ± 0.91	57.87	49.1470	309.9169
F 1	90.96 ± 1.55	82.99 ± 0.85	68.95	76.4392	
F 2	89.83 ± 2.17	86.97 ± 1.46	79.20	58.0331	815.4552
		80.50 ± 2.27	76.28		
B 2	106.24 ± 3.37	110.06 ± 1.65	108.39	62.1922	312.4790
G. Ball	129.16 ± 1.42			62.1025	

Heritability and number of gene pairs

Estimates of heritability in the broad sense are high and the number of effective factor pairs computed only slightly higher than one (Table 7). The different methods of calculation give nearly identical results. When the number of factor pairs are calculated from frequency distributions (Table 8) most estimates indicate either one or two pairs. The percentage values obtained fit best Powers' (1955) Genetic Model 1 which gives further support to the assumption that the genes are isodirectional.

Hypothesis

On the basis of these observations the hypothesis is proposed that lipoxidase activity is governed by one major and one minor gene pair in the Stewart x Golden Ball cross. The genes conditioning lower lipoxidase activity are carried by Stewart and those inducing higher activity by Golden Ball. Since a small amount of phenotypic dominance of higher lipoxidase activity was apparent from the F1 mean, the major factor pair is designated AA in Golden Ball and aa in Stewart.

Theoretical frequency distributions of genotypes

The above hypothesis was tested by computing theoretical frequency distributions for genotypes of the main factor pair and comparing the combined genotype distributions of a segregating population with the obtained. The distributions, theoretical genotype means, standard errors of single determination, and X^2 tests for goodness of fit are presented in Table 9. There is excellent agreement between obtained and theoretical frequency distributions in the two backcrosses, and in F2 a reasonably close fit is obtained with a P value of 0.2 - 0.1.

Table 7. Estimates of heritability and number of effective factor pairs calculated from means and variances for lipoxidase activity

Method of calculation	Heritability in percent 1	2	No. of factor pairs 1	2
Burton	91.2	93.4		
Mahmud and Kramer	94.9	93.4		
Mather			-	1.1
Castle - Wright			1.3	1.3
Weber			1.3	1.3
Burton - Wright			1.4	1.3

1 = Genetic variance estimated according to author
2 = " " from Table 6

Table 8. Quotients (expressed as percentages) between frequency distribution classes of designated populations and number of effective factor pairs for lipoxidase activity

Estimate	Lower tail of curve								Upper tail of curve							
	B 2 / F 1		B 1 / P 1		F 2 / P 1		F 2 / B 1		B 1 / F 1		B 2 / P 2		F 2 / P 2		F 2 / B 2	
	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No
1	32	2	15	3	3	3	7	4	4	5	47	1	75	1	160	1
2	48	1	43	1	6	2	14	3	7	4	35	2	25	1	71	1
3	60	1	41	1	8	2	17	3	14	3	29	2	26	1	89	1
4	60	1	46	1	11	2	20	2	21	2	30	2	20	1	68	1

Table 9. Obtained frequency distributions of segregating populations and theoretical frequency distributions of genotypes for lipoxidase activity, with theoretical means, standard errors of single determinations, and X^2 test for goodness of fit between obtained and theoretical data

Lipoxidase activity	Frequency distribution for lipoxidase activity*)										
	B 1			F 2				B 2			
	Obt.	Theor.		Obt.	Theor.			Obt.	Theor.		
		aa	Aa		aa	Aa	AA		Aa	AA	
25		1									
30	1	2									
35	5	5		[2]							
40	6	6		[6]	1						
45	5	4		[6]	5						
50	3	1		[5]	13						
55	1		1	12	15						
60	2		1	9	9						
65	2		2	7	3						
70	2		4	5		1					
75	4		4	5		3			1		
80	[3]		4	9		8		[1]	1		
85	[3]		2	9		15		[4]	3		
90	[1]		1	12		20		[3]	4		
95	[1]		1	20		20		5	4		
100				14		14		4	3		
105				9		8		1	1		
110				8		3		1		1	
115				7		1	2	2		2	
120				9			5	1		3	
125				5			9	4		4	
130				7			11	3		3	
135				[8]			10	1		2	
140				[3]			6	2		1	
145				[4]			3	1			
150				[4]			1				
155				[1]							
$\bar{x}$		36.54	72.99		51.30	89.73	128.55		90.35	122.13	
s_d		5.6707	8.7429		5.6707	8.7429	8.0442		8.7429	8.0442	
D.F.		13			22				13		
X^2		3.7873			29.1479				4.2063		
P		0.99			0.20 - 0.10				0.99 - 0.98		

*) Obtained frequency distributions enclosed in blocks were used in predicting means of genotypes

The X^2 tests thus give evidence that the obtained frequency distributions of the segregating populations are those expected on the assumption that they are composed of their respective genotype distributions. The frequency distribution of the B1 population consists of two distributions, each following the normal curve, one fluctuating about the mean of aa and the other about the mean of Aa. The B2 population distribution is made up of the Aa and AA genotype distributions. Finally, the F2 distribution is composed of three, namely the aa, Aa and AA distributions.

Obtained frequency distributions of genotypes

The obtained frequency distributions of the three segregating populations are now partitioned into the respective genotype distributions and their means calculated (Table 10). All obtained genotype means are in close agreement with their respective theoretical means in Table 9.

In the B1 population 20 plants are of the aa genotype and 19 plants of the Aa genotype giving an excellent 1:1 ratio. The B2 population consists of 18 Aa and 15 AA plants. The F2 gives a very close fit to a 1:2:1 ratio (47:93:46).

Analysis of F3 lines

The analysis so far has been concerned with single plants whose seeds had been tested for lipoxidase activity. However, as outlined in Materials and Methods, progenies of F2 plants together with Stewart and Golden Ball were also grown that same year on a line basis. It should be pointed out that in testing an F2 plant its seed (F3) was taken to determine lipoxidase activity, whereas in testing the progeny of an F2 plant (=F3 line) a bulk sample of seed (F4) was used.

