

SPECIFIC COMBINING ABILITY ESTIMATES  
IN WINTER WHEAT CROSSES

by

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## INTRODUCTION

The breeder of self-pollinated crops in general is faced with two major problems: (a) the choice of the best parents for hybridization and (b) the selection of best segregates within these hybrid progenies. The choice of the parents may be an obvious one in dealing with simply inherited characters like resistance to some diseases, but when the principal character is a complex one, the choice of the parents is not easy.

The inheritance of yield is complex. It is conditioned by a large number of factors whose expression is also subject to the effect of the environment. The individual genes can no longer be studied separately and also here the effects of the environment must be accounted for.

To cope with such a situation, several statistical approaches have been developed. Instead of following the individual genes, here gene action may be expressed in terms of means, variances and covariances. Based on these methods, the combining ability and heritability estimates may be studied and this information utilized to devise the best and most efficient breeding method which may be used.

The present study was undertaken on 1100  $F_3$  lines representing eleven crosses of wheat varieties to determine the following: (1) specific combining ability of yield, (2) heritability estimates in broad and narrow sense, and (3) possible association of kernel color with yield.

## REVIEW OF LITERATURE

Combining Ability

Very frequently more desirable segregates are obtained from certain crosses than others. Some varieties are good parents, as judged by their ability to transmit high yield and quality to their progeny in crosses, whereas others are less desirable. Although the importance of combining ability has been known and applied for many years in the breeding of hybrid corn, studies in self-pollinated crops have been limited.

The difference in the ability of corn inbreds to combine well in crosses was studied by Sprague and Tatum (22, p. 931-32). They divided combining ability into two categories, general and specific, and offered the following definitions. The term "general combining ability" was used to designate the average performance of a line in hybrid combinations.

The term "specific combining ability" was used to designate those crosses in which certain combinations do relatively better or worse than others on the basis of the average performance of the lines involved.

Harrington (9, p. 36-37) was one of the first who suggested that an analysis of characters which could be



studied in an  $F_2$  population may be useful in predicting the value of a given cross, although it had distinct limitations with respect to characters like baking quality, which could not be studied in an  $F_2$  generation.

Harlan et al. (10, p. 198-199) made perhaps the most extensive study involving a total of 378 crosses in 28 varieties of barley in all possible combinations of two each. These crosses were carried in bulk plots with no selection until the eighth generation and then space planted. Plant selections were then made from each cross and tested in progeny rows the next year. Since each variety was crossed with the other 27, the potential of each variety as a parent in crosses, could be determined from the average yield of the selections made in crosses involving each parent. The varieties Atlas, Club Mariout, Minia, Trebi, and Sandrel produced an unusually high percentage of superior selections. The crosses involving Glabron produced very few superior selections. Some varieties that had not been sufficiently promising in nursery tests to be grown in plots were found to be superior parents.

Immer (12, p. 205-206) studied the extent of heterosis for number of heads per plant, seeds per

head, weight per seed, and yield per plant between six crosses in barley.

As an average of all crosses, the  $F_1$  exceeded the average of the parents by 8.3% in number of heads per plant, 11.1% in number of seeds per head, 4.9% in weight per seed, and 27.3% in yield per plant.

The average yield of six crosses in  $F_2$  and  $F_3$  in replicated trials, exceeded as an average of the parents by 24% and 13% respectively. In  $F_4$  the average increase in a single year test was 5% over the average of the parents.

Based on these studies, it was suggested that the average yield performance of different crosses may be determined by means of replicated yield trials in  $F_2$  or  $F_3$  generations and such yield trials may be used to discard those crosses which are not performing well.

Kalton (14, p. 671-672) studied the bulk  $F_2$ ,  $F_3$  and  $F_4$  populations of 25 soybean crosses grown in replicated trials in successive years and evaluated for seed yield, date of maturity, plant height and lodging resistance in comparison with three of the parental varieties.

While the bulk populations varied considerably from one generation to the next, behavior was

relatively consistent for height, maturity, and lodging. Yield differences were not consistent, and it was concluded that elimination of the poorer crosses on the basis of single year test was not possible. Yield differences between parental varieties was not considered a good criterion of the bulk population yield performance of crosses in early segregating generations.

The results in this study appear to justify the conclusion that soybean varieties differ widely in combining ability for factors determining the agronomic characters studied in this investigation.

Weiss, Weber, and Kalton (25, p. 811), working with soybeans, studied whether or not heterosis as measured by yields of spaced plants in  $F_1$  generation, could serve as a criterion of the recombination potentialities of a cross. When the degree of heterosis as expressed in  $F_1$  was compared with the mean yield of  $F_5$  selections, no relationship among crosses was apparent. Thus, in this study the degree of heterosis of  $F_1$  plants could not be used as a reliable criterion to predict the yield potentialities of segregates from a cross.

