BREEDING FOR INCREASED PROTEIN
IN WINTER WHEAT

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IN WINTER WHEAT

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PART II

INTRODUCTION

The first three parts of this dissertation are separate and complete manuscripts to be submitted to *Crop Science* for publication. The format of each manuscript conforms to the style of *Crop Science*.

PART I

RESPONSE OF SIX WINTER WHEAT CROSSES
TO HIGH AND LOW SELECTION
FOR GRAIN PROTEIN

Response of Six Winter Wheat Crosses to High and Low Selection for Grain Protein[1]

ABSTRACT

Six winter wheat (Triticum aestivum L. em Thell) populations involving three high-protein (HP) and one "normal"-protein (NP) genotypes were studied to determine the effectiveness of selection for higher grain protein. The high-protein parents used were 'Atlas 66', 'Flex', and Danne/Nap Hal. The three HP X HP crosses studied were Atl 66/Flex, Flex/D-NH, and Atl 66/D-NH. Three NP X HP crosses were also studied--KS73114/Atl 66, KS73114/Flex, and KS73114/D-NH. Head selections were taken at random from F_2 populations and grown as F_3 head rows. One hundred rows/cross were harvested with selection based on agronomic characteristics. Each cross was divided into four equal sized grids to reduce environmental bias. Percent grain protein was determined by the Kjeldahl procedure, and five high protein and five low protein lines/grid were selected for a total of 20 high and 20 low protein lines/cross. The high-low selections were grown as F_4's in replicated tests at Stillwater in 1979-80.

For grain protein all crosses exhibited highly significant positive differences between high- and low-protein selection groups, with differences ranging from 0.5 to 1.0% protein. No significant differences for grain yield between high- and low-protein groups were observed for three crosses. Two crosses exhibited an inverse protein-yield relationship. One combination showed a positive difference between high and low groups

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for grain yield. Realized heritability estimates for grain protein ranged from 0.385 to 0.611. Phenotypic correlation coefficients were negative for all crosses and statistically significant, ranging from -0.320 to -0.599. The use of grids in this study resulted in an average 9.2% increase in efficiency of selection for grain protein.

Additional index words: *Triticum aestivum* L. em Thell, Grain yield, Grid selection, Realized heritability.

INTRODUCTION

Increasing the protein content of bread wheat (Triticum aestivum L. em Thell) has been a concern of plant breeders for many years. Middleton et al. (12) in 1954 reported on the elevated grain protein of a group of new cultivars, one of which was 'Atlas 66.' All cultivars of this group had either 'Frontiera' or 'Frondoso' in their parentage. Frontiera and Frondoso were developed in Brazil from the same cross. Atlas 66 has been widely used in breeding programs where emphasis was placed on grain protein (4, 6, 7, 8, 9). Morris et al. (13) reported that chromosome 5D of Atlas 66 carries at least one major gene for grain protein and that chromosome 5A carries a gene or genes with lesser effect for grain protein. The USDA Wheat Collection was screened for protein and lysine content at the University of Nebraska by Johnson et al. (8). They identified 'Nap Hal' as one of several potentially useful sources of high protein and high lysine. Another source of high protein, 'Flex,' was released as germplasm by the South Dakota Agric. Exp. Stn. in 1973 (15).

It is commonly known that increased nitrogen fertilization increases the protein content of the grain. McNeal et al. (10) studied the effects of four N fertilizer rates on agronomic and quality characters of tall-, medium- and short-statured spring wheats. They found that increased N fertilization rates resulted in increases in percent protein and protein yield both in the straw and in the grain. They also reported an inverse relationship between grain yield and grain protein. No trends were observed in the effects of plant height on the quality traits studied.

Johnson et al. (7) studied the responses of a normal protein cultivar 'Lancer' and a high protein cultivar C.I.14016 to five fertilizer rates in ten trials over three years. They reported significant grain protein responses to N fertilization at all locations. Both cultivars responded to increased fertility by having increased grain protein content. However, the high protein line C.I.14016 consistently produced higher levels of grain protein than Lancer over all N levels at all locations. The authors concluded that C.I.14016 was a more efficient producer of protein than Lancer. In this experiment, no relationship between grain yield and grain protein was found, indicating that the higher grain protein content of C.I.14016 was not the result of reduced grain yield.

The effectiveness of selection for grain protein has been measured by using stratified (high vs. low) selections based on protein content (6, 11). Haunold et al. (6) studied crosses of Atlas 66 x 'Wichita' and Atlas 66 x 'Comanche.' F_2 plants were classified for grain protein content, either high- or low-protein, and F_3 and F_4 progeny rows were grown and evaluated for grain protein content. The correlation between F_2 plants and their F_3 progeny rows for grain protein was positive and statistically significant. The actual grain protein content of the F_4 progenies of high- and low-protein selections in the F_3 agreed well with predicted responses.

McNeal et al. (11) utilized a recurrent selection scheme for improving grain protein of spring wheat cultivars. Nine high protein genotypes from the USDA Wheat Collection were crossed at Bozeman, Mont., and grown to the F_3 when protein analysis was made. High and low selections from each cross were made and the best high protein selections were put into a crossing block for the second cycle of selection. High and low protein selections were made in the F_3 of the second cycle also. Then high and low protein F_4's from each cycle were compared with each other and the high protein parents. Their results indicated significant and consistent differences between the high and low protein selections. In the second cycle, both the high and low protein selections were higher for grain protein than the corresponding selections in the first cycle. In each case, both the high and low protein selections averaged higher than the high protein parent for grain yield. The authors concluded that progress could be made in selecting for higher grain protein content.

Broad-sense heritability estimates based on parent-offspring regression for grain protein have been reported by several workers (5, 6, 9). Halloran (5) reported heritability estimates of 0.48 (F_3-F_4), 0.52 (F_4-F_5) and 0.71 (F_3-F_5) for grain protein in a soft white spring wheat cross. Haunold et al. (6) calculated realized heritability estimates (F_3 on F_2) for grain protein of 0.36 and 0.25 for two Atlas 66 crosses. Lofgren et al. (9), also working with Atlas 66, reported that regression of F_4 on F_3 gave heritability estimates of 0.25 and 0.69 for grain protein.

The importance of additive genetic effects for grain protein has been reported by Chapman and McNeal (1). In five spring wheat crosses involving Frontiera as a high protein parent, significant additive genetic effects for grain protein were detected for each cross. Three of the crosses were high protein (HP) x low protein (LP) crosses, and in these crosses the additive effects were greater than in HP x HP crosses. The authors concluded that if the parents are very different for grain protein content, increased additive genetic effects will be expressed and that a potential for selection for higher grain protein exists.