Table 10. Obtained frequency distributions of genotypes for lipoxidase activity, with number of plants and mean of each genotype

Lipoxidase activity	Frequency distribution for lipoxidase activity						
	B 1		F 2			B 2	
	aa	Aa	aa	Aa	AA	Aa	AA
30	1						
35	5		2				
40	6		6				
45	5		6				
50	3		5				
55		1	12				
60		2	9				
65		2	7				
70		2		5			
75		4		5			
80		3		9		1	
85		3		9		4	
90		1		12		3	
95		1		20		5	
100				14		4	
105				9		1	
110				8			1
115				2	5		2
120					9		1
125					5		4
130					7		3
135					8		1
140					3		2
145					4		1
150					4		
155					1		
N	20	19	47	93	46	18	15
$\bar{x}$	38.50	72.50	50.37	90.46	128.48	90.28	124.83
s	± 1.29	± 2.48	± 1.29	± 1.18	± 1.66	± 1.63	± 2.58

The data from lines were analyzed by the same methods as those from single plants. Obtained frequency distributions of parental and F3 lines, and theoretical and obtained distributions of genotypes, with number of lines, means, variances, and X^2 test are presented in Table 11.

There is close agreement between the obtained frequency distributions of Stewart and Golden Ball and the normal curve. The obtained mean of the F3 population is not statistically different from the arithmetic mean (97.59), while the geometric mean is significantly lower (85.85). Environmental and genetic variability evidently follow the arithmetic scale. Slight phenotypic dominance of higher lipoxidase activity is suggested but not significant.

A comparison of the obtained population means in Tables 6 and 11 shows that the line means are approximately 13 units higher than the plant means. This may have been due to the higher moisture content of the line seeds during harvest and the shorter duration of storage before testing. The lines were cut with a sickle and the sheaves placed on high stubble when a rain storm wetted them so thoroughly that threshing was delayed for a week. The single plants, on the other hand, dried up quickly and were pulled a few days after the storm. The lines were tested for lipoxidase a few months after harvest but the single plant material one year later. (See page 38a).

Environmental variance of lines is larger than that of plants while genetic variance is smaller (environmental and genetic variances of F3 are 68.9522 and 789.1432, respectively). Lines were grown in 18 1/2 foot rows, one foot apart, and comprised a much greater land area than the single plant material. That genetic variation between lines was not as great as between plants may be attributed to the

Goodwin and Waygood (1954)* found lipoxidase activity to increase during germination of barley seeds. At 24, 48 and 110 hours after beginning of soaking, the activities of mitochondria were 512, 704 and 782 μl O_2 /mg.N / h., respectively.

According to Irvine (private communication, 1963), there is evidence that lipoxidase activity decreases during storage.

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* Goodwin, B.C., and Waygood, E.R. 1954. Succinoxidase inactivation by a lecithinase in barley seedlings. Nature 174: 517 - 519.

Table 11. Obtained frequency distributions of parental and F3 lines and theoretical and obtained frequency distributions of genotypes for lipoxidase activity, with number of lines, means, total variances, and X^2 test for goodness of fit.

Lipoxidase activity	Frequency distribution for lipoxidase activity*)								
	Obtained			F 3 Theoretical			F 3 Obtained		
	Stewart	G.Ball	F 3	aa	Aa	AA	aa	Aa	AA
40	1								
45	1		[1]				1		
50	3		[4]	1			4		
55	6		[5]	4			5		
60	2		[4]	9			4		
65	1		3	9			3		
70			4	5			4		
75			6	1			6		
80			3				1	2	
85			4		1			4	
90			5		1			5	
95			6		4			6	
100			8		8			8	
105			5		12			5	
110			7		13			7	
115			7		10			7	
120			8		6	1		7	1
125		1	6		2	3		2	4
130			7		1	5		1	6
135		3	10			7			10
140		1	[6]			6			6
145		3	[3]			4			3
150		3	[1]			2			1
155		3	[2]			1			2
160		1	[1]						1
165		1							
N	14	16	116	29	58	29	28	54	34
$\bar{x}$	51.19	143.99	101.67	60.23	106.25	133.95	60.54	101.94	134.12
s	±1.65	±2.43	±2.72				±1.90	±1.74	±1.58
V	38.2598	94.6806	858.0954						
D.F.	5	7	21						
X^2	1.5833	2.3333	27.1686						
P	0.9.	0.9	0.2-0.1						

*) Obtained frequency distributions enclosed in blocks were used in predicting means of genotypes.

smaller number of lines tested.

When theoretical genotype distributions are computed for the F3 lines and these tested against the obtained distribution the same P values are obtained as for the F2 population. Partitioning of the F3 distribution into obtained genotype distributions results in genotype means which agree well with the theoretical. The F3 is thus composed of 28 aa, 54 Aa, and 34 AA lines fitting a 1:2:1 ratio very closely.

Comparison of genotype means within populations

The obtained means of genotypes make it now possible to evaluate the effects of major and minor factors. Differences between genotype means within a population are given in Table 12.

The difference in means between the aa and AA genotypes represents the effect of the major gene pair on lipoxidase activity. It is the same, within the limits of random sampling, whether F2 single plants or their progenies were tested.

The difference between Aa and AA in B2 is not significantly different from that between aa and Aa in B1. In F2, Aa-AA is slightly smaller than aa-Aa but not significantly so. Neither allele of the major factor pair shows genic dominance in the single plant data.

In F3, the difference Aa-AA is significantly smaller than aa-Aa indicating a slight degree of genic dominance of higher lipoxidase activity. F2 and F3 are not statistically different, however, since there is good agreement between them with respect to aa-Aa and aa-AA. The difference between the two Aa-AA estimates is also smaller than twice the standard error of difference.

