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SEED SIZE OF WHEAT - ITS INHERITANCE AND INFLUENCE ON YIELD

by

PETER DOUGLAS BROWN

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ABSTRACT

The purpose of this study was to determine the influence of seed size on yield of wheat under local conditions and to study the inheritance of kernel weight in relation to the feasibility of increasing seed size through selection.

The study to determine the effect of seed size upon yield was performed in field trials during two summers. Two varieties, Neepawa and Glenlea, were separated on the basis of seed size using nested hand screens. The results indicate that yield varies positively with seed size. Yield differences of at least 19 per cent were observed for the extreme seed sizes. The largest seed size outyielded the average seed size by at least 4 per cent. Differences in yield components due to seed size differences were not detected. The yield advantage of the large sizes was maintained at all seeding rates (constant seed number) tested. By sowing a constant weight of seed it was shown that it is possible to obtain equal yields regardless of seed size.

Using seven parents varying in seed size (hence weight), seven sets of crosses were made in the greenhouse to obtain the F_1, F_2, reciprocal backcrosses, and in some cases the F_3 generations. With this material it was found that the minimum number of genes determining seed weight was 2. The average heritability estimates ranged between 24 and 80 per cent. In all the crosses there was additive gene action for seed weight

although in some there was also dominance and epistasis. However, due to lack of randomization of genetic material estimates of gene action and some of the estimates of gene number may not be accurate. There was minimal transgressive segregation for either large or small seed size in the F_2 and F_3 samples of all the crosses.

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INTRODUCTION

> "... no matter what treatment was given to the seed
> grain it was in vain except when they also, with
> great care, picked out the largest grain ..."
>
> Virgil

The main objective of this program was to obtain information about the influence of seed size of wheat on yield and to investigate its inheritance. A field study was conducted to determine whether it was possible to obtain increased yields using large seed of local wheat varieties. Glenlea, one of the varieties used in these experiments, derives its yield advantage in part from its greater seed size compared with other wheat varieties such as Neepawa. It would be interesting to know the yield differences between Glenlea and Neepawa when the same size of seed was planted. The experiments were set up to determine whether increased yields could be obtained with either Glenlea or Neepawa just by using larger than normal seed. If this were the case there would be immediate practical implications: the grower would be able to separate the seed on the basis of size and plant only the large seed. The plant breeder, using this information, could include selection of the heavier, heterozygous kernels in the breeding program and obtain a plant having a larger seed size thus having an increased yield potential.

These experiments also studied the effect of the interaction between seed size and seeding rate upon yield. Does the effect of seed size upon yield remain the same regardless of seeding rate or is it possible to get equal yields at a higher seeding rate? By seeding a constant weight of seeds it was possible to see whether planting more small seeds makes up for the greater vigour of the large seed.

Knowing that seed size does influence yield resulted in a study of the inheritance of this characteristic. The ultimate goal would be to increase the seed size, hence yield. The experiment was set up to determine the number of genes involved and the heritability of this trait. With this information it would be possible to predict just how great a yield increase could be made and whether it would be easier to select for kernel weight than for yield itself. The greatest potential for increased yield would come from crosses in which there was transgressive segregation for large size. This would indicate a combination of genes resulting in a heavier seed. Another source of genes for large size would be the large durum wheats. The feasibility of transferring these genes from the tetraploid to the hexaploid should be explored. Two characteristically round seeded parents were included. The purpose for using these parents was to combine the round and long characteristics resulting in a distinctively large plump kernel with a good yield potential.

LITERATURE REVIEW

2.1 Effect of Seed Size Upon Seedling Vigour and Yield

Yield, whether it be total plant weight or seed harvested, has always been one of the major concerns of the producer. There are reports of studies being done to determine the effects of seed size upon yield dating back into the last century (Hicks and Dabney, 1896). Attempts were being made to find some easy way to improve yield. The results of this early work (Eitingen, 1928; Kiesselbach, 1924; Waldron, 1910) on various plant species indicate that yield increases could be attained by using larger, heavier seed.

Experimental results with most crops show that the potential per cent germination does not vary with seed size. That is, the viability of the seed is not dependent upon the size of the seed (Dermirlicakmak, Kaufmann and Johnson, 1963; Hunter and Kannenberg, 1972; Kaufman and McFadden, 1963; Kneebone and Cremer, 1955; Pinthus and Osher, 1966). The actual emergence of a sample of seeds can vary positively with the size of seed. This is shown in experiments where depth of planting and seed size are 2 variables. In some cases depth of planting reduces rate of emergence but not the final emergence (Hunter and Kannenberg, 1972). Working with flax, Harper and Obeid (1967) showed that at 6 centimeters the large seeds germinated faster than the medium or small seed. Often this speed is necessary to avoid the "damping off" fungi which would reduce the number of seedlings emerging (Rogler, 1954). The larger seeds with their greater food reserves in the cotyledons or endosperm are able to grow from a greater depth before requiring photosynthates to provide the energy and material for growth. It has also been shown that the coleoptile length and seed size are positively related. For this reason large seeds can be planted deeper and can be expected to emerge resulting in a potentially better stand and yield compared with smaller seed. Boyd, Gordon and LaCroix (1971), working with barley found that as seed size increases germination resistance in barley decreases. From this it could be expected that the rate of emergence would be positively related to seed size. In this way the visible germination varies positively with seed size.

Seed size has been shown to influence traits during the time of vegetative growth. Seedling vigour is positively related to seed size. This has been demonstrated in a number of ways. The fastest and most obvious method of indicating seedling vigour is visual inspection. Kaufmann and McFadden (1963) found that plants from large seeds "appeared more vigourous" than those from small seeds. In an earlier paper Kaufmann and McFadden (1960) found that although emergence was the same regardless of seed size, plants arising from large seeds were more vigorous and the second leaf stage appeared sooner. Kneebone and Cremer (1955) working with grass species native to North America and Kittock and Law (1968) working with wheat used rate of emergence to show the positive relation between seedling vigour and seed size. A continuation of this method is seedling growth rate; the work with native grasses and wheat mentioned above, in addition to work with barley (McDaniel, 1969), smooth bromegrass (Trupp and Carlson, 1971), rye-grass (Thomas, 1966), and birdsfootrefoil (Carlton and Cooper, 1972) indicate that the seedlings from large seeds grew faster than those from smaller seeds. Experiments with other legumes such as alfalfa and sainfoin (Carlton and Cooper, 1972) showed no relation between seed size and vigour although in the case of the latter there was a correlation with vigour at small seed sizes. A more precise indication of seedling vigour can be obtained by making a quantitative measurement. The weight of barley shoots (Boyd, Gordon, and LaCroix, 1971) and oats, barley, rye and corn seedlings (Hicks and Dabney, 1896) showed again the positive relation between seed size and vigour. Other effects that are positively related to seed size are the number of leaves and stem diameter of soya beans and the earliness of peas as reported by Hicks and Dabney (1896) and the basal diameter and leaf area reported by Eitingen (1928). In an attempt to determine the influence of seed size on the results of barley yield trials, Kaufmann and McFadden (1963) noted that plants from large seeds headed and ripened faster. This information indicates that seed size influences numerous characteristics associated with the growth habit of the plant.

In the experiments with smooth bromegrass and rye-grass mentioned above, the advantage conferred by large seeds upon growth rate diminished with time although in the case of the work with bromegrass by Trupp and Carlson (1971) this effect was still noticeable 93 days after seeding. Many of the studies on seedling vigour showed that during the initial stages of growth, seed size was correlated with vigour but that these correlations decrease as the plants become older. Nevertheless, even though specific effects and correlations decrease, the long term cumulative effect of seed size often continues (Thomas, 1966). This information indicates that crops with a limited growing season such as spring wheat and barley might have a yield advantage when large seed is used but that with crops having a long period of growth as with winter cereals (Bowman and Rothman, 1967) and perennial grasses, the initial advantage of seed size might not be revealed in the final yield. Though not applicable to cereals, the record long term effect due to seed size may be held by the oak tree. Planting 3 sizes of acorns resulted in trees with differences in height, basal diameter, dry weight and number and area of leaves after periods of 5 and 8 years (Eitingen, 1928).

The effect of seed size upon yield is the most important consideration when studying cereals. Much work has been done in this respect using wheat (Austenson and Walton, 1970; Christian and Grey, 1941; Geizler and Hoag, 1967; Kiesselbach, 1924; Pinthus and Osher, 1966; Waldron, 1941, 1943), oats (Kiesselbach, 1924), barley (Dermirlicakmak, Kaufmann and Johnson, 1963; Kaufmann and McFadden, 1960, 1963), rye (Vageler, 1927) and corn (Hunter and Kannenberg, 1972). Most of the results indicate that by using large seed increased yields can be attained. With corn these increases were not significant. These plants, however, were growing under optimum conditions so that this might explain the lack of significance. Conditions of stress magnify the yield advantage of large seeds. Geiszler and Hoag (1967) found that when the wheat plants were under stress due to disease the yield of the plants arising from small seed was significantly less than that of the larger sizes. Working with oats, Frey and Wiggans (1956) showed that under favourable conditions plants derived from light weight seed were able to recover from their handicapped start by heading time. When environmental conditions were unfavourable, the result was a yield differential in favour of the heavier seeds. A number of workers using wheat (Christian and Grey, 1941) and barley (Kaufmann and McFadden, 1960) showed that the stress due to inter-plant and inter-row competition gave the plants from the large seeds an advantage. Citing barley as an example the small "seeded" plants yielded 83 per cent that of the plants from large seeds under field conditions in the absence of competition. When alternation of large and small seeds provided inter-plant and inter-row competition the yields of plants from small seeds were no more than 57 per cent that of the yields from large "seeded" plants.

To validate the claim that large "seeded" plants out yield those arising from small seeds and to provide meaning to the numerical data describing these yield differentials the rate of seeding must be noted.

When the same number of large and small seeds is planted the yield from large "seeded" plants was significantly greater than that from small "seeded" plants. When a constant volume is seeded which is the case with the drill in commercial farming practices or a constant weight is seeded as may be done experimentally, there will be more small seeds planted compared to large seeds and the yield differences diminish. Using a constant weight as the seeding measure, Waldron (1941) found that the large outyielded the small seeded plants by 10 per cent. Geiszler and Hoag (1967) found that the lower seeding rate of large seeds obtained by seeding a constant volume resulted in small non-significant yield differences in favour of the large seeds when the plants were growing under good environmental conditions. Under conditions of stress, however, the large seeds displayed a significant advantage. Kiesselbach (1924) showed that when equal numbers of large and small seeds were grown the large "seeded" plants outyielded the small but that when equal volumes of each size were sown there were no yield differences and he theorized that the lack of vigour of the small seeds was compensated for by the greater number.