The type of gene action in relation to combining

ability was studied by Sprague and Tatum (21) and Carnahan et al. (2, p. 515-516). They assumed that general combining ability was the result of additive gene action, while the specific combining ability was due to the effect of dominance and epistasis. This information may have a very important bearing in visualizing an efficient breeding procedure in self-pollinated crops where ultimately it is the additive part which is going to be fixed.

The results of Johnson and Hoover (13, p. 595-598) with sweet clover, and Grissom and Kalton (8, p. 289-293) with brome grass, indicate that combining ability is an inherited character. No such work, however, has been reported in the case of small grains and other self-pollinated crops.

### Heritability

In recent years, studies on quantitative genetics have been directed toward the separation of phenotypic variance into genotypic and environmental portions. Information on heritability estimates are of value to plant breeders as a measure of efficiency in selection and an index of transmissibility in a segregating population.

Warner (24, p. 427) gives an excellent review of historical development of methods for estimating heritability in literature prior to 1952. These methods in general were reported to fall into three main categories:

1. Parent offspring regressions.
2. Variance component of analysis of variance.
3. Approximation of non-heritable variance from genetically uniform populations to estimate total genetic variance.

Fisher (4, p. 399-433) first separated the genetic variance into three components: (1) that due to additive effect of genes, (2) that due to dominance deviations arising from interactions of alleles (intra-allelic interaction), and (3) an epistatic part associated with interactions of non-alleles (inter-allelic interaction or epistasis). The techniques for partitioning phenotypic variance into these components have been discussed by Mather (17).

Robinson, et al. (21, p. 353-359) defined heritability as the additive genetic variance in percent of total variance. Panse (20, p. 283-302) suggested the use of the ratio of additive genetic variance to the total variance as a measure of the degree of

heritability. Lush (15, p. 356-357) has classified heritability estimates into two categories: (1) in the broad sense, heritability refers to the functioning of the whole genotype as a unit and is used in contrast with the environmental effects; (2) in the narrow sense, heritability includes only the average effects of genes transmitted additively from parent to progeny.

Bartley and Weber (1, p. 487-493) obtained heritability estimates in a narrow sense by regression of progeny means on their parents in F<sub>2</sub> and F<sub>3</sub> generations for four agronomic characters in three soybean crosses. Heritability values for seed yield were consistently low in F<sub>2</sub> and F<sub>3</sub> progenies. Heritability estimates for maturity date and plant height in general were fairly high in all cases. Heritability values for lodging in F<sub>3</sub> progenies were somewhat variable in all cases. Heritability estimate for seed yield varied from 10-44%, for maturity date 75-92%, for plant height 59-62%, and for lodging 43.6%.

Weber and Moorthy (25, p. 209) studied heritability estimates for oil content, seed weight and yield in soybeans. Flowering time gave the highest value, 75.7% and seed weight the lowest, 54.3%, and that for

oil content was 54.7%. The heritability for seed yield was erratic, due to large environment variance and averaged zero.

Grafius, et al. (7, p. 256) studied heritability estimates for yield in barley. The estimates of the additive genetic variance were obtained from the mean squares for progeny of different females and the progeny of different males. The theoretical aspect of this method has been discussed in the mathematical model developed by Grafius (6, p. 253-257). A heritability estimate of 4.5% and 9.0% for yield from  $F_2$  data and 35% from  $F_3$  data, was obtained by using this method.

Wallace, et al. (23) reported heritability estimates of 8.6% for yield, 8.1% for culm number per plant, 14.4% for weight per seed and 20.3% for height in oats, using the component of variance method in  $F_3$  generation.

Mahmud and Kramer (16, p. 609), working with soybeans, calculated heritability estimates in several ways. One was by utilizing the variability among spaced  $F_2$  plants in relation to the variability among spaced plants of the non-segregating parents. They further used the regression of  $F_3$  lines on  $F_2$  plants and  $F_4$

progeny on  $F_3$  lines, in terms of percent deviation from the mean of the respective populations. By using these methods, it was found that heritability values range from 69% to 77% for yield, 74% to 91% for height, and 92% to 100% for maturity.

Fluzat and Atkins (5, p. 419) obtained heritability estimates for a number of agronomic characters in barley by using the  $F_2$  variable method. The heritability values were quite high for heading date, maturity date, and plant height ranging from 74% to 92%. The heritability values for kernel weight, grain yield and number of heads on the other hand, ranged from 21.2% to 50%.