Comparison of genotype means between populations

The differences between obtained means of the same genotype in different populations are shown in Table 13. If only one factor pair were involved in lipoxidase activity all means of the same genotype in different populations should be similar, within the limits of random sampling.

The agreement between the means of Stewart and the aa genotype in B1 is good, while the means of the aa genotype in F2 and F3 are higher than can be explained by chance. The means of F1 and the Aa genotype in F2 and B2 are similar, whereas the mean of Aa B1 is significantly lower. There are no significant differences between the means of the AA genotypes in the single plant data. The AA genotype in F3, however, is significantly lower than Golden Ball.

The deviations of aa F2 and F3, and Aa B1 may be explained by supposing one minor factor pair with a high degree of genic dominance of higher lipoxidase activity (gene B). A small amount of phenotypic dominance and no or slight genic dominance of higher activity for the major gene A has already been pointed out. Some interaction between A and B is also evident.

On the basis of the proposed gene model, the mean of the aa genotype in F2 consisting of 1bb + 2Bb + 1BB is then expected to be higher, on account of the higher frequency of B, than the means of aa B1 (1bb + 1Bb) and Stewart (bb). The means of F1 and the Aa genotypes in F2 and B2 will differ little from each other while the mean of Aa B1 will be significantly lower. The AA genotype means of F2 and B2 will be close to the mean of Golden Ball.

Interaction between the A and B genes is indicated by the fact

Table 12. Differences between obtained means of genotypes within a population for lipoxidase activity

Population	Genotypes compared		
	aa - Aa	aa - AA	Aa - AA
B 1	34.00 ± 2.79		
F 2 (plants)	40.09 ± 1.74	78.11 ± 2.10	38.02 ± 2.04
F 3 (lines)	41.40 ± 2.57	73.58 ± 2.47	32.18 ± 2.35
B 2			34.55 ± 3.05

Table 13. Differences between obtained means of the same genotype in different populations for lipoxidase activity[1)]

Populations compared						Genotypes		
St.	Bl	Fl	F2	B2	G.B.	aa	Aa	AA
x	x					1.97 ± 1.63		
x			x			13.84 ± 1.63		
x			x			(9.47 ± 2.54)[2)]		
	x		x			11.87 ± 1.82	17.96 ± 2.74	
	x	x					18.59 ± 2.89	
	x			x			17.78 ± 2.97	
		x	x				-0.63 ± 1.90	
		x		x			-0.81 ± 2.21	
			x	x			-0.18 ± 2.01	-3.65 ± 3.07
			x		x			0.47 ± 2.16
			x		x			(9.94 ± 3.08)
				x	x			4.12 ± 2.92

1) All means calculated from frequency distributions
2) Values in parentheses from F 3 lines

that the population mean and the genotype means of B1 are still lower than expected under the above hypothesis. A or B alone and in single dose seem to be less effective than when together.

Agreement between F2 and F3 data

The mean of the aa genotype in F3 should be comparable to the mean of the aa genotype in F2 if the seeds from the aa F2 plants sown carried the B genotypes in approximately 1:2:1 proportion. This appears to be the case since there is good agreement between the Stewart-F2 and Stewart-F3 differences.

F2 and F3 data differ, however, with respect to the AA genotype. Several AA F3 lines apparently contained a higher proportion of bb and Bb plants. The lower lipoxidase activity of these lines was then reflected in the lower AA genotype mean. The skewed frequency distribution of the obtained AA genotype in Table 11 supports this assumption. The four lower classes - 120 to 135 - contain 21 lines of which 10, the highest number in the distribution, are in class 135. The five upper classes - 140 to 160 -, on the other hand, are composed of only 13 lines.

Gene effects

The effects of major and minor genes are summarized in Table 14. The difference in lipoxidase activity between Stewart and Golden Ball is 92.42 when single plants were tested and 92.99 when lines were tested. The nearly identical results are remarkable since the data from lines lie approximately 13 units higher than those from plants. They strongly support the assumptions made earlier that environmental and genetic effects are additive.

The difference between the aa and AA genotypes represents the

effect of the major factor (AA) which is 78.11 in F2 plants and 73.58 in F3 lines. The two values are not significantly different.

By subtracting the major gene effect from the overall difference between Stewart and Golden Ball, the effect of the minor gene (BB) is obtained. It is 14.31 for plants and 19.41 for lines. Another estimate of the minor gene effect is obtained by comparing the means of the Aa genotype of the two backcrosses. This difference is 17.78. The three estimates are not statistically different as is apparent from their standard errors.

It can be concluded that the major factor for lipoxidase activity has approximately 4 1/2 times the effect of the minor factor in the Stewart x Golden Ball cross.

Predicted gains

Since plant breeders are interested in the gain they can achieve through selection, genetic gains were calculated for varying selection intensities (Table 15). Selection in F2 of plants with the lowest lipoxidase activity - those in class 35 comprising approximately 1 percent of the population - would result in an expected genetic gain of 52.19 units. The estimated mean of the selections in F3 would be 37.64 which is nearly identical with the mean of Stewart.

Saving all plants of classes 35 to 50, approximately 10 percent of the F2 population, would result in an expected reduction in lipoxidase activity of 44.80 units. The estimated mean of the next generation would be 45.03, approximately 8 units higher than Stewart. Rapid progress should be possible in selection for low lipoxidase activity in this material.