In general, the correlation between grain yield and grain protein is negative. Halloran (5) reported a negative but non-significant ($r = -0.13$) correlation coefficient between grain protein and grain yield, and concluded that it should be possible to select lines equal to the standard protein parent for grain yield from the cross studied. Ellison et al. (2) studied six spring wheat crosses and reported correlation coefficients between grain protein and grain yield ranging from highly significant negative values through near-zero values to low non-significant positive values. They concluded that the improvement of grain protein depends to a degree on the parental genotypes involved.

The objectives of this study were to determine 1) the effectiveness of selection for grain protein, and 2) the relationship between grain protein and grain yield in a series of winter wheat crosses involving high protein genotypes.

MATERIALS AND METHODS

The test populations consisted of six winter wheat crosses-three high protein (HP) x high protein (HP) crosses and three high protein (HP) x normal protein (NP) crosses. The three high protein parents used were Atlas 66 (Atl 66), Flex, and Danne/Nap Hal (D-NH). The normal protein parent used was KS73114, a sister line of the cultivar 'Newton' released by the Kansas Agric. Exp. Stn. in 1977. The three HP x HP crosses were Atl 66/Flex, Flex/D-NH, and Atl 66/D-NH. The three HP x NP crosses were KS73114/Atl 66, KS73114/Flex, and KS73114/D-NH. The parents were crossed in the greenhouse in the spring of 1976 to produce the F_1's. These F_1's were grown in the field at Stillwater, Okla., in 1976-77 as part of a thesis study (4). The results of that experiment indicated these six populations had potential for improving grain protein.

F_2 populations of each cross were grown at Lahoma, Okla., in 1977-78. Two hundred head selections were taken at random from each population and 192 were planted as F_3 head rows in 1.2 m rows at Stillwater, Okla., in Oct. 1978. The parents and check cultivars were also included in the nursery. Prior to harvest, each cross was divided into four equal grids and 25 rows were selected from each grid on the basis of agronomic characteristics. A 30 cm section of each of the 100 rows per cross was harvested by hand in June 1979. Grain yield was measured on each row and then a sample of the grain was taken for protein determination by the Kjeldahl method. On the basis of grain protein content only, five high protein and five low protein lines from each grid were selected, resulting in 20 high and 20 low protein selections per cross. For each cross, the 20 high protein and 20 low protein lines selected in

F_3 were grown as F_4's in a replicated test in 1979-80 along with parent cultivars. The nursery was planted 27 Oct., 1979 at Stillwater, Okla., and standard nursery management and fertilizer regime was followed. The experimental design was a split-plot design with grids as main plots and entries as sub-plots with two replications. The three HP x HP crosses were planted in single 1.2 m plots, the HP x LP crosses were grown in two 1.2 m rows. A 0.9 m section was harvested from each F_4 row. Mean grain yield from each cross is reported on a 30 cm^2 of row basis. Grain protein on the F_4 plots was determined by near infrared analysis.

Analysis of variance was conducted on each cross to determine if differences existed between the high-low protein selections for grain yield and grain protein. Heritability estimates for grain yield were obtained by regressing means for F_4 rows on the F_3 means. Realized heritability estimates for grain protein were calculated by the following formula: $\frac{\text{High - Low F4}}{\text{High - Low F}_3}$. Phenotypic correlation coefficients between grain yield and grain protein were calculated on the F_4 data. Efficiency of grid selection was estimated on the F_3 data by variance components utilizing the following formula:

$$\sqrt{\frac{\sigma^2_w + \sigma^2_a}{\sigma^2_w}} \times 100$$

where σ^2_a is the among grid component and σ^2_w is the within grid component.

RESULTS AND DISCUSSION

The crosses utilized in this study were initially part of a thesis study on grain protein (4). Based on the results of that thesis study, six crosses were chosen as most promising for further investigation. As referred to earlier, the F_3 nursery of each cross was divided into four equal grids and an equal number of rows were selected from each grid (3). This was done to minimize the variation due to environmental differences across the field.

F_3 frequency distributions for grain protein of the HP x HP crosses are shown in Fig. 1. The two crosses involving Atl 66 had a greater percentage of lines with higher grain protein than the Flex/D-NH cross. The same trend was observed for the HP x NP crosses (Fig. 2). The KS73114/Atl 66 cross had a higher overall mean than the other crosses of this category. The KS73114/Flex and KS73114/D-NH crosses were lower in grain protein than all the other crosses.

The F_4 means for grain yield and grain protein for the high-low protein selection groups are given in Table 1. For grain yield, non-significant differences between high and low protein selections were observed for three crosses, Atl 66/Flex, Atl 66/D-NH, and KS73114/Flex. Significant negative differences were observed for two crosses, Flex/D-NH and KS73114/Atl 66. One cross, KS73114/D-NH, displayed a positive and significant difference for grain yield in the F_4. Thus only two of the six crosses showed a significant negative response for differences in grain yield in response to selection for grain protein in the F_3. The non-significant differences in three crosses indicate that selections might be recovered that have high protein and potential for grain yield. For grain protein, all crosses exhibited highly significant positive differences between the high and low protein selection groups, with actual differences ranging from 0.5 to 1.1% protein. This indicates that selection for higher or lower grain protein is effective from one generation to another, which agrees with reports by other workers (6, 11).

The heritability estimates (regression analysis) for grain yield ranged from a high of 0.226 to a low of 0.047 with one negative estimate (interpreted as zero) for the cross KS73114/Flex (Table 2). These low estimates agree with the generally known low heritability estimates for grain yield. Realized heritability estimates were calculated for grain protein and are listed in Table 2. These values ranged from 0.385 up to 0.611 and are considered to be intermediate in magnitude. The level of these heritability estimates is reflected in the positive and significant differences for high-low protein groups shown in Table 1. The heritability estimates reported in this study are in the same range as those reported by others (5, 6, 9).

Phenotypic correlation coefficients between grain yield and grain protein were calculated on the F_4 data (Table 2). In all crosses, values were negative, intermediate in magnitude and statistically significant, ranging from -0.320 to -0.599.

The efficiency of grid selection which was estimated using the among-grid and within-grid variance components is shown in Table 3. Values ranged from 104.6% for the cross Atl 66/Flex up to 117.0% for the Atl 66/D-NH cross. In this study grid selection resulted in an average 9.2% increase in efficiency of selection for grain protein. Verhalen et al. (14) reported selection responses ranging from 20 to 35% for fiber length in upland cotton (Gossypium hirsutum L.) utilizing grid selection. For grain protein, the results of this study indicated that the use of grids to reduce environmental variation did improve the efficiency of selection for grain protein.