In an attempt to explain the yield differential due to differences in seed size the results of two experiments can be cited. Working with barley, McDaniel (1969) showed that seed weight, seedling vigour and mitochondrial metabolism are related in germinating seedlings. Knowing that mitochrondrial metabolism provided readily available energy for protein synthesis and ion uptake he showed that heavy seeds had a greater initial quantity of mitochondrial protein compared with light seeds. His conclusion was that heavy seeds produced seedlings with a greater energy production potential thus resulting in faster growth. Bremner, Eckersall, and Scott (1963) used a combination of 2 embryo sizes and 2 endosperm sizes, which were achieved by removing part of the endosperm, to determine the relative importance of embryo size and endosperm size in causing the effects associated with seed size differences in wheat. Their observations and conclusions are as follows. Plants from small embryos have a faster initial growth rate than those from large embryos. Their explanation for this was that a small embryo has a relatively larger scutellum compared with the large embryo and thus the enzymes in the scutellum could obtain relatively more energy for growth from the endosperm. This initial advantage quickly diminished and as long as the endosperm was the energy source the seedlings from the large and small embryos grew at the same rate. In a small seed the small endosperm means that this energy source is exhausted sooner and the growth rate is dependent only upon the leaves so that the rate of growth decreases. Conversely, seedlings having a large endosperm can grow faster because the energy source is both the endosperm and the leaves. This advantage continues even after the endosperm supply runs out as the seedlings from large seeds have a greater photosynthetic area relative to those seedlings from small seeds. In summing up this experiment the authors stated that, "the dominating factor in the seed-size/plant-size relationship in wheat is the extent of the energy source available to the developing seedling: this determines the size of the plant and the extent of its leaf surface at the time of exhaustion of reserve material when it becomes wholly dependent on photosynthesis."

What then is the yield advantage of large seeds? This will probably depend upon conditions such as the crop, the variety, the seeding rate and the environmental conditions. The results of Kaufmann and McFadden working with large and small seeds have already been mentioned; under conditions of no competition between sizes the small yielded 83 per cent of the large (Kaufmann and McFadden, 1960) under field conditions. Again working with barley sown at a constant number of seeds, Dermirlicakmak, Kaufmann and Johnson (1963) showed that large seed outyielded medium sized seed by 3.9 per cent and small seed by 12.6 per cent. The yield differential between large and small wheat seeds, sown at a constant number of seeds was over 20 per cent in the experiment conducted by Pinthus and Osher (1966). From this information it is clear that seed size has an effect on yield.

2.2 Effect of Seeding Rate Upon Yield

The effect of seeding rate on the yield of cereals has been investigated on numerous occasions. From the results, it would appear that under present farming practices and within an optimum rate range, the seeding rate is not too critical. There are too many factors which alter the influence of seeding rate. Conditions that favour heavier seeding rates are "large seed size, germination below 90 per cent, late seeding or a need for hastening maturity, deep seeding, a rough seed bed, abundant moisture reserves, high fertility, or a high incidence of weeds, insects or disease" (1972 Field Crop Recommendations for Manitoba; Siemens, 1971). It has been shown that when weeds, insects and diseases are controlled chemically, low seeding rates produced significantly more than high seeding rates (Pelton, 1969). This effect is most pronounced during years of moisture stress when the lower rates result in a slower use of available moisture. Often a higher than required seeding rate is used to compensate for poor farming practices.

The component of yield response to seeding rates was not identical for all varieties of wheat, oats or barley. In general as the rate of seeding increased, the number of plants increased (Guitard, Newman and Hoyt, 1961) although the yield per plant decreased (Severson and Rasmusson, 1968), 1000 kernel weight decreased (Guitard, Newman, and Hoyt, 1961; McNeal, Berg _et al_., 1960; Severson and Rasmusson, 1968) and the number of kernels per head decreased (Finlay, Reinbergs and Daynard, 1971; Guitard, Newman and Hoyt, 1961; Severson and Rasmusson, 1968). The component of yield which Austenson and Walton (1970) found to be most important and most closely correlated with seed size in the wheat varieties Pembina, Thatcher and Manitou was the number of heads per plant. In other experiments where this factor was noted both decreases (Guitard, Newman and Hoyt, 1961; McFadden, 1970; Severson and Rasmusson, 1968) and increases (Finlay, Reinsberg and Daynard, 1971; McNeal and Berg *et al*., 1960) in the number of heads were recorded as the rate of seeding was increased.

For wheat grown in Manitoba the recommended rate of seeding is 1-2 bushels per acre (1972 Field Crop Recommendations for Manitoba). As the extremes of this rate are approached slight yield decreases might be noticed when the plants are growing under average conditions. When growth conditions are at the optimum a seeding rate at the lower end of the recommended rate could be used whereas when adverse conditions are encountered the reverse applies. The general consensus seems to be that within limits seeding rate has little or no influence upon yield.

2.3 Inheritance of Seed Size

Grafius (1956) defined yield as the product of three components: weight per seed, number of seeds per head and the number of heads per unit area. Of these three components it has been found (Sharma and Knott, 1964) that kernel weight is the least subject to environmental variation. In any attempt to increase yield by altering one component it would make sense to begin by improving the seed weight. Knott and Talukdar (1971) transferred the seed weight of Selkirk by backcrossing into Thatcher which although it has a high number of seeds per head has a low kernel weight. They demonstrated that an increase in kernel weight resulted in a decrease in the other two yield components. In spite of these decreases, the backcrossed lines were 19 per cent heavier and yielded 6 per cent more than

Thatcher indicating that the reduction in the number of kernels per unit area was insufficient to compensate for the increased seed weight.

Severeal studies to determine the number of genes involved in seed weight have been made. Copp and Wright (1952) examined the inheritance of kernel weight in a wheat cross made between parents differing greatly in this trait. They were able to recover both parental types and from this concluded that only a few genes were involved in the inheritance of kernel weight in this particular cross. In a cross between Selkirk and Chagot wheat, Sharma and Knott (1964) found that seed weight is controlled by relatively few genes, perhaps as few as 4. They reported heritability estimates ranging from 37-69 per cent, indicating that it should be possible to breed for large seed size. Estimates of the number of genes influencing seed weight in other wheat crosses range from monogenic to trigenic (Quisenberry and Reitz, 1967). Worzella *et al*. as reported by Quisenberry and Reitz (1967) reported a cross in which there was multigenic control of kernel weight. Working with oats, Murphy and Frey (1962) found that the kernel weight distribution was normal, indicating quantitative inheritance. Their heritability estimate for kernel weight was 36 per cent. It has been reported (Quisenberry and Reitz, 1967) that in wheat chromosomes 1B, 3D, 4A, 5B, 6A, 6B and 6D are associated with kernel weight. In a study on the inheritance of kernel weight involving six spring wheat crosses, Sun *et al*. (1972) found that additive genetic variation made up a large part of the total genetic variation for kernel weight with the dominance effect being less important and epistasis being found in only one cross. With the high proportion of additive genetic variance and the high heritability (51-85 per cent) for kernel weight in mind they concluded that this trait can be changed through selection programs. In summary, the available information suggests that kernel weight is controlled by few genes possibly between 1 and 4 and that the heritability of this trait is high enough that a selection program to change the kernel weight would be successful.

Because one of the parents used in this genetic study belongs to the varietal group _Triticum_ _aestivum_ L. em Thell. sphaerococcum, a brief description of the genetics of shot wheat is included. In this hexaploid wheat the sphaerococcum effects are controlled by a hemizygous-ineffective recessive gene located on chromosome 3B (Sears, 1947). A more recent paper (Schmidt, Weibel _et_ _al_., 1963) reports the appearance of a spontaneous mutation in common wheat giving the sphaerococcum effect. This gene which is non-allelic to the sphaerococcum gene is incompletely dominant in effect. This information shows that one gene can have a very pronounced effect on the seed weight.

MATERIALS AND METHODS

3.1 Influence of Seed Size Upon Yield

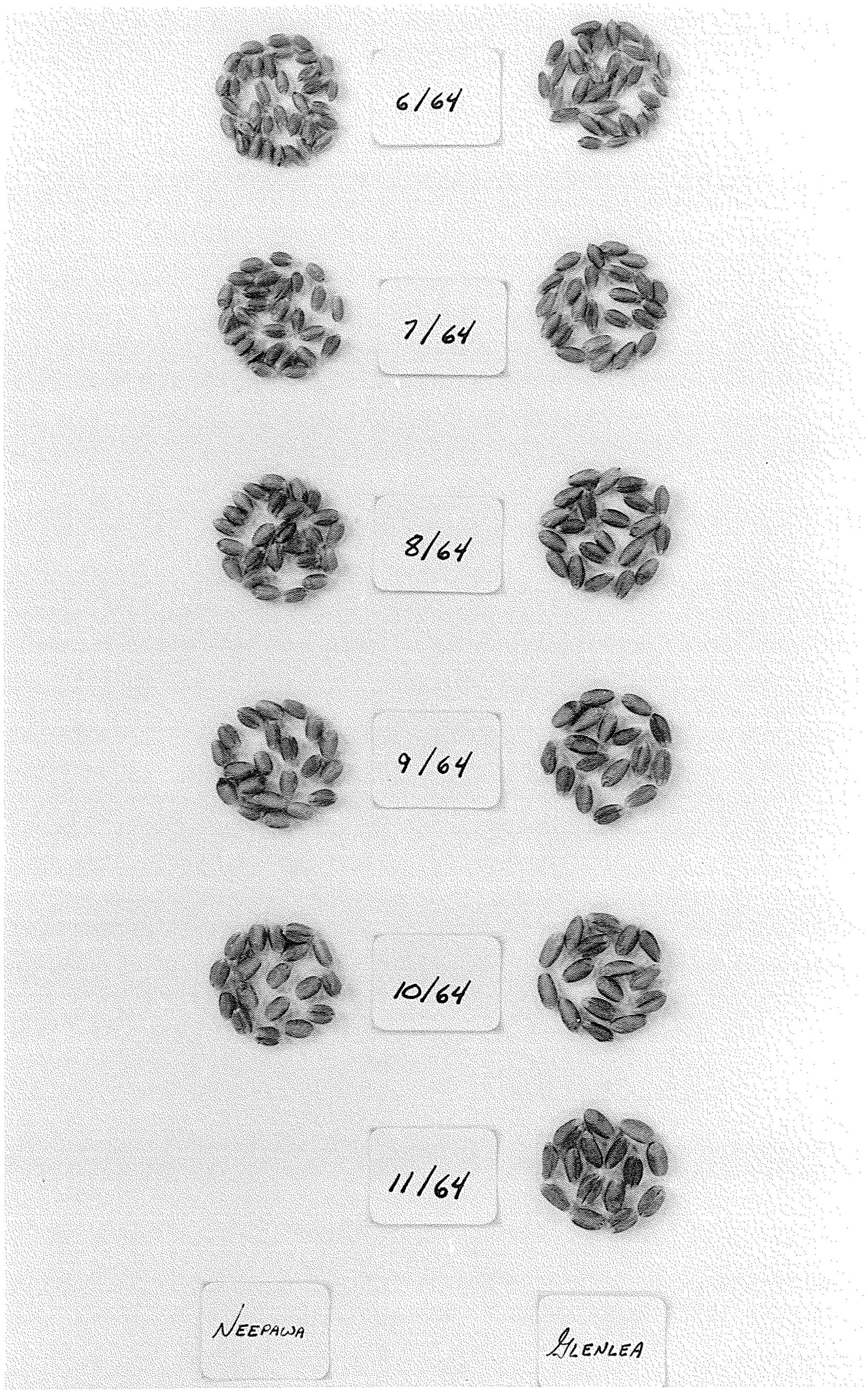
The test of the effect of seed size upon yield was performed during the summers of 1971 and 1972 on the experimental fields at the University of Manitoba. The dates of seeding were May 5 and May 3 respectively. Two wheat varieties, Glenlea, a recently licensed utility wheat, and Neepawa, a common bread wheat, were used. The seed of each variety was separated on the basis of size using nested hand screens with varying sizes of oblong holes. The seed staying above a screen with a given size of hole was designated as that seed size. The 1000 kernel weights of the different classes of seed size were measured.