Comparable results will be obtained if F3 lines are tested

Table 14. Gene effects for lipoxidase activity*

Genes	Effect	
	Plants	Lines
G. Ball - Stewart	92.42 ± 1.70	92.99 ± 3.14
Major gene	78.11 ± 2.10	73.58 ± 2.47
Minor gene 1	14.31 ± 2.70	19.41 ± 4.00
" " 2	17.78 ± 2.97	

* Means were calculated from frequency distributions
1 (G.B. - St.) - (AA - aa F2)
2 Aa B2 - Aa B1

Table 15. Predicted gains for lipoxidase activity at different selection intensities with heritability = 0.934

Plants with lipoxidase activity	Percent of F 2	Selection differential	Predicted gain
30.1 - 35.0	1.1	55.88	52.19
30.1 - 40.0	4.3	52.98	49.48
30.1 - 45.0	7.5	50.42	47.09
30.1 - 50.0	10.2	47.97	44.80
30.1 - 55.0	16.7	43.90	41.00

for lipoxidase activity. However, selection will start one year later and at a much greater cost of land and labor. It will be far more efficient to grow spaced single plants of F2 and the parents in a randomized experiment. Besides testing for lipoxidase activity, selection may be practised for other relatively simple inherited characters which can effectively be determined on single plants. The progenies of the selected F2 individuals may again be planted in similar fashion, etc., until progeny testing for yield and other complex inherited characters is begun. The same procedure can also be used with backcrossed plants.

Effect of environment

Promising lines need not be tested at many locations for lipoxidase activity since environmental variance is additive and small in comparison to genetic variance. This investigation confirms the findings of Irvine and Anderson (1953b) who tested seven varieties at seven stations in the durum-growing area of Western Canada. Environment had little effect on semolina lipoxidase activity. The mean square for stations (17) was just significant at the 5% level while that for varieties was extremely high (939).

The manometric assay for lipoxidase determination developed by Irvine and Anderson (1953a) and used in the present study should be extremely valuable to the durum breeder in assessing early generation breeding material for lipoxidase activity and thereby macaroni quality.

Stem Solidness

Frequency distributions of populations

Frequency distributions for stem solidness index and X^2 test for normality of nonsegregating populations are presented in Table 16.

The agreement between obtained and theoretical distributions is much better for the F1 and Golden Ball populations than for Stewart. Here a relatively low P value is obtained, because the obtained distribution of Stewart consists of only three classes of which the first contains too many plants. This is probably caused by errors in classification since there are only small differences in hollowness between culms of Stewart.

The frequency distributions of the segregating populations fall between those of the parents which indicates isodirection of the factors conditioning stem solidness.

A clear cut segregation of 24 hollow to 15 partial solid plants (like F1) is obtained in the B1 population. The hollow plants, however, are slightly more solid than Stewart. In B2, approximately half the plants appear to be of the F1 type while the other half is like Golden Ball. Two valleys are apparent in the F2 frequency distribution, a very broad one in the lower part corresponding to the gap in B1, and a narrow one in class 56 coinciding with the low point in B2. These results give strong evidence of one major factor pair differentiating Stewart and Golden Ball in stem solidness.

In addition, at least one minor gene pair must be involved, because the distributions of hollow plants in B1 and F2 are shifted somewhat toward higher index values so that their means lie approxi-

Table 16. Frequency distributions for stem solidness index, number of plants per population, and goodness of fit test for normality of nonsegregating populations

Solidness index[1]	Frequency distribution for solidness index											
	Stewart		B 1	F 1		F 2	B 2	G.Ball	
	O[2]	T[3]	O	O	T	O	O	O	T
14	14	8				5			
16	19	22	1			10			
18	6	9	10			17			
20			8			7			
22			5			3			
24						7			
26						2			
28						2			
30						1			
32						2			
34			1	2	1	3			
36			1	3	1	5			
38			2	2	2	7			
40			1	1	3	5	1		
42			1	4	4	9			
44			2	3	5	11	3		
46			2	4	5	13	2		
48			1	4	5	20	2		
50			3	6	4	19	3		
52			1	5	3	15	4	2	1
54				4	3	14	6	3	2
56				1	2	12	3	5	7
58					1	14	4	11	12
60						22	10	18	17
N	39		39	39		225	38	39	
D.F.	2			11				4	
X^2	5.9091			11.5333				2.2136	
P	0.10-0.05			0.50-0.30				0.70-0.50	

1) Classes are designated by upper limit of class
2) Obtained
3) Theoretical

mately three units higher than the mean of Stewart. The F1-like plants in F2 and B2 also seem to have higher means than the F1.

No significant differences exist between the populations of the different cross combinations in either backcross and between cross combinations and progenies in F2 (Table 17).

Means and variances

Means and variances are given in Table 18. The obtained means of F1, F2 and B2 lie closer to the arithmetic than to the geometric means. No significant differences exist between obtained and theoretical means of B1. All three scaling values are very close to zero: $A = -4.64 \pm 4.18$, $B = 2.72 \pm 2.11$, $C = 3.72 \pm 4.37$. Environmental and genic variability evidently follow the arithmetic scale.

Partial phenotypic dominance of solidness is apparent from the F1 mean which is approximately 9 units higher in solidness index than the parental average. In the segregating populations, the differences between obtained and arithmetic means are not greater than can be explained by chance. There appear to be no interallelic interactions.

Environment has little effect on stem solidness in the parental varieties as their small variances show. Variation in F1, however, is very great. The environmental variances of the segregating populations lie between those of the parents and F1 and are small in relation to genetic variances.

Genic dominance of solidness is evident from the smaller genetic variance of B2 as compared with that of B1.