In a replicated space planted study of parents and  $F_1$  and  $F_2$  generations of three interspecific crosses in cotton, Hutchinson, Panse, and Govinde (11, p. 757-775) found that the environment was responsible for the greatest proportion of the total variance of agronomic characters (viz. staple length, ginning percentage) among  $F_2$  plants. This makes selection very doubtful for these characters.

Nandpuri (19, p. 70-71) studied heritability values in three crosses of wheat for date of heading, plant height and number of tillers. On an average of



three crosses in two years, the heritability value for date of heading was 93.2%, plant height 88.4%, and number of tillers 24.4%. Based on these values, it was suggested that a great part of total  $F_2$  variation was due to genetic variation for heading date, whereas for number of tillers it was mostly environmental.

McNeal (18, p. 348-349) studied heritability for yield and yield components in wheat. Regression coefficients of  $F_3$  on  $F_2$  was too low to be of any value in selection. Tillers per plant had the highest  $b$  value of .356 and also the highest  $r$  value of 0.973 between  $F_2$  plants and  $F_3$  progenies.

#### Association of Kernel Color with Yield

There appears to be very little information available on association of kernel color with yield.

An attempt was made by McNeal (18, p. 348-349) to investigate whether a relationship exists between kernel color with either yield or yield components in  $F_3$  lines of a wheat cross. F test for heads per plant, kernels per head, grams per kernel, spikelets per head and plant yield showed no differences between the three color classes of any of these plant characteristics.

Based on this study, McNeal suggested that intensity of red kernel color was not associated with yield differences.

## MATERIALS AND METHODS

Six winter wheat varieties were used to make the eleven crosses used in this study. The six varieties and their characteristics are as follows:

**White Holland:** This variety originated in The Netherlands and was grown for many years in the Willamette Valley of Oregon, until it was replaced by higher yielding varieties. White Holland is a tall growing, moderate yielding variety with soft white kernels.

**Cappelle Desprez:** This variety was developed in France, and for many years was one of the most widely grown winter wheat varieties in northern Europe. Cappelle Desprez has never been grown commercially in Oregon, but in trial plots has yielded very well. It has soft, pale red kernels.

**Redmond (Alba):** Alba was developed in Belgium and introduced and grown rather widely in the Willamette Valley under the name of Redmond. Redmond is a high yielding, stiff-strawed variety and has soft, white kernels.

**Heines VII:** This variety is another of the widely grown European wheats that has yielded well in trial plantings in Oregon. Heines VII has been a high yielding variety and has soft, red kernels.

Nord Desprez: A variety similar to Cappelle Desprez described above.

Burt: This variety was developed at Pullman, Washington and has been grown rather extensively in the Columbia Basin of the Pacific Northwest. Burt is a winter wheat variety with hard, white kernels.

The eleven wheat crosses were:

1. White Holland x Cappelle Desprez
2. White Holland x Nord Desprez
3. White Holland x Heines VII
4. White Holland x Redmond
5. Burt                    x Cappelle Desprez
6. Burt                    x Nord Desprez
7. Burt                    x Heines VII
8. Burt                    x Redmond
9. Redmond                x Cappelle Desprez
10. Redmond               x Nord Desprez
11. Redmond               x Heines VII

The crosses were made by hand pollination in 1956. The F<sub>1</sub> plants were grown in the field in 1957-58. Plots of space planted F<sub>2</sub> plants were grown from each cross in 1958-59 and 100 random individual plant selections were made within each cross. These plants were pulled and threshed individually and F<sub>3</sub> lines from each

F<sub>2</sub> plant were grown in 1959-60, together with the six parents and harvested in the summer of 1960. The plantings were made on the Hyslop Agronomy Farm in a systematic arrangement with the two parent varieties spaced every twenty rows. These plants were then turned over to the writer for the detailed studies reported in this thesis.

### Measurements

Data were taken on yield and kernel color. Each row was harvested individually on the basis of 5-foot row length and yield was measured in grams. F<sub>3</sub> plants were classified into three kernel color classes:

(1) Red, (2) White, and (3) Segregating. The classification was done by comparing the color of the corresponding parents with the progeny. The segregating class represented the heterozygous F<sub>2</sub> genotypes for kernel color, while the red and white classes would represent the homozygous classes.

## METHOD OF ANALYSIS

Frequency distributions were calculated in tabular form for yield classes (with 25 gms as class interval) and kernel color for each of the  $F_3$  lines of the eleven crosses. Besides these, three other statistics were calculated for each of the eleven crosses, namely parental mean, cross mean, and coefficients of variability.