In 1971 a randomized complete block design with 14 treatments was used. These treatments, as listed in Table 1, included 3 seed sizes of Neepawa and 5 seed sizes of Glenlea planted at a constant rate of 250 seeds per row and the same planted at a constant weight per row. Each treatment consisted of 2 rows 1 foot apart and 18 feet long with 2 feet between treatments. All 14 treatments were repeated in three blocks. 16.5 feet of each row were harvested and various yield measurements were made.

In 1972 a split plot design was used. Four seeding rates 200, 300, 400 and 500 seeds per rod row made up the main plot treatments while 5 seed sizes (6/64-10/64) of Neepawa and 6 seed sizes (6/64-11/64) of Glenlea made up the sub-plot treatments. For this experiment the smallest

PLATE 1

Seed sizes of Neepawa (left) and
Glenlea (right) used in the 1972
Seed Size Test.


6/64
7/64
8/64
9/64
10/64
11/64
Neepawa
Glenlea

size of both Neepawa and Glenlea were hand cleaned keeping only the sound seed while discarding the shrivelled and broken kernels. Each treatment replicated three times consisted of 4 rows 18 feet long with 1 foot between rows. A total of 33 feet, 16.5 feet coming from each of the central rows was harvested. Various measurements were made before and after harvest.

TABLE 1

TREATMENTS FOR THE 1971 SEED SIZE TEST

Treatment No.	Variety	Seed Size	Seeding Rate		
1	Neepawa	6	250	seeds/row	
2	"	7.5	250	"	(7.65 g/row)
3	"	9	250	"	
4	Glenlea	6	250	"	
5	"	7	250	"	
6	"	8	250	"	(9.91 g/row)
7	"	9	250	"	
8	"	10	250	"	
9	Neepawa	6	7.65	grams/row	
10	"	9	7.65	"	
11	Glenlea	6	9.91	"	
12	"	7	9.91	"	
13	"	9	9.91	"	
14	"	10	9.91	"	

PLATE 2

Seed size and head types of the parents involved in the genetic study.


4B723
4B249
4B233
R4B233
Glenlea
Rescue
R6B437

3.2 Inheritance of Seed Size

The study to determine the number of genes involved in the inheritance of seed size and the heritability of this trait was performed in the greenhouse during the period of October, 1971 through to February, 1973. Seven crosses (Table 2) using 7 different lines of wheat (Table 3) were investigated. In the case of the Glenlea x 4B233 cross, the integrity of the cross was checked by counting chromosomes of the seedling root tips and discarding all selfed plants as indicated by counts of 28 or 42. For all the crosses, two generations of emasculation and manual pollination were required to obtain the genotypes necessary to perform a quantitative analysis.

TABLE 2

CROSSES MADE IN THE STUDY OF INHERITANCE OF SEED SIZE

Hexaploid Crosses

Glenlea x R4B233
Glenlea x Rescue
Glenlea x R6B437
R4B233 x R6B437

Tetraploid Crosses

4B249 x 4B233
4B723 x 4B233

Hexaploid x Tetraploid Cross

Glenlea x 4B233

TABLE 3

CHARACTERISTICS OF THE PARENTAL MATERIAL USED IN THE CROSSES

		Size Classification		
Parent	Chromosome Number	Visual	Length(1)	1000 kernel weight
Glenlea	42	long	7.1 mm	32.4 grams
R4B233	42	long	7.0	40.4
Rescue	42	intermediate	5.3	24.9
R6B437	42	round	3.9	20.3
4B233	28	very long	8.8	66.2
4B249	28	very long	8.8	53.9
4B723	28	round	4.9	22.6

(1) Seed length expressed in millimeters per seed, obtained on the basis of the length of 10 seeds.

In October of 1972 the parents, the first and second filial generations, the reciprocal backcrosses and in the case of some crosses the third filial generations were planted in the greenhouse. Crosses in which the F_1, F_2, B_1C or B_2C had not been obtained were not included in this planting. Each cross was planted as a separate unit. The F_1, B_1C and B_2C were each planted in single rows in the centre of the unit. One row of each parent was planted alongside these generations. F_2 seeds, and F_3 seeds, if available, were planted in several rows to one side of the block with rows of either parent interspersed. This design represents a deviation from true replication and randomization and, therefore, the analysis of generation means may not be reliable. However, the design used should not seriously affect the estimation of intrageneration variances and of heritabilities.

The rows in the greenhouse benches were 4 inches apart with the seeds being placed approximately 1 inch apart within the row. The seeds were all soaked 24 hours and given at least a 3 day cold treatment (at $4^{o}C$) to break dormancy and ensure even germination. To distinguish the primary tillers from the secondary and tertiary tillers the heads were marked with a dated tag at the heading stage. In the analysis of this experiment only the primary tillers were used. When ripe the plants were harvested with each head being threshed individually. The number and weight of seeds per head were recorded.

3.3 Statistical Analysis

To assist in the interpretation of these experiments a variety of statistical procedures was employed. The analysis of variance of the randomized complete block and split-plot design is straight forward; specific examples and the steps in analysis of variance were obtained from the books Statistical Methods (Snedecor and Cochran, 1967) and Methods of Plant Breeding (Hayes and Immer, 1942). For both years the analyses on Glenlea and Neepawa were performed separately. Assistance in estimating the missing observation from the split-plot design was given by the formula:

$$Y = \frac{rW + b(a_j b_k) - a_j}{(r-1)\ (b-1)}$$ (Steel and Torrie, 1960)

where Y = the missing subunit observation

W = the sum of the observed subunits in the whole unit from which the observation is missing

$a_j b_k$ = the sum of observed subunits receiving the same treatment $a_j b_k$ as the missing plot

a_j = the sum of the observed subunits receiving the j'th level of A

r = the number of replicates

b = the numbers of subtreatments

3.4 Genetic Analysis

Determination of the number of genes involved in the inheritance of seed weight is possible using a variety of formulae. Variances can be used to give some idea of the number of genes involved with the inheritance of a quantitative character in two populations. The variances of the homozygous parent and the F_1 are usually small relative to the F_2 population which is segregating. As the number of genes involved increases the variance of the nonsegregating populations will remain fairly constant whereas the F_2 variance will increase. One formula suggested by Sewell Wright as reported by Burton (1951) can be used to estimate the minimum number of genes controlling the expression of a single character.

The formula is:

$$n = \frac{.25\ (.75 - h + h^2)\ (P_2 - P_1)^2}{V_{F_2} - V_{F_1}}$$

where $h = (F_1 - P_1)/(P_2 - P_1)$

P_1 = the mean of the small parent

P_2 = the mean of the large parent

F_1 = the mean of the F_1 population

F_2 = the mean of the F_2 population

Va = the variance of the a'th population

This formula is based on the following assumptions:

1. no linkage exists between pertinent genes;
2. one parent supplies only plus factors and the other only minus factors among those in which they differ;
3. all genes are of equal effect;
4. the degree of dominance of all the plus factors is the same;

and,

5. there is no interaction between pertinent nonallelic genes.

As mentioned this formula estimates the minimum number of genes involved. If these assumptions are invalid a much smaller value than the true gene number will be given.

Wright (1934) has proposed another formula for estimating the number of factors involved in the inheritance of a trait. Basically, this formula is the comparison of the ratio of the extreme plus and minus types with the variance due to genetic variation. The extreme plus and minus value is obtained by squaring the difference between the two parents. This explains the necessity for the assumption that one parent supplies the plus factors while the other provides the minus factors. The genetic variance can be obtained by subtracting the variance of a segregating population from the variance of a nonsegregating population thereby separating the total variation into its genetic and environmental components. The F_1 or parents can be used to give an estimate of the variance of a nonsegregating population. The F_2, F_3 or backcross populations could be used as estimates of variance of a segregating generation. According to Wright the variance of the backcrosses would be half as great as the variance of the F_2.

The formula he gives, which is also used by Sinnot, Dunn and Dobzhansky (1950) is:

$$n = (P_2 - P_1)^2 \ / \ 8({}^{V}F_2 - {}^{V}F_1)$$

with the symbols representing the same variables as before. This formula also estimates the minimum number of genes involved.

It is possible to modify this basic formula by Wright. Weber (1950) used the cube root of the product of the variances of the parents and F_1 to obtain a more accurate estimate of the environmental variance. In addition he made use of the backcross variances to estimate the total variance of a segregating population. Instead of using the cube root of the product of the nonsegregating generations, their average could be used. Therefore, this formula became:

$$n = (P_2 - P_1)^2 \;/\; 8(V_{F_2} - \sqrt[3]{V_{P_1} \,.\, V_{P_2} \,.\, V_{F_1}})$$

$$n = (P_2 - P_1)^2 \;/16(V_{BC} - \sqrt[3]{V_{P_1} \,.\, V_{P_2} \,.\, V_{F_1}})$$

$$n = (P_2 - P_1)^2 \;/\; 8(V_{F_2} - \frac{V_{P_1} + V_{P_2} + V_{F_1})}{3}$$

It seems obvious that all sorts of combinations can be made to obtain the different desired variances. For all these formula the same assumptions as those listed for the formula reported by Burton apply except that instead of assuming equal dominance effects these latter formulae assume no dominance affects.