In conclusion, the results of this study indicate that selection was effective in identifying lines with high grain protein content, but that no such accompanying trends were observed for grain yield in connection with selection for high grain protein content. The heritability estimates for grain protein reported in this study ranged from low to intermediate, suggesting that this high protein material could be effectively handled in a breeding program emphasizing increased grain protein. Also, the generally accepted inverse relationship between grain yield and grain protein was observed in this study, although some lines having higher protein content and acceptable yield levels were identified.

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Table 1. Response of grain protein and grain yield to high and low selection for grain protein in six winter wheat crosses.

Cross	Grain Protein Protein Selection Group High	 Low	 Dif- ference	Grain Yield Protein Selection Group High	 Low	 Dif- ference
	%			g		
Atl 66/Flex	18.2	17.1	1.1***	27.6	29.9	-2.3
Flex/D-NH	16.8	15.8	1.0***	25.9	29.3	-3.4**
Atl 66/D-NH	17.6	16.7	0.9***	24.5	25.9	-1.4
KS73114/Flex	15.3	14.8	0.5***	31.4	31.1	0.3
KS73114/Atl 66	16.6	15.5	1.1***	34.3	35.9	-1.6*
KS73114/D-NH	15.4	14.5	0.9***	25.9	24.2	1.7*

*, **, *** Significant at the 0.05, 0.01, and 0.001 levels of probability, respectively.

Table 2. Heritability estimates (h^2) and phenotypic linear correlation coefficients (r) for grain protein and grain yield in six winter wheat crosses.

Cross	Grain protein Realized h^2	Grain yield h^2 (Regression)	r
Atl 66/ Flex	0.611	0.181 ± 0.054	-0.488**
Flex/D-NH	0.476	0.149 ± 0.065	-0.320*
Atl 66/D-NH	0.529	0.075 ± 0.068	-0.486**
KS73114/Flex	0.385	-0.003 ± 0.051	-0.599***
KS73114/Atl 66	0.579	0.047 ± 0.053	-0.359*
KS73114/D-NH	0.500	0.226 ± 0.073	-0.359*

*, **, *** Significant at the 0.05, 0.01, and 0.001 levels of probability, respectively.

Table 3. Estimated efficiency of grid selection for grain protein in six winter wheat crosses.

Cross	Efficiency
	—— % ——
Atl 66/Flex	104.6
Flex/D-NH	106.8
Atl 66/D-NH	117.0
KS73114/Flex	109.5
KS73114/Atl 66	111.2
KS73114/D-NH	106.2

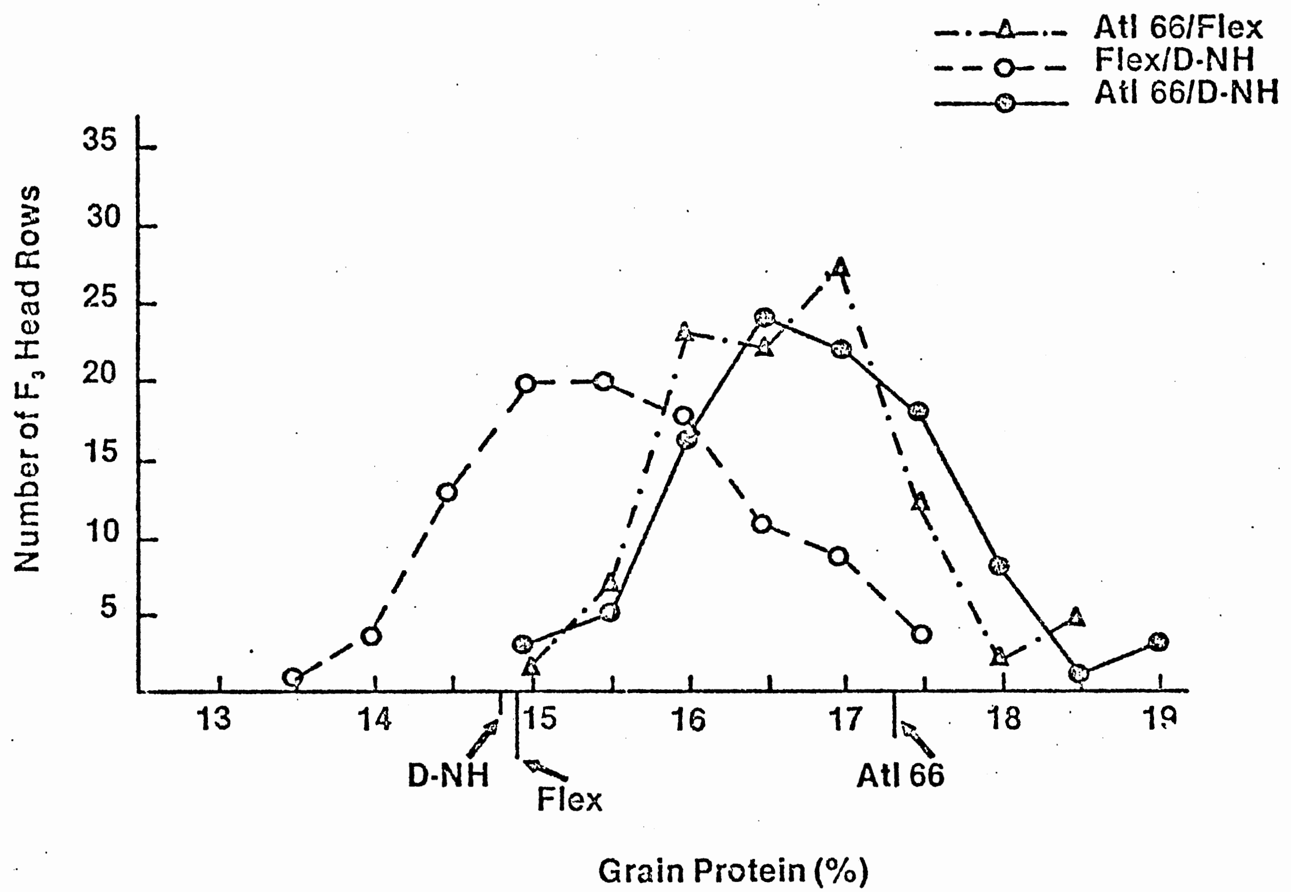

Fig. 1. F_3 frequency distributions for three HP X HP winter wheat crosses for grain protein. (Grain protein values for parental genotypes are shown on the x-axis.)