The analysis of variance of a completely randomized experiment was used to test the significance of specific combining ability of the six parents used in this study and also to test if there was any relationship between kernel color and yield.

Heritability values were obtained in the broad and narrow sense respectively for yield. The formulas used to estimate heritability values have been derived from the method used by Grafius et al. (7). These are as follows:

$$H_{bs} = \frac{\text{Within cross M.S.} - \text{Within parent M.S.}}{\text{Within cross M.S.}} \div$$

$$\frac{\sigma^2_h + \sigma^2_a}{\sigma^2_h + \sigma^2_a + \sigma^2_e}$$

$$H_{ns} = \frac{\text{Among Parent M.S.} - \text{Within Parent M.S.}}{n}$$

$$= \frac{\sigma^2_a}{\sigma^2_a + \sigma^2_h + \sigma^2_e}$$

Where

$H_{bs}$  = Heritability in broad sense

$H_{ns}$  = Heritability in narrow sense

$\sigma^2_h$  = Non-additive genetic variance

$\sigma^2_a$  = Additive genetic variance

$\sigma^2_e$  = Environmental variance

and where

Within cross M.S. =  $\sigma^2_h + \sigma^2_a + \sigma^2_e$

Among parent M.S. =  $\sigma^2_e + n \sigma^2_a$

Within parent M.S. =  $\sigma^2_e$

Where  $n$  = the weighted average number of plant rows in each parent sub-class and was calculated from the formula:

$$n = \frac{1}{K-1} \left[ \sum n_o - \frac{\sum n_o^2}{\sum n_o} \right]$$

Where

$K$  = number of parental sub-classes

$n_o$  = number of observations in a particular parental sub-class

The theoretical heritability estimates were calculated for the F<sub>2</sub> and for the F<sub>4</sub> to F<sub>8</sub> generation by assuming the following:

1.  $\sigma^2_a$  remains constant in each generation.
2.  $\sigma^2_h$  is reduced by one-half in the subsequent generation.
3. No epistasis.
4.  $\sigma^2_e$  remains constant.
5. No selection was practiced.



## EXPERIMENTAL RESULTS

### Comparison of Parent and Progeny Means

The mean of each of the  $F_3$  crosses and the corresponding parent means are presented in Table I. The cross mean was calculated by taking the average of the 100  $F_3$  lines of each cross. The parent mean was obtained from the average of the corresponding yield of the two parents used to make the cross. Almost all cross means exceeded the parent means except the two crosses, White Holland x Nord Desprez and Burt x Nord Desprez. The coefficient of variability of the eleven crosses ranged from a low of 14.70% to a high of 32.08%.

The two-way contingency table of yield classes with different seed color classes, red, white, and segregating, is presented in Table II.

### Specific Combining Ability

Analysis of variance of the eleven cross means is presented in Table III. Mean square was significant at 1% which shows that the population means of eleven crosses are significantly different. Since this mean square alone does not indicate which of the crosses

were specifically different from each other, it was necessary to separate the among crosses sum of squares into the components representing the crosses with a common parent and to obtain a test of significance for the mean squares representing the specific combining ability of the six parents.

Table IV presents the analysis of variance calculated for different combinations of the six parents. The means squares for specific combining ability were found to be significant at 1% for White Holland, Burt and Nord Desprez, whereas it was not significant for Redmond, Cappelle Desprez and Heines VII. Mean squares for Redmond and Heines VII were significant at 5%; the conclusions, however, in this study are based on 1% significance level.

#### Heritability Estimates

The heritability estimates obtained in this experiment were computed for yield in both broad and narrow sense.

The analysis of variance of the six parents for yield has been presented in Table V. However, when the within cross mean square of all eleven crosses was used to obtain estimate of heritability, a negative value

was obtained. Later examination of the values for the coefficients of variability revealed a possible reason. It was apparent that there was a large range of variation among coefficient of variability values. A single representative heritability value may not be the best estimate because of the large differences in coefficients of variability. It appears possible, therefore, that in certain of these crosses, the possibility of a genotype x environment interaction may exist, resulting in a net negative heritability estimate. The eleven crosses were divided into two different groups on the basis of their coefficients of variability (Table VI) and then heritability estimates were computed in order to find which crosses were contributing to the negative value.

Group A consisted of 5 crosses, whereas Group B consisted of 6 crosses. The analysis of variance was computed on the corresponding parents to obtain  $\sigma^2_a$  and  $\sigma^2_e$  of the two groups. It was found that Group A contributed to the negative part and Group B to the positive part of the net heritability observed. The within cross mean square of Group B is presented in Table V, and using this, a heritability estimate of 39.16% and 20.33% was obtained in broad and narrow sense respectively.