Another method of estimation has been proposed by Panse (1940) which is not based on the assumption of complete concentration of plus and minus genes in opposite parents and thus could provide a more accurate estimate of the number of genes involved. Panse used the F_2 and F_3 generations to separate the variance due to additive effects from the total genotypic variance. In place of the F_3 the variances of the two second backcrosses (that is, first backcross crossed to the parental line) could be used.

Mather (1949) discusses the implications of using either the Wright method or Panse method of estimation of number of effective factors comparing the methods and illustrates what happens when the assumptions do not hold.

To determine the nature of the gene action and the degree of dominance expressed in the inheritance of seed weight a comparison of the theoretical arithmetic and geometric F_1 and F_2 population means with the actual means can be made. In the arithmetic scheme the essential point is that a particular gene substitution always adds the same amount to the phenotypic value regardless of the remaining genotype. In the geometric case a given gene substitution is always assumed to multiply the phenotypic value by the same amount. The same per cent increment results with the substitution of a geometric gene whatever the residual genotype (Charles and Smith, 1939). The theoretical means were calculated according to the formula given by Powers and Lyon as reported by Weber (1950). These formulae are shown in Table 4.

Heritability is the inherited portion of the total observed variability; it is the degree to which the characteristics of a plant are repeated in its progeny (Briggs and Knowles, 1967). The basic formula for calculation of heritability is:

$$h = Bh/(Vh + Ve)$$

where Vh = the variance due to the genotype, and

Ve = the variance due to the environment.

TABLE 4

FORMULAE FOR ESTIMATING ARITHMETIC AND GEOMETRIC MEANS

Generation or Backcross	Arithmetic Mean	Geometric Mean
F_1 generation	$\frac{P_1 + P_2}{2}$	Antilog. of $\frac{\log P_1 + \log P_2}{2}$
F_2 generation	$\frac{P_1 + 2F_1 + P_2}{4}$	Antilog. of $\frac{\log P_1 + 2 \log F_1 + \log P_2}{4}$
BC to P_1	$\frac{F_1 + P_1}{2}$	Antilog. of $\frac{\log F_1 + \log P_1}{2}$
BC to P_2	$\frac{F_1 + P_2}{2}$	Antilog. of $\frac{\log F_1 + \log P_2}{2}$

Subdivision of the genotypic variance into variances due to additive (Vg), dominance (Vd) and epistatic (Vi) gene effects leads to a distinction between "broad" and "narrow" sense heritabilities. With the former, the genotypic variance consists of all 3 types of genic expressions. With "narrow" sense heritability only the additive genetic variance makes up the numerator and the formula becomes:

$$h = Vg/(Vg + Vd + Vi + Ve).$$

Heritability indicates the utility of the observed variability. It is for this reason that it was calculated. The heritability estimates resulting from this experiment must be considered with caution because of the method in which these plants were grown. That is, all plants were grown in the greenhouse, in only one location and for only one year. This makes the separation of the genotypic variance from the variation due to time and location impossible.

Warner (1952) in his review of the literature has classified the actual methods of calculating heritability and has placed them into the following 3 categories:

a) parent-offspring regressions,

b) variance components from an analysis of variance and

c) use of the variance of genetically uniform populations to estimate the nonheritable environmental variability.

In this experiment, genetically uniform populations were used to estimate the nonheritable environmental variation. Formulae used in this experiment based on this format are as follows:

$$h = \frac{V_{F_2} - \frac{1}{2}(V_{P_1} + V_{P_2})}{V_{F_2}}$$ (Briggs and Knowles, 1967)

$$h = \frac{V_{F_2} - \sqrt{V_{P_1} \cdot V_{P_2}}}{V_{F_2}}$$ (Mahmud and Kramer, 1951)

$$h = (V_{F_2} - V_{F_1})/V_{F_2} \qquad \text{(Burton, 1951)}$$

In all these formulae the numerator includes not only the variance due to additive gene effects but also due to dominance deviations from the additive scheme plus variance due to the interaction of nonallelic genes; all of these components form the total genetic variance. In addition to this the numerator includes variance due to interation of the genotype and the environment. The result is that these formulae give a maximum heritability estimate.

The exception to this formula format was the formula derived by Warner (1952) in which the necessity of estimating environmental and total genetic variances is eliminated by calculating an estimate of the additive effect of genes from the total variance of the F_2 and the two backcrosses. This formula is:

$$h = \frac{2V_{F_2} - (V_{B_1C} + V_{B_2C})}{V_{F_2}}$$

This formula is based on the assumptions that the genotype and environmental variances are independent and that the genic effects are additive over the various loci. Warner discusses the effects on the heritability estimate when these assumptions do not hold true.

RESULTS AND DISCUSSION

4.1 Influence of Seed Size Upon Yield

In both 1971 and 1972 the seed lots of Neepawa and Glenlea were separated using nested hand screens which had oblong holes varying in width from 6/64 to 11/64 of an inch. The resulting 1000 kernel weights on the basis of this separation are listed in Table 5. In 1972 the smallest seed size of each variety was hand picked discarding all discoloured, cracked and broken seed. The difference in 1000 kernel weight due to this process of visual inspection was +1.45 grams in the case of Neepawa and -0.38 grams for Glenlea; with these differences being so slight it was probably unnecessary to perform this operation. Preparatory to planting, the germinability of the seed was measured. The 1972 results of this test are shown in Table 6. In all cases the per cent germination was high (greater than 85.0 per cent) and no corrections in seeding rate were made.

In 1972 the germination in the field was measured by making three 1 foot paired counts of the emerged seedlings in the centre rows. Paired counts were made so as to avoid unconscious bias of the results. The germination in the first replicate was counted as the 1-2 leaf stage. Weather conditions forced a 1 week delay in counting the other 2 replicates; at this time the growth was so rapid that the plants were in the 3-4 leaf stage so that distinguishing individual plants was impossible.

TABLE 5

1000 KERNEL WEIGHTS OF THE DIFFERENT CLASSES OF SEED SIZE

Variety	Seed Size	1000 kernel weight in grams [a]	
		1971	1972
Neepawa	6/64	18.08	18.89
	7/64)	30.66	24.73
	8/64)		33.03
	9/64	40.00	41.18
	10/64		48.31
Glenlea	6/64	18.80	19.03
	7/64	28.40	28.75
	8/64	36.64	38.18
	9/64	49.04	49.35
	10/64	56.00	56.91
	11/64		61.73

(a) Determined on the basis of 3 samples of 100 seeds at constant moisture.

TABLE 6

GERMINATION TESTS - 1972

	Seed Size		%		Average Field Germination Counts per foot				
Variety	Sieve Size	1000 Kernel Wt.	Germination On Filter Paper	Seeding Rate	200	300	400	500	Average
Neepawa	6/64	18.89	96.1		11.3	13.8	17.5	19.9	16.5
	7/64	24.73	96.4		9.5	13.6	21.5	21.8	17.0
	8/64	33.03	94.0		9.0	16.9	21.8	24.7	19.0
	9/64	41.18	94.2		11.3	16.0	17.5	19.1	15.6
	10/64	48.31	99.0		9.2	15.9	18.0	21.5	17.0
				Mean	10.3	15.3	19.3	21.4	
				Per cent of theoretically possible	85.4%	85.0%	80.3%	71.2%	
Glenlea	6/64	19.03	86.9		11.0	11.7	20.0	21.8	16.3
	7/64	28.75	88.9		9.1	13.3	19.5	20.2	14.2
	8/64	38.18	89.3		7.7	-	15.7	17.2	13.5
	9/64	49.35	89.3		11.0	14.0	17.3	19.5	16.3
	10/64	56.91	90.9		9.2	13.4	19.2	20.4	16.0
	11/64	61.73	90.3		10.3	15.5	19.2	20.7	17.0
				Mean	9.6	13.4	18.5	20.2	
				Per cent of theoretically possible	80.0%	74.3%	77.2%	67.3%	

The cursory results of these counts are presented in Table 6. Due to the incompleteness of the results no statistical analysis was performed. The trends, however, are apparent; as the seeding rate increased from 200 to 500 seeds the number of seedlings per foot increased in a slightly less than linear fashion. It is interesting to note that in this test seed size had no effect upon the germination with the average germination being the same regardless of seed size. Although germination did not appear to be influenced by seed size one could note differences in growth rate between plots of seedlings arising from small seeds and those grown from large seeds. The latter appeared much fuller, more lush than the former.

The rate of seeding did have an effect at the seedling stage. As the number of seeds per row increased from 200 to 500 the number of seedlings per foot also increased. These increases, as shown in Table 6, are not constant when compared with the number of seedlings theoretically possible. In this case, as seeding rate increases the comparison with the number theoretically possible, given in the table as a per cent of that which is possible, decreases. A feasible explanation for this phenomenon is that increased crowding of the seeds results in a decrease in the per cent germination.

In these tests the most important results are the relative yields per plot. The yield results of the 1971 seed size test are presented in Tables 7 and 8. Table 7 summarizes the results of seeding at a constant rate of 250 seeds per row. The yield differences due to differences in

TABLE 7

YIELD DATA FROM 1971 SEED SIZE TEST

Seeding at a constant rate of 250 seeds per row

			Yield Data		Mean Yield Per Plot	
Variety	Seed Size	1000 kernel wt.	1000 kernel wt.	Test weight	grams	% of mean
Neepawa	6/64	18.08 gm.	36.1 gm.	62.9	1295**	84**
	7.5/64	30.66	36.9	64.1	1541	100
	9/64	40.00	38.8	64.5	1674	109
Glenlea	6/64	18.80	48.5	62.5	1989*	81*
	7/64	28.40	51.0	63.8	2207	90
	8/64	36.64	51.2	64.0	24.56	100
	9/64	49.04	52.2	63.5	2430	99
	10/64	56.00	52.1	63.6	2563	104

** Treatment differences are significant at 1% level.

* Treatment differences are significant at 5% level.