Heritability and number of gene pairs

Heritability is high and the number of factor pairs calculated

Table 17. Analyses of variance of backcross and F 2 populations for stem solidness index

Variations	D.F.	Variance	F	nec. F	
				5%	1%
B 1					
Cross combinations	3	54.9368	0.32	2.87	4.40
Plants	35	170.1366			
B 2					
Cross combinations	3	47.7974	1.58	2.88	4.42
Plants	34	30.3221			
F 2					
Cross combinations	1	252.6620	0.96	7.71	21.20
Progenies	4	264.0624	1.25	2.41	3.41
Plants	219	211.7668			

Table 18. Means and variances for stem solidness index

Population	Mean			Variance	
	Obtained	Theoretical		Environmental	Genetic
		Arithmetric	Geometric		
Stewart	15.08 ± 0.20			1.5466	
B 1	28.10 ± 2.03	30.42 ± 0.50	26.27	19.8943	141.1475
F 1	45.77 ± 0.97	36.42 ± 0.22	29.51	36.9717	
F 2	42.03 ± 0.97	41.10 ± 0.51	36.75	13.6640	199.2192
		40.62 ± 1.11	38.64		
B 2	53.13 ± 0.91	51.77 ± 0.52	51.42	8.6951	23.0439
G.Ball	57.77 ± 0.39			5.8138	

only slightly greater than one (Table 19). Estimates from frequency distributions indicate either one or two isodirectional gene pairs (Table 20).

Hypothesis

Based on these findings the hypothesis is proposed that Stewart and Golden Ball are differentiated by one major and one minor factor pair for stem solidness. Golden Ball carries the genes for solid stem A and B, and Stewart their alleles a and b.

Theoretical and obtained frequency distributions of genotypes

Theoretical frequency distributions were computed for genotypes of the main factor pair A-a and the combined genotype distributions of a segregating population tested against the obtained by means of X^2. Table 21 gives the distributions, theoretical genotype means and standard errors of a single determination, with X^2 tests for goodness of fit.

The agreement between obtained and theoretical frequency distributions is very good for all three segregating populations. This furnishes conclusive evidence that the obtained distributions of B1, F2 and B2 are indeed composed of their respective genotype distributions.

The theoretical genotype distributions served as the basis for partitioning the obtained population distributions into obtained genotype distributions. From these were then calculated the obtained genotype means (Table 22). They agree very well with their respective theoretical means. The number of plants obtained for the different genotypes fit a 1:1 ratio in both backcrosses and a 1:2:1 ratio in F2.

Table 19. Estimates of heritability and number of effective factor pairs calculated from means and variances for stem solidness index

Method of calculation	Heritability in percent 1	2	No. of factor pairs 1	2
Burton	82.6	93.6		
Mahmud and Kramer	98.6	93.6		
Mather			-	1.0
Castle - Wright			1.3	1.1
Weber			1.1	1.1
Burton - Wright			1.4	1.3

1 = Genetic variance estimated according to author
2 = " " from Table 18

Table 20. Quotients (expressed as percentages) between frequency distribution classes of designated populations and number of effective factor pairs for stem solidness index

Estimate	Lower tail of curve								Upper tail of curve							
	B 2 / F 1		B 1 / P 1		F 2 / P 1		F 2 / B 1		B 1 / F 1		B 2 / P 2		F 2 / P 2		F 2 / B 2	
	%	No	%	No	%	No	%	No	%	No	%	No	%	No	%	No
1	13	3	3	5	6	2	260	1	10	3	57	1	21	1	37	2
2	9	4	28	2	8	2	50	1	25	2	50	1	22	1	43	1
3	27	2	-		14	2	36	2	25	2	51	1	24	1	48	1
4	32	2	-		-		30	2	29	2	64	1	29	1	46	1

Table 21. Obtained frequency distributions of segregating populations and theoretical frequency distributions of genotypes for stem solidness index, with theoretical means, standard errors of single determinations, and X^2 test for goodness of fit between obtained and theoretical data

Solidness index	Frequency distribution for solidness index*)								
	B 1			F 2				B 2		
	Obt.	Theor.		Obt.	Theor.			Obt.	Theor.	
		aa	Aa		aa	Aa	AA		Aa	AA
12					1					
14				[5]	4					
16	1	2		[10]	10					
18	10	3		17	16					
20	8	6		7	15					
22	5	5		3	8					
24		3		7	2					
26		1		2						
28				2						
30			1	1						
32			1	2		1				
34	1		1	3		1				
36	1		1	5		2				
38	2		2	7		4			1	
40	1		2	5		7		[1]	1	
42	1		3	9		10			1	
44	[2]		2	11		12		[3]	1	
46	[2]		2	13		14		[2]	2	
48	[1]		2	20		15		[2]	2	
50	[3]		1	19		14		3	2	
52	[1]		1	15		11	2	4	2	1
54				14		9	5	6	2	2
56				12		6	12	3	2	4
58				14		3	16	4	1	5
60				[22]		3	22	10	2	7
$\bar{x}$		19.755	41.392		17.634	46.625	57.224		49.216	57.047
s_d		2.6355	6.0804		2.6355	6.0804	2.7729		6.0804	2.7729
D.F.		16			22				10	
X^2		13.0549			21.7685				5.1955	
P		0.70 - 0.50			0.50 - 0.30				0.90 - 0.80	

*) Obtained frequency distributions enclosed in blocks were used in predicting means of genotypes

Table 22. Obtained frequency distributions of genotypes for stem solidness index, with number of plants and mean of each genotype

Solidness index	Frequency distribution for solidness index						
	B 1		F 2			B 2	
	aa	Aa	aa	Aa	AA	Aa	AA
14			5				
16	1		10				
18	10		17				
20	8		7				
22	5		3				
24			7				
26			1	1			
28			1	1			
30				1			
32				2			
34		1		3			
36		1		5			
38		2		7			
40		1		5		1	
42		1		9			
44		2		11		3	
46		2		13		2	
48		1		20		2	
50		3		19		3	
52		1		13	2	3	1
54				9	5	3	3
56				4	8	1	2
58				2	12	1	3
60				3	19	2	8
N	24	15	51	128	46	21	17
$\bar{x}$	18.92	43.37	18.40	45.97	57.28	50.07	57.15
s	± 0.35	± 1.47	± 0.47	± 0.60	± 0.35	± 1.20	± 0.67

Comparison of genotype means within populations

Table 23 shows the differences between genotype means within the B1, F2 and B2 populations. The difference of 38.88 units in solidness index between the means of the aa and AA genotypes in F2 represents the effect of the major gene pair on stem solidness.