The variances of the different components for the Group B crosses are partitioned and presented in Table VII. The  $\sigma^2_p$ , which is total phenotypic variance, has been broken up into  $\sigma^2_e$ ,  $\sigma^2_a$  and  $\sigma^2_h$  components.

The theoretical values of heritability estimates were calculated for the  $F_2$  and from the  $F_4$  to  $F_8$  generation and are presented in Table VII.

Progress of homozygosis may be studied from Table VII. Although in absence of any precise test of significance, it is difficult to say exactly when homozygosity is approached; it is, however, apparent that for all practical purposes, homozygosity may be said to be approached for yield somewhere from  $F_6$  to  $F_8$  generations. The values of heritability estimates in Table VII are all theoretical values except for  $F_3$  and they serve to show the general pattern considering that the assumptions underlying them are fulfilled.

#### Association of Kernel Color with Yield

Analysis of variance performed on the means of three kernel colors is presented in Table VIII. The mean square is not significant at 1%, which shows that the population means of the seed color classes (red,

white and segregating) is the same. The results indicate that there is no association of kernel color with yielding ability in these crosses.

Table I: Cross means, parent means, and coefficient of variability for eleven crosses in F<sub>3</sub> generation for yield.

| Cross         | Cross<br>mean<br>gms. | Parents<br>mean<br>gms. | Coeff. of<br>var.<br>% |
|---------------|-----------------------|-------------------------|------------------------|
| White Holland |                       |                         |                        |
| x Capp. Desp. | 249.6                 | 221.1                   | 17.96                  |
| x Nord Desp.  | 203.1                 | 217.1                   | 32.08                  |
| x Heines VII  | 230.0                 | 210.0                   | 16.46                  |
| x Redmond     | 234.2                 | 184.3                   | 26.64                  |
| Burt          |                       |                         |                        |
| x Capp. Desp. | 241.2                 | 232.4                   | 27.90                  |
| x Nord Desp.  | 221.2                 | 228.4                   | 31.91                  |
| x Heines VII  | 239.5                 | 220.9                   | 28.94                  |
| x Redmond     | 215.7                 | 195.6                   | 24.96                  |
| Redmond       |                       |                         |                        |
| x Capp. Desp. | 245.0                 | 220.0                   | 20.79                  |
| x Nord Desp.  | 265.4                 | 216.0                   | 14.70                  |
| x Heines VII  | 249.1                 | 208.2                   | 19.68                  |