TABLE 8

YIELD DATA FROM 1971 SEED SIZE TEST

Seeding at a constant average weight of 7.65 gm. per row for Neepawa and 9.91 gm. per row for Glenlea

Variety	Seed Size	1000 kernel wt.	Yield Data (N.S.) 1000 kernel wt.	Yield Data (N.S.) Test weight	Mean Yield Per Plot grams	Mean Yield Per Plot % of mean
Neepawa	6/64	18.08 gm.	38.3	64.5	1666	108
	7.5/64	30.66 gm.	36.9	64.1	1541	100
	9/64	40.00 gm.	38.5	63.9	1630	106
Glenlea	6/64	18.80	50.5	64.4	2356	96
	7/64	28.40	50.3	64.0	2404	98
	8/64	36.64	51.2	64.0	2456	100
	9/64	49.04	51.1	64.1	2324	95
	10/64	56.00	50.4	64.1	2440	99

(N.S.) No significant differences were detected among treatments.

seed size are significant at the 1 per cent and 5 per cent levels for Neepawa and Glenlea respectively. It should be pointed out that in the case of Neepawa the large size outyielded the small size by 25 per cent and the yield increase of the large size compared to the average size was 9 per cent. Similarly, in the case of Glenlea, the yield extreme was 23 per cent with the large size outyielding the average size by 4 per cent. Figure 1 shows graphically the increase in yield that is realized with increasing seed size. The correlation coefficients given are for the best straight line. Table 8 shows what happens when the seeding rate is a constant weight. The weights chosen were 7.65 grams per row for Neepawa and 9.91 grams per row for Glenlea. These weights were used because they were the weight of 250 seeds of the average size of each variety. The result of this seeding rate is that many more small, light weight seeds were planted per row with the number of seeds per row diminishing as seed size increases. As the table shows the yields in all the plots of each variety were quite similar; no significant differences within Neepawa or Glenlea were detected. In both Tables 7 and 8 the 1000 kernel weight and test weight of the harvested grain are reported. This data shows that these parameters are the same within each variety at all sizes of seeds. There were significant differences between the two wheat varieties for both 1000 kernel weight and total yield per plot.

Table 9 and 10 show the yield data for the 1972 seed size-seed rate test. As reported in Table 9, extremes in the seed size of Neepawa

FIGURE I. SEED SIZE versus YIELD - 1971

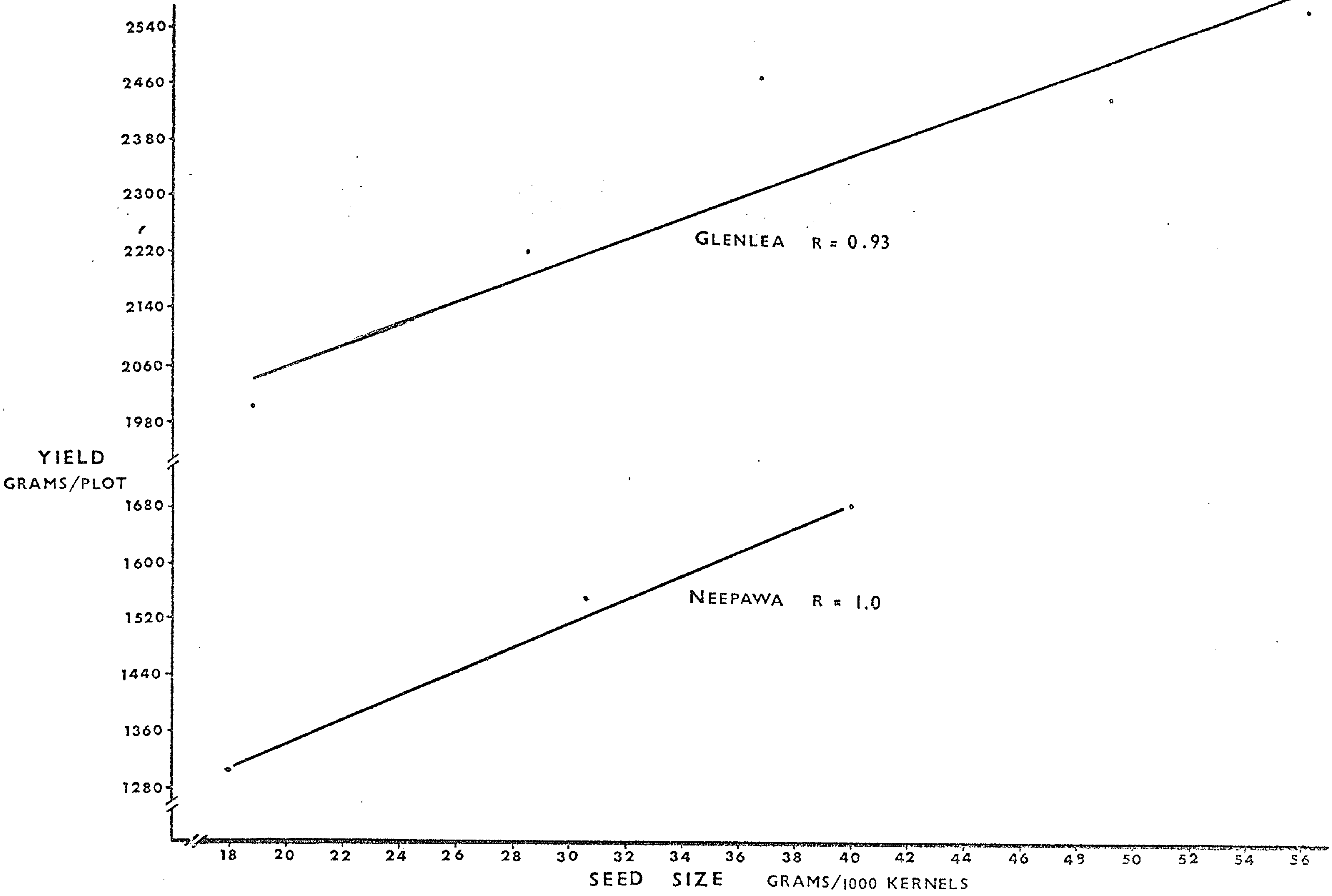


TABLE 9

YIELD OF NEEPAWA AT DIFFERENT SEEDING RATES AND SEED SIZES - 1972

(Yield is presented as a percent of the sample mean)

Seed Size		Seeding Rate (Seeds/Rod Row)				Seed Size Mean(a)	
Seive size	1000 kernel wt.	200	300	400	500		
6/64	18.89 gm.	79.8	93.3	86.3	91.2	87.6	(837)
7/64	24.73	111.6	106.3	91.4	99.6	102.2	(976)
8/64	33.03	79.3	114.2	104.8	104.6	100.7	(962)
9/64	41.18	104.7	94.8	107.0	102.0	102.0	(976)
10/64	48.31	103.5	118.8	106.7	100.6	107.4	(1026)
Seeding Rate Mean (N.S.)		95.7 (914)	105.5 (1008)	99.3 (948)	99.6 (951)	100.0	(955)

(-) Indicate actual average yield in grams for the given class.

(a) Treatment differences were significant only at 10% level of probability.

(N.S.) No significant differences were detected among treatments.

TABLE 10

YIELD OF GLENLEA AT DIFFERENT SEEDING RATES AND SEED SIZES - 1972

(Yield is presented as a percent of the sample mean)

Seed Size		Seeding Rate (Seeds/Rod Row)				Seed Size Mean **	
Seive size	1000 kernel wt.	200	300	400	500		
6/64	19.03 gm.	88.0	81.6	94.0	86.7	87.6	(1028)
7/64	28.75	110.4	93.6	102.5	87.5	98.6	(1157)
8/64	38.18	97.4	92.5	112.4	97.6	100.0	(1174)
9/64	49.35	108.9	111.7	101.9	102.0	106.1	(1246)
10/64	56.91	94.0	99.2	100.4	101.4	100.9	(1185)
11/64	61.73	101.1	119.9	99.7	107.0	106.9	(1255)
Seeding Rate Mean (N.S.)		100.0	99.7	103.2	97.0	100.0	(1174)
		(1174)	(1171)	(1212)	(1139)		

(-) Indicates actual average yield in grams.

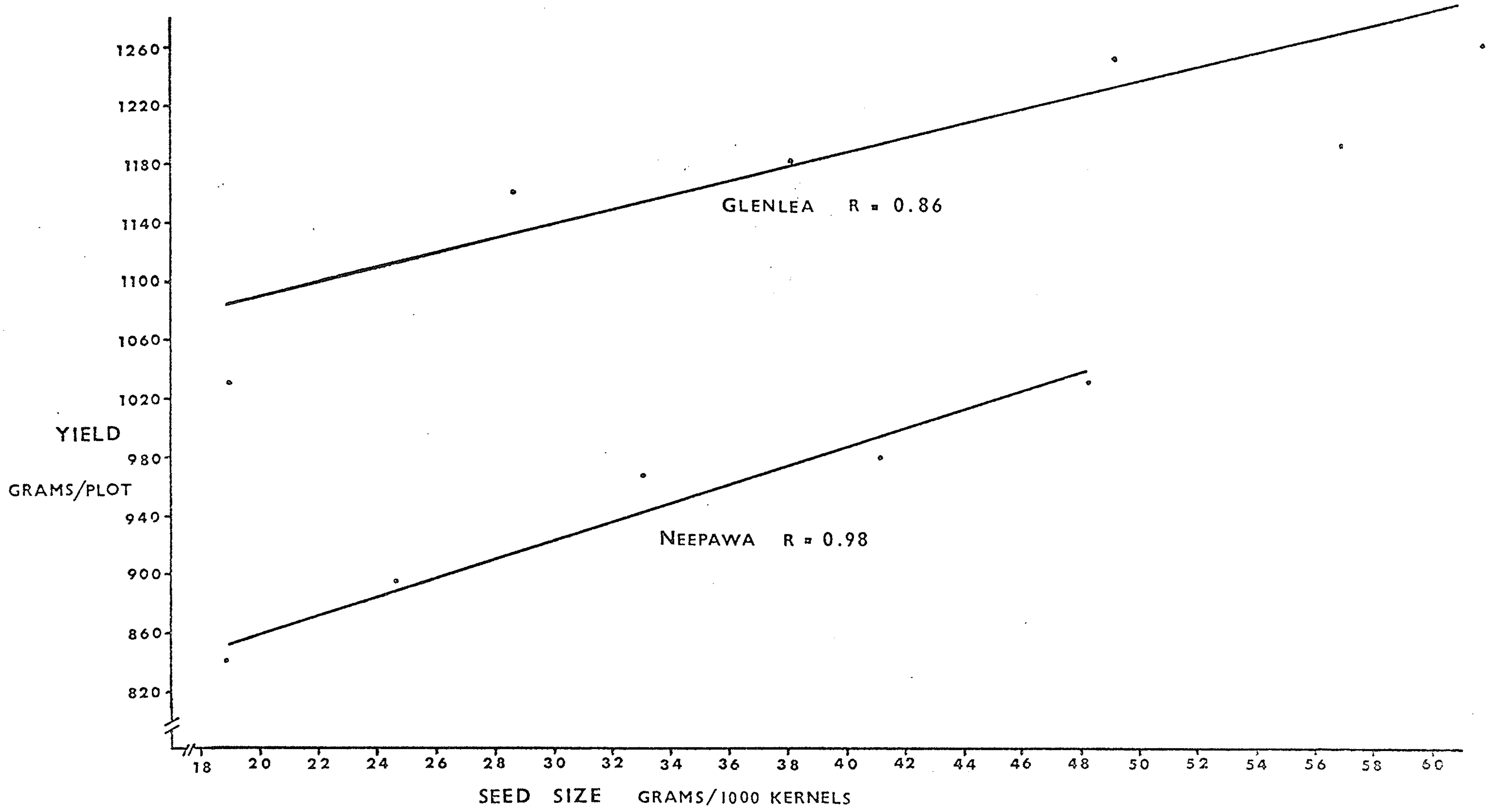
** Treatment differences are significant at 1% level.