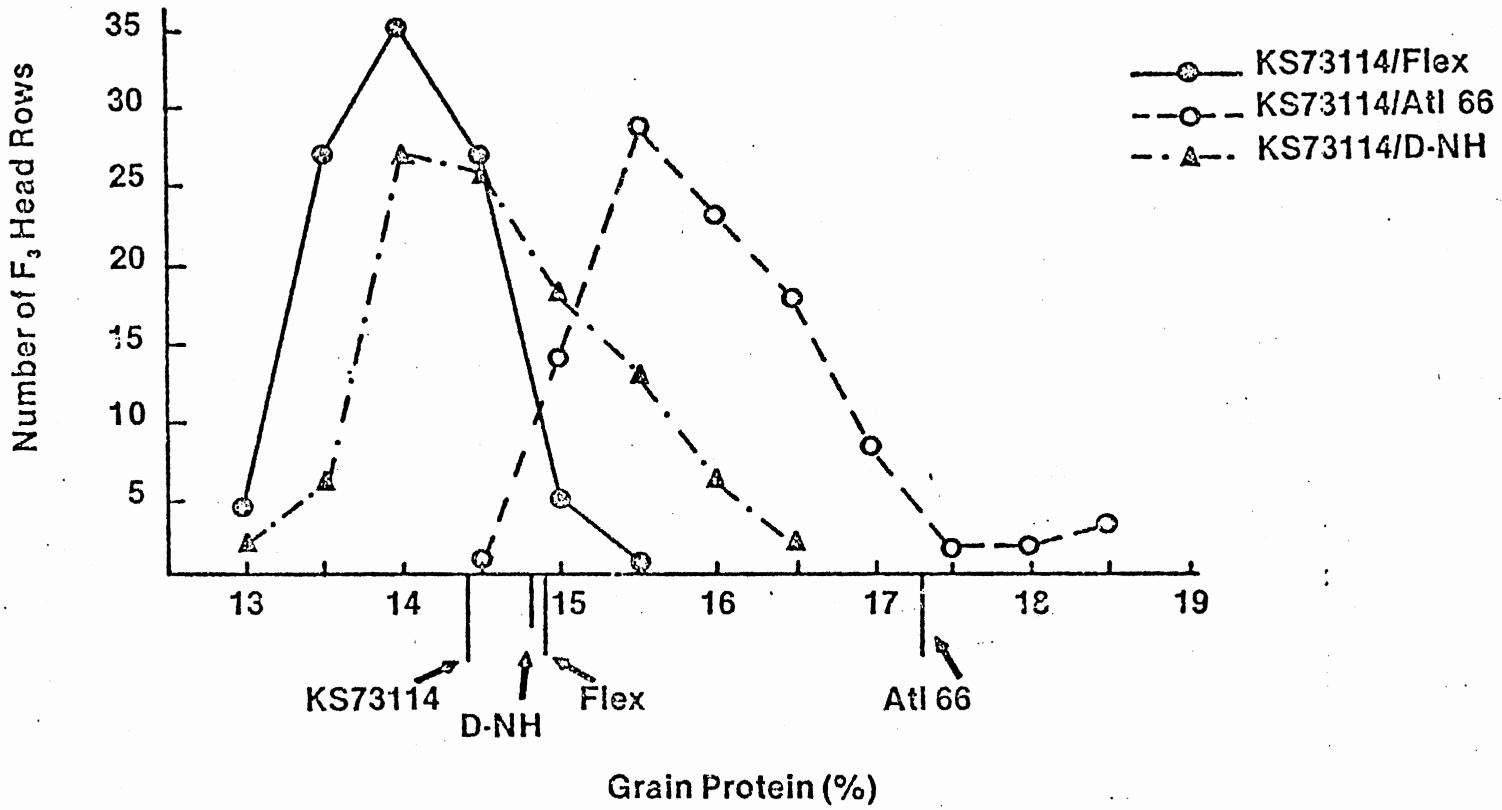

Fig. 2. F_3 frequency distributions for three HP X NP winter wheat crosses for grain protein. (Grain protein values for parental genotypes are shown on the x-axis.)

PART II

ANALYSIS OF F_1'S AND F_2'S OF A WINTER WHEAT CROSS FOR GRAIN PROTEIN AND OTHER TRAITS

Analysis of F_1's and F_2's of a Winter Wheat Cross for Grain Protein and Other Traits[1]

ABSTRACT

Seven winter wheat (Triticum aestivum L. em Thell) genotypes reported to have elevated grain protein were crossed in a diallel mating system to produce F_1's and F_2's. The seven parents were also crossed with two normal protein lines, producing 14 test cross F_1's. The 21 diallel F_1's, 14 test cross F_1's, parent and check cultivars were planted in hill plots in 1979-80. The F_2 populations were grown at two locations in 1979-80. Combining ability analysis was conducted on the diallel F_1's and additive genetic effects were found to be predominant for grain protein in this material. GCA and SCA effects were calculated for the parents and F_1's. The two F_1's that had the largest positive SCA effects for grain yield had the greatest negative effects for grain protein, and the converse was also true. The breeding potential of the seven parents was evaluated by the average performance of their test cross F_1's. Three potentially useful high protein parents were identified on the basis of their test cross arrays. Means, standard deviations, and L.S.D. values were calculated for the F_2 populations on data from two locations. Analysis of variance indicated significant genotype x environment interactions for kernels/spike, kernel weight, grain yield, percent spike fertility, and grain protein. Three F_2 populations with yield potential and elevated protein levels were identified.

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Additional index words: Triticum aestivum L. em Thell., Spike fertility, Grain yield, Diallel cross, Hill plots, GxE effects, Combining ability.

INTRODUCTION

Increasing grain protein in common wheat (Triticum aestivum L. em Thell) is a prime objective in a number of wheat breeding programs throughout the world. Johnson et al. (8) have screened over 12,00 common wheat entries in the USDA Wheat Collection in attempts to identify sources of high protein. They (8) also studied several 'Atlas 66' derived lines in the International Winter Wheat Performance Nursery over a number of locations. The Atlas 66 derivatives showed consistently higher protein values above the general level of grain protein in the nurseries. Heyne (7), studying Atlas 66 and 'Atlas 50' crosses, reported that the major problem in evaluating lines for higher protein content was the variation due to the environment. Significant genotype x environment effects for grain protein were reported by Miezan et al. (9) and Diehl et al. (4). Soil nitrogen levels have been shown to have a direct effect on grain protein content, due to residual mineral N levels in the soil (12) and the amount of available moisture (15).