The means of the Aa and AA genotypes in B2 are only 7.08 units in solidness index apart while those of the aa and Aa genotypes in B1 are 24.45 units apart. In F2, the difference Aa-AA (11.31) is also much smaller than the difference aa-Aa (27.57). Partial genic dominance of the major gene for solid stem is clearly evident.

Comparison of genotype means between populations

Differences between means of the same genotype in different populations are given in Table 24. The means of the aa genotypes in B1 and F2 are similar and significantly higher than the mean of Stewart. The means of F1 and the Aa genotype in F2 are the same, while the mean of Aa B1 is somewhat lower and the mean of Aa B2 is significantly higher. No differences exist between the means of the AA genotypes.

The data may be explained by supposing one minor factor pair with partial genic dominance for solid stem (gene B). The aa genotype means of B1 and F2 will then be significantly higher than Stewart. The means of F1 and Aa F2 will be similar, whereas the mean of Aa B1 will be lower and that of Aa B2 higher. The AA means in F2 and B2 will approach the mean of Golden Ball.

The mean of the aa genotype in B1 is, however, higher than expected. Here probably more Bb than bb plants were sampled. The skewed distribution of the aa B1 genotype in Table 22 supports this assumption.

Table 23. Differences between obtained means of genotypes within a population for stem solidness index

Population	Genotypes compared		
	aa - Aa	aa - AA	Aa - AA
B 1	24.45 ± 1.51		
F 2	27.57 ± 0.76	38.88 ± 0.59	11.31 ± 0.69
B 2			7.08 ± 1.37

Table 24. Differences between obtained means of the same genotype in different populations for stem solidness index*)

Populations compared						Genotypes		
St.	B1	F1	F2	B2	G.B.	aa	Aa	AA
x	x					3.83 ± 0.42		
x			x			3.31 ± 0.52		
	x		x			-0.52 ± 0.59	2.60 ± 1.58	
	x	x					2.28 ± 1.77	
	x			x			6.70 ± 1.89	
		x	x				0.32 ± 1.16	
		x		x			4.42 ± 1.56	
			x	x			4.10 ± 1.34	-0.13 ± 0.76
			x		x			0.27 ± 0.52
				x	x			0.40 ± 0.77

*) All means calculated from frequency distributions

Gene effects

Table 25 summarizes the effects of major and minor genes. Stewart and Golden Ball differ by 42.46 units in stem solidness index. Of these, 38.88 units - the difference aa-AA in F2 - is accounted for by the major factor (AA). The remainder, 3.58 units, is due to the minor factor (BB). The other estimate of the minor gene effect, 6.70 units, is the difference between the Aa means of the backcrosses. The two latter estimates are not significantly different since the difference between them is smaller than twice its standard error.

The major factor for stem solidness has thus approximately 8 times the effect of the minor factor in the Stewart x Golden Ball cross.

Effect of environment

The above analysis was made on the material of the complete randomized block experiment of 1957. As mentioned in Materials and Methods, F2 plants of the same cross had also been grown a year earlier. Of these, two F1 progenies with 123 and 141 F2 plants each were examined for stem solidness. Their frequency distributions were similar to those of the six progenies from 1957. The analysis of variance performed on all F2 data shows no significant differences between years and between progenies (Table 26).

Variations in weather had no detectable influence on the expression of stem solidness, though the two summers differed substantially in temperature and hours of sunshine. The growing period from May to August in 1957 was warmer, dryer, and sunnier than the same period in 1956. Mean temperatures of the four summer months were 61.8°F. in 1956 and 73.3°F. in 1957. Total precipitation was 12.9 and 11.9 inches,

and hours of sunshine 1095 and 1172, for 1956 and 1957 respectively.

This confirms the findings of Platt (1941) who tested Golden Ball and two solid common wheats for three years at from 12 to 17 stations in Canada. Golden Ball was essentially solid-stemmed at all points where it was grown while the other wheats varied in degree of solidness from year to year and locality to locality. Roberts and Tyrell (1961) grew the durums Golden Ball and Melanopus and five T. aestivum varieties under shaded cages in the field. Shading had no effect on the durums but lowered stem solidness and resistance to sawfly in the bread wheats.

Predicted gains

Excellent progress can be made in selection for stem solidness in the Stewart x Golden Ball cross as the predicted gains in Table 27 indicate. If all F2 plants with a solidness index of 59 or 60 were selected, comprising approximately 10 percent of the population, a gain of 16.23 units would be expected and the Golden Ball solidness should be recovered.

It has to be pointed out, however, that estimates of heritability in the broad sense were used in calculating the expected gains. The actual genetic gains realized will be lower because both major and minor factors show partial genic dominance of solid stem.

Analysis of progenies

From all B1 and B2 plants and from approximately 80 percent of the F2 of 1957, progenies were grown in 1958 and classified for stem solidness.

In both backcross populations two types of segregating lines could be distinguished: one in which a great variation occurred -

Table 25. Gene effects for stem solidness index*

Genes	Effect
G. Ball - Stewart	42.46 ± 0.44
Major gene	38.88 ± 0.59
Minor gene 1	3.58 ± 0.74
" " 2	6.70 ± 1.89

* Means were calculated from frequency distributions
1 (G.B. - St.) - (AA - aa F2)
2 Aa B2 - Aa B1

Table 26. Analysis of variance of all F 2 populations examined

Variation	D.F.	Variance	F	nec. F	
				5%	1%
Years	1	50.3940	0.23	5.99	13.74
Progenies	6	222.1998	0.94	2.12	2.85
Plants	481	235.9231			

Table 27. Predicted gains for stem solidness index at different selection intensities with heritability = 0.936

Plants with solidness index	Percent of F 2	Selection differential	Predicted gain
59 - 60	9.8	17.34	16.23
57 - 60	16.0	16.58	15.51
55 - 60	21.3	15.76	14.75
53 - 60	27.6	14.83	13.88

like in F2 - from hollow to solid with different intermediate classes; and the other type in which the intermediates resembled each other, as did the hollow or the solid plants.