(N.S.) No significant differences were detected among treatments.

resulted in a yield differential of 19 per cent. The largest seed size outyielded the average of the 3 middle seed sizes by 5.7 per cent. For Neepawa the difference due to seed size was significant only at the 10 per cent level. This degree of significance is due to a few extreme values that are quite out of line with all the others. As shown in Table 10 differences in the seed size of Glenlea resulted in yield differences significant at the 1 per cent level. The yield extreme between the largest and smallest seed sizes was 19 per cent. In this test Glenlea outyielded the average of the 4 medium seed size classes by 5.5 per cent. For both Neepawa and Glenlea the main plot treatment, seeding rate, has no effect upon yield; no significant differences for these treatments were obtained. In spite of a few extreme values, it can be seen that at any of the seeding rates used seed size increases result in yield increases. Similarly, at any given seed size an increase in seeding rate does not result in an increase in yield. The effect of seed size upon yield has been plotted in Figure 2. As in Figure 1 the correlation coefficients given are for the best theoretically straight line. For both Neepawa and Glenlea there is a linear increase in yield with increasing seed size for most of the seed sizes.

In an attempt to account for the increases in yield with increasing seed size the components of yield, the number of heads per row and the weight of seed per head were measured. The number of heads per row was measured in a manner similar to the method used for counting emerged

FIGURE 2. SEED SIZE versus YIELD - 1972



seedlings. Paired counts of the stems were made in the centre rows. The weight of seed per head was obtained by collecting at least 20 heads per plot and getting the average weight per head. The results, shown in the appendix, are all nonsignificant and contrary to expectations the product of the head counts by head weights by a constant of 33 bears no relation to the observed plot yields.

4.2 Inheritance of Seed Size

The data for the 7 crosses are given in the form of frequency distributions in Tables 11-17. Each primary tiller was the source of one observation; the weight and number of seeds per head were recorded. It is the average kernel weight of the sample that, after having been multiplied by 1000 to make presentation easier, is reported in the frequency tables. The means, therefore, are actually the 1000 kernel weights of the given generation. The estimates of the number of genes involved in the inheritance of seed size for the various crosses as derived from the formulae listed in the previous section are listed in Table 18. It should be pointed out again that this is the minimum number of effective factors involved in the inheritance of this trait. For this reason attention was drawn to the maximum value given by one of the formulae for each cross. It could be expected that the actual number of genes determining the inheritance of seed size might be as great as or greater than this value. The heritability estimates expressed as a per cent are given in Table 19. Where possible standard

TABLE 11

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS GLENLEA x R6B437

Generations	Class Centres (grams/1000 kernels)																										Statistics		
	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	n	$\bar{x}$	s^2
Glenlea									1	1	2	5	6	4	4	6	2	2	1	1							35	34.0	24.4
R6B437				1	1	4	5	2	1		2																16	19.8	17.3
F_1										1		1	4	6	7	2	2										23	34.3	9.5
BC(Glenlea)						1	2	2	1	1		3	1														11	24.3	24.4
BC(R6B437)						1	4	2	2			1															10	21.7	10.7
F_2	1	1	3	1	1	16	15	31	35	44	52	59	41	58	46	33	23	9	6	3			1				489	29.9	49.7
F_3			2	2	1	13	23	23	21	36	47	38	38	52	39	36	22	11	9	4							427	30.3	47.1

TABLE 12

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS R4B233 x R6B437

Generation	Class Centres (grams/1000 kernels)																										Statistics		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	n	$\bar{x}$	s^2
R4B233							3	2	2	5	3	6	2	9	2	5	1	5	5	3	3	1	1			1	59	38.9	77.9
R6B437			4	12	12	7	6	3	4																		48	20.5	11.4
F_1									1		1	1	2		3	3	3	2	2								18	40.3	27.0
BC(R4B233)										1	1	1		1	1		1		2	1							9	39.6	58.3
BC(R6B437)					1							2															3	28.7	57.5
F_2	1					7	11	4	12	16	20	20	27	19	14	24	12	12	7	7	2	1					216	35.7	59.3
F_3	1	4	4	12	15	20	22	35	26	43	49	40	43	19	33	17	24	11	4	6	9	1	2	1			443	32.6	74.4

TABLE 13

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS GLENLEA x RESCUE

Generation	Class Centres (grams/1000 kernels)																			Statistics		
	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	n	$\bar{x}$	s^2
Glenlea							1		1	1	2	5	4	6		2	2	1	2	27	36.7	33.3
Rescue			3	3	5	9	3	2	4	4	4	2	1	1	1					42	24.9	41.0
F_1										2	3	3	2	1	4	1			1	17	35.7	23.7
BC(Glenlea)						2		1	3		1	1	1	3		2	1	1		16	33.4	59.0
BC(Rescue								1		4	1	1	2	1						10	31.6	16.0
F_2	1	1	2	1	6	9	10	17	17	18	22	26	16	17	5	7	1	4		178	30.8	42.7

TABLE 14

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS GLENLEA x R4B233

Generation	Class Centre (grams/1000 kernels)																									Statistics		
	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	n	$\bar{x}$	s^2
Glenlea		2		1	1	2	5	9	9	4	4	6	2	4	2	1		1								53	30.6	44.4
R4B233								2		1	2	4	3	4	3	5	5	7	4	2	2					44	42.3	44.0
F_1							1				1		1	3	5	2	1	1								15	39.8	27.6
BC(Glenlea)														1		3				1						5	43.9	22.0
BC(R4B233)								1			2	1	2	1		3	3	1	1	3						18	41.9	47.7
F_2	1		2	4	7	8	17	28	31	40	43	33	42	56	35	43	32	28	24	14	4	3	2	1		498	37.4	64.9
F_3		2	3	4	4	16	15	28	32	35	39	57	48	46	36	42	28	23	24	9	10	5	1	1	1	511	37.2	72.9

TABLE 15

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS 4B233 x 4B723

Generation	Class Centres (grams/1000 kernels)																																						Statistics		
	7	9	11	13	15	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	83	n	$\bar{x}$	s^2
4B233																	1	1		1	1	1		3	1	3	1	1	5	2	4	6	6	3	1				1	42	63.8	91.2
4B723				1	1	2	3	7	5	5	3	1																												28	22.5	13.4
BC(4B233)							1								1				1						1				1											5	43.8	300.8
F_2	1	2	6	3	11	8	9	11	9	12	11	6	8	13	8	11	15	17	11	28	17	13	10	10	3	7	4		2		1									267	36.6	177.5
F_3		1	5	9	9	8	8	6	6	7	9	14	13	9	9	15	12	12	16	22	16	18	11	11	7	8	6	1		1										269	37.7	175.5

TABLE 16

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS 4B233 x 4B249

Generation	Class Centres (grams/1000 kernels)																							Statistics		
	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	n	$\bar{x}$	s^2
4B233																1			1		1		1	4	66.7	29.5
4B249							1				4	3	4	2	2	1	1	1						19	53.9	23.4
F_1												1		1	2						1			5	58.3	49.8
BC(4B233)															1	1	1			1				4	61.7	16.1
BC(4B249)														2	1		1	2	1					7	60.4	18.3
F_2	1	1			1	1	1	2	2	3	11	7	6	10	11	10	10	5	4	7	8	1		102	57.0	70.8

TABLE 17

FREQUENCY DISTRIBUTIONS FOR SEED SIZE OF VARIOUS GENERATIONS OF THE CROSS GLENLEA x 4B233

Generations	Class Centres (grams/1000 kernels)																																	Statistics		
	17	19	21	23	25	27	29	31	33	35	37	39	41	43	45	47	49	51	53	55	57	59	61	63	65	67	69	71	73	75	77	79	81	n	$\bar{x}$	s^2
4B233											1									1		2		2	4	4	3	8	3	4	3		1	36	69.0	62.1
Glenlea			1	2	3	6	5	5	4	5	2		1	1			1																	36	31.5	31.7
F_1										2		1		2	1	1	1																	8	42.5	27.5
BC(Glenlea)					1							1					1																	3	39.0	126.8
F_2	1	2	3				1	4	3	2	5	2	4			3	1			1					1									33	36.3	113.1

TABLE 18

ESTIMATES OF THE NUMBER OF GENES INVOLVED IN THE INHERITANCE OF SEED SIZE

	Glenlea x R6B437	R4B233 x R6437	Glenlea x Rescue	Glenlea x R4B233	4B233 x 4B723	4B233 x 4B249	Glenlea x 4B233
$n = \frac{.25(.75-h+h^2)\,(P_2-P_1)^2}{V_{F_2}-V_{F_1}}$	.96	$\underline{2.19}$	1.23	.53	(a)	1.03	2.23
$n = \frac{(P_2-P_1)^2}{8(V_{F_2}-V_{F_1})}$	.62	1.32	.91	.45	(a)	.98	2.06
$n = \frac{(P_2-P_1)^2}{8\left(V_{F_2}-\frac{V_{P_1}+V_{P_2}+V_{F_1}}{3}\right)}$	.77	2.07	$\underline{1.73}$	.64	$\underline{1.70}$ (b)	.56	$\underline{2.43}$
$n = \frac{(P_2-P_1)^2}{8\left(\frac{V_{F_2}+V_{B_1C}+V_{B_2C}}{2}-\frac{V_{P_1}+V_{P_2}+V_{F_1}}{3}\right)}$	$\underline{1.00}$	.87	.66	.59	(a)	$\underline{1.12}$	(a)
$n = \frac{(P_2-P_1)^2}{8\left(V_{F_2}-\sqrt[3]{V_{P_1}\cdot V_{P_2}\cdot V_{F_1}}\right)}$	.74	1.40	1.60	.55	1.49 (b)	.54	2.34
$n = \frac{(P_2-P_1)^2}{8\left(\frac{V_{F_2}+V_{B_1C}+V_{B_2C}}{2}-\sqrt[3]{V_{P_1}\cdot V_{P_2}\cdot V_{F_1}}\right)}$	.95	.72	.64	.51	(a)	1.03	(a)
Average estimate	.84	1.43	1.13	.56	1.60	0.89	2.25

(a) Component of formula is missing making calculation meaningless.