Table II: Frequency distribution of kernel color within yield classes

| Cross                          | Yield<br>Color | 50-<br>75 | 76-<br>100 | 101-<br>125 | 126-<br>150 | 151-<br>175 | 176-<br>200 | 201-<br>225 | 226-<br>250 | 251-<br>275 | 276-<br>300 | 301-<br>325 | 326-<br>350 | 351-<br>375 | 376-<br>400 | 400<br>and 7 | Total |
|--------------------------------|----------------|-----------|------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|--------------|-------|
| White Holland<br>x Capp. Desp. | Seg.           |           |            |             |             | 3           | 7           | 11          | 14          | 11          | 10          | 3           | 3           | 1           |             |              | 63    |
|                                | Red            |           |            |             |             | 2           | 2           | 1           | 15          | 5           | 5           | 1           | 3           |             |             |              | 34    |
|                                | White          |           |            |             |             |             |             | 1           | 1           | 1           |             |             |             |             |             |              | 3     |
| White Holland<br>x Nord Desp.  | Seg.           | 4         | 2          | 1           | 6           | 7           | 17          | 18          | 10          | 10          | 6           | 4           |             | 1           |             |              | 86    |
|                                | Red            | 1         | 1          |             | 3           | 1           | 2           | 2           |             |             |             |             | 1           |             |             |              | 11    |
|                                | White          |           |            |             |             | 1           |             |             | 1           |             | 1           |             |             |             |             |              | 3     |
| White Holland<br>x Redmond     | White          | 1         | 1          | 3           | 5           | 9           | 7           | 15          | 17          | 18          | 12          | 6           | 3           | 2           | 1           |              | 100   |
| White Holland<br>x Heines VII  | Seg.           |           |            |             |             | 6           | 13          | 18          | 22          | 14          | 10          |             | 1           |             |             |              | 84    |
|                                | Red            |           |            |             | 1           | 2           | 2           | 3           | 3           |             | 2           |             |             |             |             |              | 13    |
|                                | White          |           |            |             |             |             | 1           |             | 1           | 1           |             |             |             |             |             |              | 3     |
| Burt x<br>Heines VII           | Seg.           | 2         |            |             | 1           |             | 12          | 11          | 13          | 10          | 8           | 8           | 2           | 4           | 1           |              | 72    |
|                                | Red            |           |            | 2           | 2           | 3           | 5           | 2           |             | 3           | 1           | 5           |             |             |             |              | 23    |
|                                | White          | 1         |            |             | 1           |             | 1           |             |             |             |             |             | 1           | 1           |             |              | 5     |
| Burt x Redmond                 | White          | 2         |            | 4           | 4           | 13          | 16          | 15          | 18          | 12          | 13          | 1           | 2           |             |             |              | 100   |
| Burt x<br>Capp. Desp.          | Seg.           |           | 1          | 3           | 2           | 5           | 3           | 14          | 6           | 4           | 7           | 8           | 3           | 1           | 2           |              | 59    |
|                                | Red            |           |            | 1           |             | 3           | 2           | 9           | 14          | 4           | 4           | 2           | 2           |             |             |              | 41    |
|                                | White          |           |            |             |             |             |             |             |             |             |             |             |             |             |             |              | 0     |
| Burt x<br>Nord Desp.           | Seg.           | 1         | 2          | 4           | 4           | 11          | 12          | 8           | 7           | 8           | 7           | 6           | 4           | 2           |             |              | 76    |
|                                | Red            |           |            |             |             | 2           |             |             | 3           | 4           | 1           |             |             |             |             |              | 10    |
|                                | White          | 1         |            | 1           | 1           |             | 2           | 4           | 2           |             | 2           |             | 1           |             |             |              | 14    |
| Redmond x<br>Nord Desp.        | Seg.           |           |            |             | 1           | 4           | 6           | 9           | 15          | 24          | 14          | 9           | 3           | 1           |             | 2            | 88    |
|                                | Red            |           |            |             |             |             |             | 1           | 1           | 1           | 1           | 4           |             | 1           |             |              | 9     |
|                                | White          |           |            |             | 1           |             |             |             | 1           |             | 1           |             |             |             |             |              | 3     |
| Redmond x<br>Capp. Desp.       | Seg.           | 1         |            |             | 2           | 2           |             | 6           | 9           | 4           | 3           | 4           | 3           |             |             |              | 34    |
|                                | Red            |           |            |             |             |             |             |             |             |             |             |             |             |             |             |              | 0     |
|                                | White          |           |            |             | 3           | 2           | 6           | 9           | 13          | 21          | 8           | 2           | 2           |             |             |              | 66    |
| Redmond x<br>Heines VII        | Seg.           |           |            |             |             | 6           | 4           | 9           | 24          | 9           | 7           | 4           | 3           |             |             | 1            | 67    |
|                                | Red            |           |            |             | 1           |             |             | 9           | 6           | 11          | 2           | 2           | 1           |             |             |              | 32    |
|                                | White          |           |            |             |             |             |             |             |             |             | 1           |             |             |             |             |              | 1     |

Table III: Analysis of variance of eleven crosses in  $F_3$  generation for yield.

| Source of var. | d.f. | M.S.     | F      |
|----------------|------|----------|--------|
| Among crosses  | 10   | 30933.76 | 9.63** |
| Within crosses | 1089 | 3212.46  |        |
| Total          | 1099 |          |        |

\*\*Significant at 1%

Table IV: Analysis of variance of specific combining ability of the parents in F<sub>3</sub> generation for yield.

| Source of variation  | d.f. | M.S.      | F       |
|--|------|-----------|---------|
| Among:   |      |           |         |
| White Holl. x Capp. Desp.<br>x Nord Desp.<br>x Heines VII<br>x Redmond | 3    | 37497.16  | 11.67** |
| Among:   |      |           |         |
| Burt x Capp. Desp.<br>x Nord Desp.<br>x Heines VII<br>x Redmond        | 3    | 16518.84  | 5.14**  |
| Among:   |      |           |         |
| Redmond x Capp. Desp.<br>x Nord Desp.<br>x Heines VII                  | 2    | 11611.77  | 3.61*   |
| Among:   |      |           |         |
| Capp. Desp. x White Holl.<br>x Burt<br>x Redmond                       | 2    | 1777.74   | 0.55    |
| Among:   |      |           |         |
| Nord Desp. x White Holl.<br>x Burt<br>x Redmond                        | 2    | 102682.93 | 31.96** |
| Among:   |      |           |         |
| Heines VII x White Holl.<br>x Burt<br>x Redmond                        | 2    | 9168.07   | 2.85*   |
| Error  | 1089 | 3212.46   |         |