In the backcross to Stewart, the latter type line segregated in approximately 1 hollow : 2 intermediate : 1 nearly or partly solid. Similar segregation was observed in the backcross to Golden Ball but the hollow plants were not quite hollow, the intermediates on the average more solid, and the solid plants like Golden Ball.

All three types of segregating lines were found among the F2 progenies. No differentiation was attempted among hollow lines and among solid lines, though small differences were noted within each group.

The progenies of the B1 and B2 plants were classified into three groups each, and the F2 progenies into five. Table 28 gives the number of lines obtained in the different groups and the theoretical numbers based on the frequencies of the assumed genotypes, with X^2 test for goodness of fit. Obtained and theoretical numbers agree very well as shown by the high P values.

The progeny test thus supports the results of the partitioning analysis that Stewart and Golden Ball are differentiated by one major and one minor factor pair. Due to the small effect of the minor gene (B) segregation was not detected in the progenies of the aaBb and AABb genotypes, and hollow aabb and aaBB lines as well as solid AAbb and AABB lines could not be distinguished with certainty.

Comparison with factorial analyses in tetraploid wheats

Most investigators who studied stem solidness in crosses between tetraploid wheats found solidness to be partially dominant and controlled

Table 28. Classification of progenies from B1, F2, and B2 plants for stem solidness, and obtained and theoretical numbers with X^2 test for goodness of fit

Classification of progeny	Assumed genotype of parent plant	Number of progenies from B 1		F 2		B 2	
		O[1]	T[2]	O	T	O	T
Hollow to nearly hollow, homozygous or segregating	aa bb aa Bb aa BB	24	19.50	44	46.250		
Segregating 1 hollow : 2 intermediate : 1 nearly solid	Aa bb	8	9.75	24	23.125		
Segregating like F2	Aa Bb	7	9.75	52	46.250	12	9.5
Segregating 1 nearly hollow : 2 intermediate : 1 solid	Aa BB			29	23.125	9	9.5
Nearly solid to solid, homozygous or segregating	AA bb AA Bb AA BB			36	46.250	17	19.0
N		39		185		38	
D.F.		2		4		2	
X^2		2.1282		4.6216		0.8947	
P		0.5-0.3		0.5-0.3		0.7-0.5	

1) Obtained
2) Theoretical

by one factor (Engledow and Hutchinson 1925, Putnam 1942, and Hemstad 1961). Engledow and Hutchinson, however, also noted transgressive segregation in some crosses which suggested at least two factors.

The only report in the literature where solidness was studied in tetraploid crosses involving Golden Ball is that by Putnam (1942). Golden Ball was crossed to the hollow durums Pentad, Kahla, and Pelissier, and to hollow T. turgidum "Alaska". Partial dominance of solidness was indicated from the F1 of Golden Ball x Pelissier. The F2 of all crosses segregated in 3 solid plus intermediate to 1 hollow. The intermediates had a greater range of variation than the F1. In F3, a ratio of 1 nonsegregating solid + intermediate : 2 segregating : 1 hollow progenies was obtained.

The F3 data revealed also that: solid F2 plants were either homozygous or heterozygous, some plants classified as intermediate proved to be homozygous, hollow segregates were all true-breeding, and progenies of solid heterozygotes contained more solid plants than those of intermediate heterozygotes.

These results suggest that in reality two factors - one major and one minor - were segregating. Putnam classified the F3 lines as follows (in brackets are given the assumed genotypes of F2 plants, according to our hypothesis):

1.	Hollow	(aabb or aaBb or aaBB)
2.	Intermediate segregating	(Aabb or AaBb)
3.	" nonsegregating	(AAbb)
4.	Solid segregating	(AaBB)
5.	" nonsegregating	(AABb or AABB)

The number of lines obtained in the five classes were reported

for the crosses with Pentad, Kahla and Alaska. When theoretical numbers are calculated and these tested against the obtained, the following P values are obtained: < 0.01 for G.B. x Pentad, 0.8-0.7 for G.B. x Kahla, and 0.3-0.2 for G.B. x Alaska.

Evidently one major and one minor gene pair were segregating in the crosses with Kahla and Alaska. Due to the small effect of the B gene, segregation for B was not detected in the progenies of the aaBb and AABb genotypes, and hollow aabb and aaBB lines were not distinguished.

Comparison with partitioning study in common wheat

The results of the present study in durum wheat compare very favorably with those of McNeal (1956) in common wheat. The cross Thatcher x Rescue showed slight phenotypic dominance and small amounts of genic dominance of solidness for both major and minor factors.

Thatcher and Rescue were differentiated by one major gene pair having approximately 2 1/2 times the effect of all minor modifying factors. The number of minor genes was not determined but was believed to be between two and four.

The writer calculated the number of factor pairs from McNeal's data using the same methods as employed in the present study. Estimates from means and variances ranged from 1.4 to 2.1. Most estimates from frequency distributions indicated either two or three isodirectional gene pairs. Very likely two minor factor pairs were involved in the common wheat cross, one more than in the durum cross.

Comparison with aneuploid studies in common wheat

Larson and MacDonald (1959) tested monosomic lines of S-615

(the solid-stemmed parent of Rescue) for solidness. Chromosomes 3B and 3D promoted pith development in the upper part of the culm (in the first internode and to a lesser extent in the second), while chromosomes of homoeologous group 5 were needed to produce solidness in the lower internodes. Monosomic line 3B showed the greatest difference from normal in total solidness index though only the first two internodes were significantly less solid. Large differences from normal were also noted in lines 5A and 5B, here all cuts - except one in 5A - were less solid than normal, especially those in the lower internodes.