(b) Only V_{P_1} and V_{P_2} were used, i.e., $\frac{V_{P_1}+V_{P_2}}{2}$ and $V_{P_1}\cdot V_{P_2}$.

errors of the estimates were calculated using the method outlined by Kempthorne (1957). These standard errors suggest the reliability of the heritability estimates. The formula for calculating heritability given by Warner was not too useful in the analysis of the data for two reasons. First, in two of the crosses a backcross to one of the parents was missing making the calculation meaningless. Second, in all cases the number of backcrossed plants was so small that the generation means and variances were not accurate. As a result the standard errors are large and in two of the crosses studied the combined variances of the two backcrosses was less than the variances of the F_2 thereby giving an estimate of over 100 per cent. In spite of these apparent inaccuracies, these values were included. Again a word of caution: as discussed in the previous section these values are to be considered as the maximum heritability estimates.

In an attempt to ascertain whether the gene action behaved in an additive, dominant or epistatic manner the observed means were compared with the theoretical arithmetic and geometric means calculated according to the formulae listed previously. These values, listed in Table 3 of the Appendix shed no light on this question. An alternative method suggested by Hayman (1958) and illustrated by Baker, Pesek and McKenzie (1972) was used. Both the three-parameter and the six-parameter model were used; the former to detect the presence of additive and dominant gene effects and the latter to indicate the types of epistasis involved.

TABLE 19

HERITABILITY ESTIMATES OF SEED SIZE [a]

	Glenlea x R6B437	R4B233 x R6B437	Glenlea x Rescue	Glenlea x R4B233	4B233 x 4B723	4B233 x 4B249	Glenlea x 4B233
$h = \frac{V_{F_2} - \frac{1}{2}(V_{P_1} + V_{P_2})}{V_{F_2}}$	58.1± 8.7	24.7±14.1	13.0±17.3	31.9±10.6	70.5±6.2	61.6±15.1	58.5±12.3
$h = \frac{V_{F_2} - \sqrt{V_{P_1} \cdot V_{P_2}}}{V_{F_2}}$	58.7	49.7	13.5	31.9	80.3	62.9	60.8
$h = \frac{V_{F_2} - V_{F_1}}{V_{F_2}}$	80.8± 5.6	54.4±15.4	44.5+19.4	57.5±15.3	-	29.7±41.8	75.7±12.9
$h = \frac{2V_{F_2} - (V_{B_1C} + V_{B_2C})}{V_{F_2}}$	129.4±22.5	4.7±83.6	24.3±53.3	92.6±31.6	-	151.4±20.5	-
Average	80.2	33.4	23.8	53.5	75.4	76.7	65.0

[a] Expressed as per cent.

The three parameters common to both models are the F_2 mean (m), the pooled additive effects (d) and the pooled dominance effects (h). In the six-parameter model i measures the pooled interactions between additive effects, j between additive and dominance effects and l, the interaction between dominance effects. This model is based on interaction between only two loci. As Table 20 shows only two crosses fit the three-parameter model satisfactorily; Table 21 shows the results of fitting a six-parameter model which includes the three types of epistasis.

For the cross, Glenlea x R6B437, an average heritability of 80.2 per cent was obtained. From the frequency distribution it can be seen that in the F_2 and F_3 there are seven samples showing a seed size smaller than that of the parents. The three-parameter model of the Hayman analysis indicates that there is both additive and dominant gene action. Failure to fit this model signals the presence of epistasis. The formulae estimating the number of genes involved in the inheritance of seed weight show that at least 1 gene was present. The presence of epistasis, however, means that this estimate is low and that there is interaction between at least two genes influencing seed size. Recall from the literature review that the gene for the sphaerococcum effect which is in R6B437 is a recessive gene. A compact head with globuse glumes is one of the sphaerococcum traits. Although not much attention was paid to this trait, the F_2's of this cross were segregating in roughly a 3:1 manner. A small sound seed is another trait of the

TABLE 20

ESTIMATES OF GENETIC PARAMETERS FOR SEED SIZE IN SEVEN WHEAT CROSSES. THREE-PARAMETER MODEL.

Parameter [(a)]	Glenlea x R6B437	R4B233 x R6B437	Glenlea x Rescue	Glenlea x R4B233	4B233 x 4B723	4B233 x 4B249	Glenlea x 4B233
m	29.6±0.3	35.4±0.4	31.8±0.4	37.8±0.3	36.6±0.8	58.4±0.6	44.1±0.9
d	7.3±0.6	9.3±0.6	5.3±0.7	5.5±0.7	20.6±0.8	4.8±1.2	18.5±0.8
h	7.5±0.9	11.1±1.2	3.7±1.3	3.0±1.3	-13.1±2.3	- 1.3±2.6	-10.8±1.9
Difference [(b)]							
P_1	0.85	-0.25	1.45	0.50	0.05	2.8	1.00
B_1C	-8.95	-0.45	-1.05	1.35	3.10	0.9	-
F_1	0.95	-0.65	2.05	0.50	-	0.55	3.80
F_2	0.30	0.30	-1.00	-0.40	0.00	-1.40	-7.80
B_2C	-4.25	-2.05	2.45	8.85	-	4.40	4.15
P_2	1.25	-0.05	0.25	-0.20	-0.05	-0.35	0.50
Chi-squared	58.6	0.93	13.0	20.2	0.17	11.7	23.2
Degrees of freedom	3	3	3	3	1	3	2

(a) Genetic parameters as defined by Hayman (1958).

(b) Difference = observed mean - expection on three parameter model.

TABLE 21

ESTIMATES OF GENETIC PARAMETERS FOR SEED SIZE IN FIVE WHEAT CROSSES. SIX-PARAMETER MODEL.

Parameter [(a)]	Glenlea x R6B437	R4B233 x R6B437	Glenlea x Rescue	Glenlea x R4B233	4B233 x 4B249
m	29.9 ± 0.3	35.7 ± 0.5	30.8 + 0.5	37.4 ± 0.4	57.0 ± 0.8
d	2.6 ± 1.8	10.9 + 5.1	1.8 ± 2.3	- 3.0 ± 2.7	1.3 ± 2.6
h	-20.2 ± 4.0	4.4 ± 10.4	11.7 ± 5.2	25.4 ± 5.7	14.2 ± 7.1
i	-27.6 ± 3.8	- 6.2 ± 10.3	6.8 ± 5.0	22.0 + 5.5	16.2 ± 6.1
j	- 4.5 ± 1.9	1.7 ± 5.1	- 4.1 ± 2.4	- 7.9 ± 2.7	- 5.1 ± 3.0
l	58.0 ± 7.6	9.6 ± 20.5	- .38± 9.8	-41.1 + 11.1	-23.2 ± 12.9

[(a)] Genetic parameters as defined by Hayman (1958).

sphaerococcum gene. Segregation of this gene would result in large and small seeds. It can be assumed that the one gene recessive for small size is the sphaerococcum gene. In addition there is another gene influencing seed size which behaves in an additive fashion.

For the cross R4B233 x R6B437 the average heritability estimate was 33.4 per cent. The average number of genes was 1.43 and the maximum estimate was 2.19. The observed generation values fir the three-parameter model of the Hayman analysis indicating an absence of epistasis. This model shows that there are both additive and dominant gene effects. Because R6B437 contributed the sphaerococcum gene these results suggest that there is at least one more gene coming from the R4B233 that behaves in an additive manner.

The average heritability of seed weight in the cross, Glenlea x Rescue, was 23.8 per cent. From Table 18 it can be seen that the average of the estimates of the number of genes is 1.13 with the maximum being 1.6. The three-parameter Hayman model shows that the genes for seed weight behave in an additive manner although failure to completely fit this model indicates the presence of some interaction. In summary for this cross there is a difference of at least two genes influencing seed weight which behave in both an additive and epistatic manner.

For the cross, Glenlea x R4B233, the average heritability was 53.5 per cent. The formula estimating the number of genes involved in the inheritance of seed weight suggest that a gene difference of one is present. Evidence that there is a minimum gene difference of at least two comes from both the Hayman analysis and the frequency distribution. The three-parameter Hayman model shows that the genes influencing seed weight behave in an additive manner. The failure of the observed data to fit this model indicates the presence of epistasis. This interaction must occur between two genes influencing seed weight. The six-parameter model shows that there are probably interactions between additive effects and between additive and dominance effects. The frequency table shows that there is transgressive segregation for large seed size; this is possible only in the presence of more than one gene influencing this trait.

In the case of the final three crosses, two involving tetraploids and one hexaploid-tetraploid cross, not all the desired generations were obtained. For the generations that were obtained in the latter cross very few of the hybrids produced seed; this fact should be kept in mind when looking at the results of the analysis of this cross. In spite of the deficiencies, it was possible to analyze the data by making appropriate adaptations to the formulae.

For the 4B233 x 4B249 cross an average heritability estimate of 75.4 per cent was obtained on the basis of limited information. The average of two estimates of the number of genes was 1.60. The data of this cross fit the three-parameter model indicating an absence of epistasis. From Table 20 it can be seen that the two genes influencing seed weight behave in an additive and dominant for small size manner.

The cross between the two large seeded tetraploids resulted in an average estimate of 0.89 genes for seed size. Failure to fit the three-parameter Hayman model, however, suggests that an estimate of one gene is too low and that inheritance of seed weight in this cross involves two genes. From Table 20 it can be seen that the genes behave in part in an additive fashion. Comparing the estimates of the different types of epistatic gene effects with their respective standard deviations does not clearly define the type of interaction involved although there probably is some interaction between additive effects. The average heritability estimate of this trait was 76.7 per cent.

The hexaploid-tetraploid cross between Glenlea and 4B233 gave a heritability estimate of 65.0 per cent. The average of the estimates of the number of genes involved in the inheritance of seed weight was 2.25. It was concluded that in this cross at least two genes were involved in the inheritance of this trait. The three-parameter model suggested that in addition to epistasis there was additive and dominance for small size gene action. The analysis of inheritance might be quite complicated. Because it is a hexaploid-tetraploid cross the heritability must be considered at either ploidy level but not an intermediate, unstable level. In determining the number of genes and their effect it should be pointed out that in some plants genes determining size may be present whereas in other plants they would be absent. This is due to the unstable nature of the chromosome number which would advance either to the hexaploid level or more likely to the tetraploid level.