\*\*Significant at 1%

\*Significant at 5%



Table V: Analysis of variance for parental and progeny (Group B) yields

| Source of variation               | d.f. | M.S.     | Expected mean square*                  |
|-----------------------------------|------|----------|--|
| Among parents                     | 5    | 17365.32 | $\sigma^2_e + n \sigma^2_a$            |
| Within parents                    | 98   | 2573.18  | $\sigma^2_e$                           |
| Total                             | 103  |          |  |
| Within progeny of group B crosses | 594  | 4229.46  | $\sigma^2_e + \sigma^2_a + \sigma^2_h$ |

\*These mean squares were not used to obtain any test of significance, but only to obtain the genetic estimates.

$n = 17.20$  = the weighted average number of plant rows in each parental sub-class and was calculated from the following formula:

$$n = \frac{1}{K-1} \left[ \sum n_o - \frac{\sum n_o^2}{\sum n_o} \right]$$

$\sigma^2_e$ ,  $\sigma^2_a$ , and  $\sigma^2_h$  = estimate of environmental, additive genetic and non-additive genetic variance in  $F_3$  respectively.

Table VI: Separation of eleven crosses into two groups on the basis of coefficient of variability to determine heritability estimates for yield in  $F_3$  generation.

| Group A       |           | Group B       |           |
|---------------|-----------|---------------|-----------|
| Cross         | %<br>C.V. | Cross         | %<br>C.V. |
| White Holland |           | White Holland |           |
| x Capp. Desp. | 17.96     | x Nord Desp.  | 32.08     |
| x Heines VII  | 16.46     | x Redmond     | 26.64     |
| Redmond       |           | Burt          |           |
| x Capp. Desp. | 20.79     | x Capp. Desp. | 27.90     |
| x Nord Desp.  | 14.70     | x Nord Desp.  | 31.91     |
| x Heines VII  | 19.68     | x Heines VII  | 28.94     |
|               |           | x Redmond     | 24.96     |

Table VII: Partitioning of phenotypic variances in group B segregates\* for yield.

| $F_n$ | $\sigma^2_a$ | $\sigma^2_h$ | $\sigma^2_e$ | $\sigma^2_p$ | H(broad) | H(narrow) |
|-------|--------------|--------------|--------------|--------------|----------|-----------|
| $F_2$ | 859.81       | 1592.94      | 2573.18      | 5025.93      | 48.80%   | 17.10%    |
| $F_3$ | 859.81       | 796.47       | 2573.18      | 4229.46      | 39.16%   | 20.33%    |
| $F_4$ | 859.81       | 398.23       | 2573.18      | 3831.22      | 32.84%   | 22.44%    |
| $F_5$ | 859.81       | 199.12       | 2573.18      | 3632.11      | 29.15%   | 23.67%    |
| $F_6$ | 859.81       | 99.56        | 2573.18      | 3532.55      | 27.16%   | 24.34%    |
| $F_7$ | 859.81       | 49.78        | 2573.18      | 3482.77      | 26.12%   | 24.69%    |
| $F_8$ | 859.81       | 24.89        | 2573.18      | 3457.88      | 25.58%   | 24.87%    |

\*  $\sigma^2_a$  = additive genetic variance

$\sigma^2_h$  = non-additive genetic variance

$\sigma^2_e$  = environmental variance

$\sigma^2_p$  = phenotypic variance

H(broad) = heritability in broad sense

H(narrow) = heritability in narrow sense

Table VIII: Analysis of variance on the means  
of three kernel color classes.

| Source of var. | d.f. | M.S.    | F    |
|----------------|------|---------|------|
| Among colors   | 2    | 194.56  | 0.06 |
| Within colors  | 897  | 3443.65 |      |
| Total          | 899  |         |      |

## DISCUSSION

Heritability estimates are of value to plant breeders since they indicate the extent to which selection for desirable characters may be effective. The selection for a quantitative character cannot be effective unless there is evidence of the presence of genetic variation. Heritability estimated in the broad sense measures the extent to which a character is under genetic control. Heritability estimates in the narrow sense, on the other hand, refer to the extent to which the offspring will resemble the parents and is thus an index of transmissibility. It is also important to realize that heritabilities are not a property of the character alone, but also depend upon the particular population and the environmental fluctuations to which the population is subjected.