Mihaljev et al. (10) utilized a diallel crossing scheme to study grain protein in four common wheat cultivars. They found a predominance of additive genetic effects in one year and non-additive in another, and a strong environmental influence on expression of SCA effects for grain protein. Significant additive genetic effects for grain protein have also been reported by other workers (2, 4, 14).

Crosses involving Atlas 66 and 'Nap Hal' were studied by workers at Nebraska (4, 16). Studies (8) have shown that Nap Hal has elevated lysine content as well as high protein content. Vogel et al. (16) found that Nap Hal has genes for higher protein concentration in the bran and that it is higher in whole-grain lysine content. They also reported that transgressive segregates for high and low grain protein were obtained from an Atlas 66/Nap Hal cross. Different genes for high protein in Atlas 66 and Nap Hal have been reported by Vogel et al. (16) and by Diehl et al. (4). Dominance of low protein has been suggested and that the low protein of the F_1's may be due to an association with heterosis for grain yield (4). Cowley and Wells (3) studied crosses of Atlas 66 and 'Hand,' a sister line of 'Flex,' and suggested that there are different genes for high protein in Atlas 66 and Hand.

Hill plots have been investigated by several workers (1, 5, 11) as an alternative to standard row plots. Garland and Fehr (5), studying hill plots in soybeans, found that the correlation between hill and row plots was positive and significant for yield, maturity, height, and lodging, and that evaluation for those characters is effective in hill plots. The genetic correlation between row plots and hill plots in wheat has been found to range from 0.99 (1) to 0.77 (11). O'Brien et al. (11) found that the yield range was greater using hill plots than standard row plots and that coefficients of variation tended to be higher. Baker and Leisle (1) stated that in some cases the number of replications might need to be increased with hills, but that in other cases one hill was as effective as a rod-row plot.

The objectives of the following study were to determine 1) the relationship between grain protein and several traits, 2) combining ability estimates for grain protein, and 3) the breeding potential in a set of high protein winter wheat genotypes.

MATERIALS AND METHODS

Seven winter wheat genotypes reported to have high grain protein were intercrossed and also crossed with two normal protein cultivars in the greenhouse in 1978 and 1979 to provide the material for this study. The high protein lines used were Atlas 66 (Atl 66), Danne/Nap Hal (D-NH), Flex, Favorit/5/Cirpiz/4/Jang Kwang/2/Atl 66/Cmn/3/Velvet (F-V), GB88-13-7-B (GB88), 'Plainsman V' (Pm V), and C.I.15322/2*Osage (322-Os). Atl 66 is a soft red winter wheat cultivar developed at the North Carolina Agric. Exp. Stn. and Flex is a hard red winter wheat cultivar released by the South Dakota Agric. Exp. Stn. Pm V is a high protein winter wheat cultivar released by Seed Research, Inc., Scott City, Kan. F-V is a germ plasm line obtained from the High Protein-High Lysine Observation Nursery distributed by the University of Nebraska. GB88 and 322-Os are presumed alien-translocation lines developed by the Okla. Agric. Exp. Stn. for pest resistance, and were found to exhibit higher grain protein levels. D-NH is a breeding line developed at Oklahoma to transfer the Nap Hal protein genes into a winter background. Two genotypes having normal protein levels, 'Newton' (Ntn), released by the Kansas Agric. Exp. Stn. in 1977, and TX71A562-6 (TX562), a breeding line from the Texas Agric. Exp. Stn. at Bushland, were also crossed with the high protein genotypes. These 14 F_1's were designated as "test crosses." The entire study consisted of 21 diallel F_1's, and 14 test cross F_1's grown at one location and 19 F_2's corresponding to the diallel set grown at two locations.

The 21 diallel F_1's, 14 test cross F_1's, seven high protein parents, two normal protein parents, and check cultivars were planted in the field at Stillwater, Okla., on 18 Oct., 1979, in hill plots using a corn jabber planter with eight seeds per hill. The hills were in rows 30 cm apart with 30 cm between hills. The experimental design was a randomized complete block with six replications. The nursery was harvested on 24 June, 1980, by pulling all plants in individual hills. The characters measured on each hill were heading date, plant height, 1000 kernel weight, grain yield, percent spike fertility, and grain protein. Heading date and plant height will not be reported in this paper. Kernel weight was measured on four heads from each hill and expressed as grams/1000 kernels. Percent fertility was also measured on four heads per hill and was calculated by the following formula: $[(\text{No. kernels/spike}) \div (\text{No. spikelets} \times 2)] \times 100$. Grain yield was measured on each hill and expressed in grams. Grain protein was measured with a near infra-red analyzer from a grain sample from each hill and given as a percent.

Standard analyses of variance indicated that genotype mean squares were highly significant for each trait. A combining ability analysis was then conducted on the diallel crosses using the Model 1, Method 4 procedure of Griffing (6). The genotype sums of squares were partitioned into general and specific combining ability sums of squares and GCA and SCA effects were estimated. Comparisons were also made between parental means, diallel array means, and test cross array means. Statistical significance was examined using an "L.S.D." test.

F_2 populations corresponding to the diallel F_1's were generated by crossing the seven parents in a diallel cross in the greenhouse in 1978. The 21 F_1's were planted in the greenhouse in 1979 to provide seed for the F_2 study. At anthesis, it was discovered that two F_1's, GB88/Flex and 322-Os/GB88, exhibited very high levels of spike sterility.

Insufficient amounts of seed were produced by these two F_1's, so the field study of F_2's contained only 19 F_2 populations. GB88/Flex had 7% spike fertility and 322-Os/GB88 had 16%. The three parents involved in these two crosses are presumed alien-translocation lines and either the loss of wheat chromatin or the presence of alien chromatin probably contributed to the high levels of spike sterility observed. For the diallel F_1 study, the reciprocals of the above crosses were made. These 19 F_2 populations and parent and check cultivars were planted in the field at two locations, Stillwater and Lahoma, Okla., in 1.2 m rows at a normal seeding rate. The experimental design was a randomized complete block with four replications. Just prior to harvest, ten heads were taken at random from each row. Percent fertility, 1000 kernel weight, and number of kernels/spike were calculated for each plot using the ten heads. The remainder of the row was harvested by hand and grain yield and grain protein (near infra-red analysis) were determined for each plot.

In the F_2 study, standard deviations were calculated for percent fertility, kernel weight, and kernels/spike. Also analyses of variance were conducted for each trait at each location and then across locations to determine the genotype x environment interactions.