Of the above mentioned chromosomes, only 5A promoted solidness in Rescue (Larson and MacDonald 1962). The long arm affected the top internode and the short arm the lower internode. Two other chromosomes, 1A and 1D, appeared to carry minor genes for solid stem; while their monosomics were not different from normal, the nullisomics were somewhat less solid throughout.

There is thus excellent agreement between aneuploid analysis and partitioning method with respect to the number of effective factors (chromosomes) for pith development in Rescue. The major factor appears to be located on chromosome 5A and the minor genes on chromosomes 1A and 1D.

Chromosome 5A probably carries Yamashita's complimentary gene C for pith in the lower internodes (Larson and MacDonald 1959). Interallelic interactions were, however, not apparent from the partitioning analysis of Thatcher x Rescue.

A study by McNeal et al. (1957) indicated that many solid-stemmed bread wheats may have the same major solidness factor but

differ in minor genes. In crosses between four Portuguese varieties with Rescue only small differences between frequency distributions occurred in F2.

Suggested chromosomes carrying genes for solid stem in Golden Ball

The major solidness factor of Golden Ball may be located on either 3B, 5A or 5B. Larson (1959b) suggested that Golden Ball has a stronger allele for solid top internode on chromosome 3B than Rescue. From the cross Golden Ball x Rescue two T. aestivum-like F4 lines were selected which were more solid than Rescue in the first internode. The increase was probably due to segregation of the genes on 3B because this is the only chromosome of the A and B genomes promoting solidness in the top internode.

Since the solidness factors on 3B and 5A have the strongest effects and may be carried by several solid-stemmed wheats, it is suggested that they are also involved in the Stewart x Golden Ball cross. Chromosomes 5B and 1A then either have no genes for solid stem in Golden Ball, or their effects are very small.

Pith inhibitors

Genes inhibiting pith development were not detected by the partitioning method. Monosomic analysis showed three chromosomes of the A and B genomes to suppress solidness: 2A in Chinese (Larson and MacDonald 1959), and 3B and 6A in Rescue (Larson and MacDonald 1962). The two latter chromosomes affect the base of the first internode only. In S-615 and probably also in Golden Ball chromosome 3B promotes solidness in the top internode. If Stewart or Golden Ball have inhibitors on chromosomes 2 and 6 of the A genome their effects must be very weak.

Association between Lipoxidase Activity and Stem Solidness

The data for lipoxidase activity and stem solidness index were tested for association by X^2 and by correlation.

The number of plants in the four genotypic groups a, b, c and d, with X^2 for independent segregation and P values, are given in Table 29. F2 progenies falling in class 80 of lipoxidase activity (Table 11) and F2 plants in classes 26 and 28 of stem solidness index (Table 22) were not used in this analysis because the frequency distributions of genotypes aa and Aa were here overlapping. No X^2 could be calculated for the B2 population since it was not possible to separate the Aa and AA genotypes for stem solidness.

The B1 and F2 populations show independent segregation between the two major factor pairs. The different F2 populations are also homogeneous.

A low P value is obtained in the backcross to Stewart because, of the 20 plants low in lipoxidase activity, only 5 were partly solid while 15 were hollow. This discrepancy from the theoretical 1 : 1 ratio was probably caused by the different sample sizes of the Aa and aa genotypes for solidness. Of the 39 plants in B1 only 15 plants were partly solid whereas 24 were hollow (Table 22).

Correlation coefficients for the B1, B2, and the three F2 populations are presented in Table 30. The backcross to Stewart indicates slight correlation between lipoxidase activity and stem solidness index, though the correlation coefficient is barely significant at the 5 percent level. This may have been due to sampling more hollow than partly solid plants in B1, as pointed out above.

Table 29. X^2 test for independent segregation between the major factor pairs of lipoxidase activity and stem solidness

Population	Number of plants					X^2	D.F.	P
	a	b	c	d	N			
B 1	10	9	5	15	39	3.1026	1	0.1-0.05
F 2 (S B)	57	12	15	7	91	1.8571	1	0.2-0.1
F 2 (B S)	51	17	21	3	92	1.5652	1	0.3-0.2
F 2 - F 3 *	62	23	23	4	112	1.5873	1	0.3-0.2
All F 2	170	52	59	14	295	0.5156	1	0.5-0.3
F 2 Homogeneity						4.4940	2	0.2-0.1

* F2 plants examined for stem solidness, their progenies tested for lipoxidase activity

Table 30. Correlation between lipoxidase activity and stem solidness index

Population	D.F.	Correlation coefficient	Significant at 5 %	1 %
B 1	37	0.335*	0.325	0.418
B 2	31	-0.016	0.349	0.449
F 2 (S B)	91	0.050	0.205	0.267
F 2 (B S)	90	-0.123	0.205	0.267
F 2 - F 3	113	-0.100	0.195	0.254

* Significant at 5 % level

Since the four other correlation coefficients are close to zero, it is concluded that there is no correlation between lipoxidase activity and stem solidness. No difficulties should, therefore, be encountered in combining the low lipoxidase activity of Stewart with the stem solidness of Golden Ball.

In the F2 of the 1957 experiment, 19 individuals fell between 30 and 50 in lipoxidase activity (Table 4) and 22 had a stem solidness index of 59 or 60 (Table 16). One of these plants had low lipoxidase activity (42.6) combined with stem solidness (59). Assuming that in this plant all factors for low lipoxidase activity and for stem solidness are represented by at least one gene, then homozygous segregants should be recovered from its progeny.

There were 47 F2 plants with lipoxidase activities of 30 to 65, and 77 individuals with solidness indices of 51 to 60. Eighteen of these plants combined low lipoxidase activity with stem solidness, in addition to the one referred to above. Selection among their progenies will be less efficient, though several lines should contain segregants with all genes for low lipoxidase and for stem solidness in the homozygous condition.

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