Using the information obtained from the four hexaploid crosses it is possible to interpret the signficance of this data. In the crosses R4B233 x R6B437 and Glenlea x R6B437 a minimum gene difference of two was detected. In both cases there was dominance for large seed size gene action indicating the presence of the sphaerococcum gene. Similarly, a two gene difference was detected for the Glenlea x R4B233 cross. It is possible to speculate that there are only 3 gene differences among these three parents. A successful cross between R4B233 and Rescue could have provided further information about the two genes that were detected in the Glenlea x Rescue cross. In connection with the Glenlea x R4B233 cross, it might be possible to obtain an increased seed size by combining the additive genes for seed size that were found in both of these parents. A yield increase might be the final result of this work.

In all these crosses both parental seed weights were recovered. This indicates that just a few genes are involved. There was very little transgressive segregation either above or below the range of the parents involved in the cross. The most noteworthy example of transgressive segregation above the range of the parents is in the F_2's and

F_3's of the cross Glenlea x R4B233. In all cases where the sample size was large enough to meaningfully plot a frequency table a normal curve with minimal skewness resulted. In spite of the few genes and the modes of gene action involved this normal curve is in line with the effects due to reduced heritability and increased environmental variation as explained by Allard (1966).

In this study seed weight was found to be due to relatively few genes or effective factors. The term "effective factor" is used to get around the assumption that the genes are not closely linked. If closely linked the gene block influencing seed weight will behave as one gene. In essence this group of genes is known as one effective factor because of its "singleness" of effect. These estimates do not include genes for seed weight that are common to both parents. When there is a combination of genes for small size and large size in each parent the detection of these genes is impossible. With this explanation it can be stated that these results indicate the minimum number of genes involved in the inheritance of this trait is two genes. In all of these crosses there was additive gene action. In some of the crosses there was also dominant and epistatic gene action.

CONCLUSIONS

5.1 Influence of Seed Size Upon Yield

These experiments permit one to draw several conclusions about the influence of seed size. Seed size does not influence the viability of the embryo. This was shown by the germination tests performed on filter paper and by the 1972 emergence counts in the field. In both these tests the differences in germination among the various seed sizes was small. Once the seedling has emerged, however, growth rate is influenced by seed size. This was obvious visually from the more luxurious growth of the plots of seedlings arising from large seeds in comparison with those from smaller seeds. Regardless of the amount of endosperm present the viability of the embryo is not altered; as the amount of endosperm increases the growth rate of the seedling increases.

In 1971 the 1000 kernel weights and test weights of the harvested seed was measured; no significant differences occurred that could be attributed to parental seed size. In 1972 both the number of heads per row length and the weight of seed per head were measured. An analysis of variance showed no significant difference between either of these components and the parental seed size. The product of head counts per foot, head weights and the constant 33, the total number of feet harvested, should have indicated the yield per plot; there was no relationship. This lack of similarity between observed yield and calculated yield indicates the presence of biased measurements. Reflection upon the method of determining the head counts and the weight of seeds per head leads to the conclusion that the method of collecting heads to determine the head weight was not entirely random. Collecting a greater number of heads and collecting bunches of heads might produce an unbiased estimate of the weight of seeds per head. In spite of this apparent bias, a few conclusions about these yield components can be drawn. First of all, the analysis of variance for the head counts and head weights showed that there were very significant (probability of 1 per cent) differences between these components and seed size when both Glenlea and Neepawa were analyzed together. When analyzed separately there were no significant differences. This suggests that the importance of each of these yield components is different with respect to the yield potential of the two varieties used in this experiment. The lack of difference in the 1000 kernel weight of the seed harvested from plants arising from various seed sizes indicates that the resulting seed is influenced more by genetic and environmental factors than by the seed size of the previous generation. The implication is that in order to sow large seed it would be necessary to screen the harvested seed every generation. Although there were yield differences among the various seed sizes the components of yield did not indicate this. Despite the possible bias of head weights one could conclude that the differences in yield components at the different seed sizes were so slight that no significant differences were detected.

The most important conclusion to be drawn from these experiments using different sizes of seed of the wheat varieties Neepawa and Glenlea is that seed size does influence yield. The graphs show the linear increase in yield with increasing seed size. In all cases there was a yield range of at least 19 per cent between the two extremes of seed size. More important is the fact that the largest seed size outyielded the average seed size by a minimum of 4 per cent and in one case by 9 per cent. The noteworthy aspect of this result is that it shows that yield increases can be achieved in a simple manner. Separation of the seed on the basis of size and planting only the large heavy seeds gives a potential for greater yields. This is a process that even the farmer can perform with a minimum of cost and time to obtain larger yields.

These experiments suggest various things about seeding rate. The 1971 test showed that by seeding at a constant weight thereby planting more small seeds compared to large seeds, the yield over the various seed sizes is about equal. The lack of vigour of the seedlings arising from small seeds can be compensated for by sowing more small seeds relative to the larger seed sizes. In 1972 when 4 seeding rates were used it was seen that the yield advantage of the large seeds was maintained. This shows that within the limits tested by this experiment rates of seeding have no effect upon yield. This is in agreement with others who have tested the effects of seeding rate upon yield. It must be added that at every rate of seeding a yield increase could be attained by increasing the seed size. In this experiment no seeding rate was high enough for the small seed size to compensate for the yield advantage of the larger seed sizes.

5.2 Inheritance of Seed Size

This study has shown that it is possible to estimate the heritability and number of genes involved in the inheritance of seed size. Average heritability estimates for this trait range between 23.8 per cent and 80.2 per cent. Very few genes were involved in the inheritance of this trait. This was indicated both by the ease with which both parental types were recovered in all the crosses and by the estimates given in the formulae. The data indicate that a minimum of two genes is involved in the inheritance of seed size. This means that there is a minimum gene difference of two between each parent used in any one of these crosses; in each of these crosses both parents could have genes in common that influence size. Using the Hayman analysis to separate epistatic from additive and dominance effects on generation means it would appear that most of these alleles behave in an additive fashion although there is some dominance and epistasis. With this information in mind it can be seen that it should be possible to increase or decrease the seed size to that of either the "large" parent or "small" parent with relative ease.

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APPENDIX

APPENDIX TABLE 1

YIELD COMPONENTS OF NEEPAWA AT DIFFERENT SEEDING RATES AND SEED SIZES - 1972

(Expressed as a percent of the sample mean)

Seed Size		Seeding Rate (Seeds/Rod Row)				
Seive Size	1000 Kernel wt.	200	300	400	500	Seed Size Mean
6/64	18.89 gm.	95.5(a)	93.6	103.3	103.9	99.1
		105.3(b)	100.7	102.1	91.2	99.8
7/64	24.73	92.6	93.3	108.1	102.5	99.1
		110.0	102.6	101.2	95.4	102.3
8/64	33.03	92.6	106.4	99.0	101.7	99.9
		115.0	88.7	91.0	93.7	97.1
9/64	41.18	98.3	104.2	104.9	103.4	103.7
		100.2	99.3	100.9	93.9	98.6
10/64	48.31	98.6	98.6	103.1	96.4	99.2
		109.8	108.1	102.7	87.5	102.0
Seeding Rate Mean		95.5	99.2	103.7	101.6	100.0 (49.5 heads/1 foot row)
		108.1	99.9	99.6	92.3	100.0 (1.24 grams/head)

(a) Number of heads per 1 foot row spacing.

(b) Weight of seeds per head.

APPENDIX TABLE 2

YIELD COMPONENTS OF GLENLEA AT DIFFERENT SEEDING RATES AND SEED SIZES - 1972

(Expressed as a percent of the sample mean)

Seed Size		Seeding Rate (Seeds/Rod Row)				Seed Size Mean
Seive Size	1000 Kernel wt.	200	300	400	500	
6/64	19.03 gm.	98.8(a)	93.1	103.4	108.5	101.0
		102.8(b)	102.5	99.2	96.8	100.4
7/64	28.75	104.3	90.7	113.3	90.4	99.7
		95.5	107.8	98.2	90.5	98.0
8/64	38.18	98.8	88.3	115.0	102.6	101.2
		111.2	97.6	101.4	92.3	100.6
9/64	49.35	93.1	91.6	100.1	102.3	96.8
		107.7	105.0	96.3	96.6	101.4
10/64	56.91	95.1	95.8	104.3	90.6	96.5
		98.3	101.1	100.8	97.0	99.3
11/64	61.73	111.1	107.5	106.3	95.1	105.0
		104.3	97.6	101.4	97.8	100.2
Seeding Rate Mean		100.2	94.5	107.0	98.2	100.0 (33.5 heads/1 foot row)
		103.3	101.9	99.5	95.2	100.0 (1.69 grams/head)

(a) Number of heads per 1f foot row spacing.

(b) Weight of seeds per head.

APPENDIX TABLE 3

OBSERVED AND THEORETICAL MEANS BASED ON ARITHMETIC AND GEOMETRIC GENE ACTION IN F_1, F_2 AND RECIPROCAL BACKCROSS POPULATIONS

Cross	Parent or Generation	Observed Means	Theoretical Means	
			Arithmetic	Geometric
714 x R6B	714	34.0		
	R6B437	19.8		
	F_1	39.3	26.9	25.9
	F_2	29.9	30.6	29.8
	$(714)^2$ x R6B437	24.3	34.2	34.2
	$(R6B437)^2$ x 714	21.7	27.1	26.1
R4B233 x R6B437	R4B233	38.9		
	R6B437	20.5		
	F_1	40.3	29.7	28.2
	F_2	35.7	35.0	33.7
	$(R4B)^2$ x R6B	39.6	39.6	39.6
	$(R6B)^2$ x R4B	28.7	30.4	28.7
714 x Rescue	714	36.7		
	Rescue	24.9		
	F_1	35.7	30.8	30.2
	F_2	30.80	33.3	32.5
	$(714)^2$ x Rescue	33.5	36.2	36.2
	$(Rescue)^2$ x 714	31.6	30.3	30.3
714 x R4B233	714	28.8		
	R4B233	42.3		
	F_1	39.8	35.5	34.9
	F_2	37.4	37.7	37.3
	$(714)^2$ x R4B233	43.5	34.3	33.9
	$(R4B233)^2$ x 714	41.9	41.1	41.0
4B233 x 4B723	4B233	63.78		
	4B723	22.55		
	F_2	36.62	-	-
	$(4B233)^2$ x 4B723	43.76	-	-
4B233 x 4B249	4B233	66.7		
	4B249	53.9		
	F_1	58.3	60.3	60.0
	F_2	57.0	59.3	59.1
	$(4B233)^2$ x 4B249	61.7	62.5	62.4
	$(4B249)^2$ x 4B233	60.4	56.1	56.1
714 x 4B233	714	31.5		
	4B233	69.0		
	F_1	42.5	50.3	46.6
	F_2	36.3	46.4	44.5
	$(714)^2$ x 4B233	39.1	37.0	36.6