RESULTS AND DISCUSSION

Diallel Analysis

The analyses of variance showed significant entry mean squares for each trait, so they will not be presented here. Phenotypic correlation coefficients were calculated among the four characters (Table 1), and only the association between grain yield and kernel weight (r=0.292) and that between percent fertility and grain yield (r=0.230) were statistically significant. As might be expected, the correlation coefficient between grain protein and grain yield was negative (r=-0.193) but low and insignificant. Also, the correlation coefficient between grain protein and percent fertility was very low and insignificant (r=0.020).

GCA and SCA mean squares are presented in Table 2. Both GCA and SCA mean squares were significant (p=0.05) for each character, indicating that both additive and non-additive genetic effects are present. The ratio of GCA/SCA variances indicates the relative importance of additive genetic effects for each trait. The GCA/SCA ratio for grain yield (0.39) indicates that both additive and non-additive effects are of major importance. The GCA/SCA ratios for kernel weight (1.39), percent fertility (2.18), and grain protein (1.11) all suggest the importance of additive genetic effects for these traits, which agrees with Bhullar et al. (2) and Mihaljev et al. (10). This is particularly important to the plant breeder, indicating that grain protein levels can be increased through 'pure-line' variety development methods.

The estimates of GCA effects and parental means (Table 3) show a high value for F-V for kernel weight. This finding was not altogether unexpected, since F-V has the highest kernel weight among the set of parental genotypes. D-NH exhibited the greatest negative effect for kernel weight which also was expected since it has the lowest kernel weight of the parents. The estimate for Flex for this trait was zero. The highest positive effects for grain yield were for Pm V (5.19), which had the highest yielding F_1's, and F-V (4.26). 322-Os had the greatest negative effect for grain yield, and also had one of the highest GCA effects for grain protein. GB88, which also exhibited a negative GCA effect for grain yield, was the highest yielding parent. Pm V, a presumed alien-translocation line, had the highest GCA effect for percent fertility. Flex had the greatest negative effect for this trait. This may be due to meiotic instability problems, since Flex is a suspected alien-translocation line, and in previous studies at Okla. State Univ., it was observed that spike fertility was lower in crosses with translocation lines (13). Also, GB88 and 322-Os, both presumed alien-translocation lines, showed negative GCA effects for percent fertility. Flex showed the highest GCA effect for grain protein, but the lowest for percent fertility. GB88 also exhibited a positive effect for grain protein which was explained by the fact that the mean of all GB88 F_1's for grain protein was higher than the parent itself. D-NH exhibited the greatest negative GCA effect for grain protein and Atl 66 also showed a negative effect.

Specific combining ability effects measure the deviation from the expected value based on the GCA effects of the parents of the hybrid. The estimated SCA effects are presented in Table 4, along with means for each trait. For kernel weight, the highest positive effect was exhibited by Pm V/Flex and the greatest negative effects by Flex/GB88 and 322-OS/Atl 66. The highest positive effects for percent fertility were shown by Flex/322-Os and Atl 66/Flex and the greatest negative effects by Pm V/Flex and Flex/GB88. The latter two hybrids were among those with the greatest negative effects for grain yield. Flex/322-Os had the highest positive effect for grain yield. The greatest negative effects for grain yield were shown by 322-Os/Atl 66 and Flex/GB88, the latter of which had only 45% spike fertility. For grain protein, the highest positive effects were shown by 322-Os/Atl 66 and Flex/GB88, while Flex/322-Os and Atl 66/Flex exhibited the greatest negative effects. The generally accepted inverse relationship between grain yield and grain protein is illustrated in this study by the SCA effects of four hybrids. The two hybrids that had the largest positive effects for grain yield, Flex/322-Os and Atl 66/Flex, had the greatest negative effects for grain protein. The converse was also true - the hybrids with the largest positive effects for grain protein had the greatest negative effects for grain yield, 322-Os/Atl 66 and Flex/GB88. However, in certain of these crosses, the degree of spike fertility must also be taken into account before generalizations are made. For instance, Flex/GB88 was low yielding, high in grain protein, and also very low in spike fertility.

The information presented in Table 5 is a measure of the breeding potential of the high protein genotypes tested. Comparisons were made between the mean of the test cross parents, Ntn and TX562, both normal protein lines adapted to the southern Great Plains, and the parental means, and the means of the diallel F_1's and test cross F_1's for each high protein parent. The comparison is expressed as a deviation from the test cross parent mean. For kernel weight, all the diallel array means and test cross array means were significantly higher than the test cross parent mean. The D-NH parental mean was significantly lower while

F-V and GB88 parental means were significantly higher than the test cross parent mean. The tester parents used in this study tended to have low kernel weight values in terms of cultivars adapted to the region. For grain yield, in no case was the high protein parent mean, diallel array mean, or test cross array mean significantly higher than the test cross parent mean. In four of these comparisons they were significantly lower. For percent fertility, the diallel array means of Atl 66, Pm V, 322-Os, and GB88 had substantially higher negative values in relation to the high protein parental and test cross array mean. This could be explained by the meiotic instability in the diallel crosses because of the preponderance of presumed translocation lines in the study. Of particular interest was the observation that in all comparisons for fertility, they were lower than the test cross parent mean. In fact, in 18 of the 21 comparisons, this difference was statistically significant. For grain protein, the results were consistent with other studies (3, 10). All high protein parental means and all diallel array means were significantly higher in protein than the test cross parent mean. The test cross array means of F-V, 322-Os, and D-NH were not significantly different from the test cross parent mean, indicating that these parents probably would not be the best high protein parents for use in improving protein content. The comparisons in Table 5 indicate that Atl 66, Pm V, and possibly GB88 would be the most useful high protein parents.

F_2 Experiment

Two tables of the data from the F_2 study are presented here. In Table 6, mean squares for kernels/spike, kernel weight, grain yield, percent fertility, and grain protein from the analysis of variance across locations are presented. A significant location effect was found for each character and differences among F_2 populations, parental genotypes, and check cultivars were significant for all traits. Also a significant genotype x location effect was observed for each trait, including protein, indicating that the influence of the environment is important and that selection for higher grain protein should be done in the environment where the cultivar will be grown.