Heritability estimates, as obtained from this study for yield, were 39.16% and 20.33% in the broad and narrow sense respectively. A single estimate of heritability was not representative for the eleven crosses due to the heterogeneity of the variances. The eleven crosses were divided into two groups based upon the values of their coefficients of variability. Group A consisted of five crosses, White Holland x Cappelle

Desprez, Redmond x Heines VII, Redmond x Cappelle  
Desprez, Redmond x Nord Desprez, and Redmond x  
Heines VII. Group B consisted of six crosses, White  
Holland x Nord Desprez, White Holland x Redmond, Burt  
x Cappelle Desprez, Burt x Nord Desprez, Burt x Heines  
VII, and Burt x Redmond.

Other workers have found the heritability values  
for yield to be comparatively low and this was true in  
the present study. One important point should be  
noted; although heritability in the narrow sense was  
only 20.33%, about 51.92% of the total genetic variance  
is due to additive genetic variance. This could be  
due to the fact that homozygosity is being approached  
in the F<sub>3</sub> generation.

Another important point should be noted. In  
studying a complex quantitative character like yield,  
we have to make certain assumptions (as has also been  
done in this study). Some of these are:

1. Genotype and environment are additive in  
their effects.
2. There is no genotype x environment interaction.
3. Epistasis is absent.
4. No selection.

In practice, however, some of these assumptions may not be satisfied. For example, epistasis may be present and this might upset the whole situation. The assumption of no selection may not be very realistic because natural selection is always operating.

By partitioning the phenotypic variance into different components and following the progress of homozygosis, it appears that homozygosis is achieved somewhere from  $F_6$  to  $F_8$  generation for yield.

If selection is made, this situation may be complicated. If more heterozygous plants were selected, the progress of homozygosity may be slowed down, or it may be enhanced, depending upon whether more of the homozygotes are selected.

In either case, however, it may be expected that the selected materials from Group A and Group B will behave differently. It can be ascertained by replicated experiments in the next generation.

The comparison of cross and parent means did not show any indication of any relationship between the two. Consequently, it is not possible to predict the potentiality of a cross from its parental yields.

The present study indicated wide differences among the specific combining abilities of the six parents

used. This could have an important implication in a breeding program based on combining ability. The improvement of yield may, in general, be approached in two ways: (1) selection of the best parents for making crosses, and (2) selection of the best segregates within the crosses. Very frequently a large number of crosses are made in the beginning, followed by elimination of inferior crosses and inferior segregates within the crosses in advanced generations. The breeder may need guidance in this screening process. A knowledge on the combining ability of the parents could be helpful in this work. Parents with low combining ability could be eliminated and the breeder may proceed with the crosses coming from high combining parents. The evaluation of parent, therefore, may be done by the help of the information on the combining ability of the parents. Hence, the parents White Holland, Burt and Nord Desprez may be selected in a breeding program because they have high specific combining ability.

The knowledge of association of character is sometimes helpful in making selection. The present study did not, however, show any indication of association of kernel color with yield. It does not appear, therefore,

possible to use kernel color as a criterion in selection for yield.



## SUMMARY

Six winter wheat crosses were used to make eleven crosses in 1956.  $F_1$  plants were grown in the field in 1957-58. Plots of  $F_2$  plants were grown from each cross in 1958-59.  $F_3$  lines were grown in 1959-60, along with six parents and harvested in the summer of 1960. Data were taken on kernel color and yield.

Frequency distributions were constructed in tabular form for yield and kernel color. Analysis of variance was used to test the specific combining abilities of the six parents. The association of kernel color with yield was tested by analysis of variance. The heritability estimates were calculated by using the formula derived from the method used by Grafius et al. (7). The principal results and conclusions of this study are as follows:

1. The six parents showed wide differences in the specific combining ability. While the parents White Holland, Burt and Nord Desprez had high specific combining ability, Redmond, Cappelle Desprez and Heines VII had low specific combining ability.

2. There was no consistent relationship observed between the yield of the parents and the yield of the progeny. It may not be possible to evaluate the merit

of progeny based on the yield of the original parents used in making crosses.

3. There appeared to be no relationship between the kernel color and yield of the  $F_3$  lines in these crosses.

4. The heritability estimates were calculated for yield in both the broad and narrow sense. A wide difference in the values of coefficient of variability of crosses necessitated the separation of the eleven crosses into Group A and Group B. Heritability estimates in Group A, however, could not be calculated, due to possibly the presence of genotype x environment interaction. The heritability estimate of the crosses in Group B were 39.16% and 20.33% in both broad and narrow sense respectively.

5. Theoretical estimates of heritability were calculated for  $F_2$  and from  $F_4$  to  $F_8$  generation and from this it was concluded that the individual plants would approach homozygosity somewhere from  $F_6$  to  $F_8$  generation.

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