The means of five traits for the 19 F_2 populations are presented in Table 7. In general, the means for kernels/spike and kernel weight for the F_2's followed the pattern of the parents for each specific hybrid. Those F_2's with a parent having high values for kernels/spike and kernel weight tended to have higher values for those same traits. For grain yield, four F_2's were not significantly different from the highest yielding parent, GB88. Only one F_2, F-V/Pm V, was higher than GB88, but it was significantly higher than either of its parents. The three highest F_2's or percent fertility all were F_2's involving Pm V, which was the parent with the highest value for percent fertility. Flex was the parent genotype having the lowest value for percent fertility, and its F_2's were correspondingly low for that trait. Four of the seven parents studied had fertility values of less than 100%. Atl 66 was the highest parent for grain protein and Flex ranked second. One F_2, 322-Os/Atl 66, was significantly higher in grain protein than the other F_2's but was among the lowest yielding and had less than 100% fertility. Several F_2's seem promising for combining high protein and higher yield levels. F-V/Flex ranked third for grain protein and fourth for grain yield. Flex/Atl 66 ranked third for grain protein, although not significantly different than F-V/Flex, and ranked fifth in grain yield, GB88/Pm V was ninth in grain protein and seventh for grain yield, but exhibited over 100% fertility.

Summary

The results of these studies, diallel F_1 crosses, test cross F_1's, and F_2's, indicate that there may be some problems with high protein parents that involve alien-translocations, but that these parents may be used if they are not crossed with other alien-translocation lines. In fact, the three more promising F_2's listed above are crosses with alien-translocation lines. Atl 66 remains the most consistent high protein source in this study, with Plainsman V, Flex, and GB88 also showing potential as high protein parents. The most promising hybrids studied were F-V/Flex, Flex/Atl 66, and GB88/Pm V. By interpolation, it can be concluded from the combining ability analysis that grain protein content was controlled mainly by additive genetic effects, which is agreement with results reported by other workers (2, 4, 10, 14). This suggests to the plant breeder that improvement of grain protein levels could be accomplished in a breeding program.

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LIST OF TABLES

Table 1. Phenotypic linear correlation coefficients among four characters of 21 F_1's from a seven-parent winter wheat diallel cross.

Character	Kernel weight	Grain yield	Percent fertility
Grain yield	0.292**		
Percent fertility	0.174	0.230*	
Grain protein	0.020	-0.193	0.038

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 2. Mean squares and GCA/SCA ratios for four characters of a seven-parent winter wheat diallel cross.

Character	Mean squares			GCA/SCA ratio
	GCA	SCA	Error	
Kernel weight	154.22**	46.91**	3.49	1.39
Grain yield	528.28**	535.44**	33.86	0.39
Percent fertility	7,810.36**	1,519.90**	103.60	2.18
Grain protein	31.14**	11.37**	0.27	1.11

** Significant at the 0.01 probability level. Degress of freedom for GCA, SCA, and error mean squares are 6, 14, and 100, respectively.

Table 3. Estimates of GCA effects and parental means for four characters from a seven-parent winter wheat diallel cross.

Parent	Kernel weight		Grain yield		Percent fertility		Grain protein	
	GCA effect	Mean	GCA effect	Mean	GCA effect	Mean	GCA effect	Mean
	g/1,000 kernels		g/hill		%			
Atl 66	-0.59	29.8	1.99	31.6	9.57	139.6	-0.16	18.3
F-V	4.52	42.3	4.26	32.8	2.55	96.7	-0.28	17.6
Pm V	-0.04	29.4	5.19	31.9	24.53	145.5	-0.69	17.2
322-Os	-1.63	26.9	-6.85	26.1	-6.06	124.2	0.48	16.4
Flex	0.00	28.9	-2.75	32.5	-26.52	94.3	1.73	16.1
D-NH	-2.67	16.5	-0.50	16.7	5.52	137.7	-1.50	15.4
GB88	0.41	34.3	-1.34	40.0	-9.59	116.9	0.42	15.1
Mean		29.7		30.2		122.1		16.6
L.S.D. (0.05)		2.1		6.7		11.7		0.6
SE	0.48		1.50		2.63		0.13	

Table 4. Estimates of SCA effects and means for four characters for the 21 F_1's from a seven-parent winter wheat diallel cross.

	Kernel weight		Grain yield		Percent fertility		Grain protein	
Entry	SCA effect	Mean	SCA effect	Mean	SCA effect	Mean	SCA effect	Mean
	– g/1,000 kernels –		—— g/hill ——		—— % ——			
Atl 66/D-NH	1.46	34.4	9.58	44.4	0.78	119.7	-0.11	15.7
Atl 66/F-V	1.74	41.9	-4.92	34.7	-7.33	108.6	0.47	17.4
Atl 66/Flex	-1.51	34.1	9.03	41.6	20.85	107.7	-1.31	17.7
Atl 66/Pm V	0.14	35.7	3.47	44.0	-1.87	136.1	-0.24	16.3
GB88/Atl 66	2.28	38.3	0.34	34.4	1.66	105.5	-0.83	16.9
322-Os/Atl 66	-4.10	29.9	-17.50	11.0	-14.08	93.3	2.01	19.8
F-V/D-NH	-1.13	36.9	-2.05	35.1	0.53	112.4	0.18	15.8
F-V/322-Os	2.06	41.1	5.77	36.5	-6.50	93.8	0.78	18.4
Flex/F-V	1.50	42.2	-2.86	32.0	2.43	82.3	-0.25	18.6
GB88/F-V	-0.55	40.6	5.47	41.8	6.21	103.0	-1.12	16.4
Pm V/F-V	-3.62	37.1	-1.41	41.4	4.66	135.6	-0.05	16.4
Pm V/D-NH	-0.41	33.1	0.00	38.1	6.97	140.9	-0.31	14.9
Pm V/Flex	4.13	40.3	-5.99	29.8	-23.86	78.0	1.47	19.9
Pm V/GB88	-0.09	36.5	2.88	40.1	2.45	121.2	0.34	17.5
Pm V/322-Os	-0.16	34.4	1.06	32.8	11.66	134.0	-1.21	16.0
D-NH/322-Os	-1.39	30.5	-9.46	16.5	-17.10	86.2	0.47	16.9
Flex/322-Os	0.61	35.2	16.07	39.8	29.77	101.0	-2.74	16.9
GB88/322-Os	2.98	37.9	4.05	29.2	-3.74	84.5	0.69	19.0
Flex/D-NH	0.68	34.2	-0.79	29.3	-6.88	76.0	0.84	18.5
Flex/GB88	-5.41	31.2	-15.45	13.8	-22.30	45.4	1.99	21.6
D-NH/GB88	0.79	34.7	2.71	34.2	15.72	115.5	-1.07	15.3
Mean		36.2		33.4		103.8		17.4
L.S.D. (0.05)		2.1		6.7		11.7		0.6
SE a ($\hat{s}_{ij} - \hat{s}_{ik}$)	0.96		3.00		5.26		0.27	
SE b ($\hat{s}_{ij} - \hat{s}_{kl}$)	0.84		2.60		4.55		0.23	

SE a is for comparison of F_1's having one parent in common; SE b is for comparison of F_1's having no parent in common.

Table 5. Comparisons of winter wheat parental, diallel array, and test cross array means with test cross parental mean (presented as deviations from test cross parental mean).

Parental group	Kernel weight	Grain yield	Percent fertility	Grain protein
	g/1,000 kernels	g/hill	%	%
<u>Atl 66</u>				
Parent	2.3	-9.8	-13.1	4.2*
Diallel array	7.8*	-9.5	-44.0*	3.4*
Test cross array	7.0*	8.9	-16.8*	1.3*
<u>F-V</u>				
Parent	14.8*	-8.6	-56.0*	3.5*
Diallel array	12.6*	-4.3	-46.2*	3.1*
Test cross array	10.0*	3.5	-32.0*	0.7
<u>Pm V</u>				
Parent	1.9	-9.5	-7.2	3.1*
Diallel array	8.6*	-2.8	-26.7*	2.7*
Test cross array	4.1*	0.3	-5.6	0.9*
<u>322-Os</u>				
Parent	-0.6	-15.3*	-28.5*	2.3*
Diallel array	7.8*	-12.2*	-53.4*	3.5*
Test cross array	4.5*	-6.0	-22.6*	0.5
<u>Flex</u>				
Parent	1.4	-8.9	-58.4*	2.0*
Diallel array	8.9*	-9.2	-68.2*	4.7*
Test cross array	9.6*	1.3	-50.6*	1.3*
<u>D-NH</u>				
Parent	-11.0*	-24.7*	-15.0*	1.3*
Diallel array	6.7*	-6.9	-42.7*	2.1*
Test cross array	4.3*	2.6	-27.5*	-0.3
<u>GB88</u>				
Parent	6.8*	-1.4	-35.8*	1.0*
Diallel array	8.2*	-10.1*	-57.4*	3.8*
Test cross array	9.4*	0.4	-38.3*	1.0*
Test cross parental mean	27.5	41.4	152.7	14.1

* Significant at the 0.05 probability level.

Table 6. Mean squares for 19 F_2's plus parent and check winter wheat cultivars for estimating G X E effects for five characters.

Source	df	Mean Squares				
		Kernel weight	Grain yield	Percent fertility	Grain protein	Kernels/ spike
Environment (e)	1	22,805.61**	116,318.89**	22,879.04**	56.16**	1,980.17*
Error a	6	85.48	1,052.97	1,264.00	1.41	165.63
Genotype (G)	29	1,456.42**	3,229.18**	8,223.69**	8.79**	1,013.76**
G X E	29	106.90**	582.23**	1,656.02**	1.26**	239.97**
Error b	174	56.68	216.71	621.95	0.25	102.48

*, ** Significant at the 0.05 and 0.01 probability levels, respectively. Error a = Rep (Environment), Error b = Rep * Genotype (Environment).

Table 7. Means, standard deviations, and L.S.D. values for 19 F_2's from a seven-parent winter wheat diallel cross for five characters from two locations.

Entry	Kernel weight	Grain yield ‡	Percent fertility	Grain protein ‡	Kernels/ spike
<u>F2</u>					
D-NH/Atl 66	25.8 ± 4.9	71.4	105.2 ± 16.3	16.7	34.3 ± 6.7
F-V/Atl 66	29.1 ± 6.2	85.0	101.5 ± 15.8	17.9	32.5 ± 6.7
Flex/Atl 66	27.8 ± 3.7	100.6	91.2 ± 13.2	18.0	27.2 ± 4.7
Pm V/Atl 66	25.6 ± 5.2	91.3	113.9 ± 19.7	17.5	33.5 ± 7.8
GB88/Atl 66	28.8 ± 4.0	88.3	95.5 ± 17.3	17.9	29.1 ± 6.6
322-Os/Atl 66	25.1 ± 4.7	71.0	92.5 ± 17.5	18.8	29.4 ± 5.9
F-V/D-NH	25.2 ± 5.8	70.6	107.4 ± 18.4	16.9	34.7 ± 7.3
322-Os/F-V	28.6 ± 5.9	72.5	91.9 ± 18.8	17.9	27.3 ± 7.6
F-V/Flex	30.3 ± 4.4	103.7	85.7 ± 15.6	18.2	25.6 ± 5.8
GB88/F-V	31.6 ± 3.9	107.0	98.2 ± 13.1	16.8	29.7 ± 5.5
F-V/Pm V	29.2 ± 3.8	117.1	113.7 ± 18.5	17.3	33.0 ± 6.3
D-NH/Pm V	25.4 ± 3.7	96.6	120.2 ± 18.2	16.1	36.1 ± 8.3
Pm V/Flex	30.6 ± 5.2	112.0	104.5 ± 15.9	17.3	29.9 ± 5.9
GB88/Pm V	26.6 ± 3.6	94.5	104.2 ± 15.2	17.6	32.0 ± 6.2
322-Os/Pm V	28.8 ± 4.7	82.9	98.3 ± 19.5	18.0	28.6 ± 6.7
322-Os/D-NH	22.8 ± 5.0	64.8	91.9 ± 20.4	16.5	30.2 ± 7.9
322-Os/Flex	27.9 ± 4.5	77.7	82.3 ± 15.6	18.0	25.3 ± 6.3
322-Os/GB88†	--	--	--	--	--
Flex/D-NH	24.4 ± 5.1	73.0	91.0 ± 19.0	17.3	31.1 ± 9.2
GB88/Flex†	--	--	--	--	--
GB88/D-NH	29.2 ± 3.3	89.4	99.7 ± 16.0	16.6	30.8 ± 6.3
F_2 mean	27.5	87.9	99.4	17.4	30.5
<u>Parent</u>					
Atl 66	21.0 ± 4.8	57.9	106.0 ± 19.6	19.7	34.4 ± 8.4
F-V	32.7 ± 6.1	86.5	94.4 ± 12.5	17.9	27.3 ± 5.5
Pm V	22.6 ± 3.3	72.0	121.5 ± 16.6	17.9	30.8 ± 5.5
322-Os	21.7 ± 2.2	67.7	96.6 ± 17.6	17.0	27.2 ± 6.6
Flex	22.3 ± 3.3	73.6	85.7 ± 12.9	18.5	26.2 ± 5.2
D-NH	12.8 ± 2.8	38.0	107.6 ± 21.5	17.4	36.8 ± 8.8
GB88	30.8 ± 2.4	116.5	98.5 ± 12.1	15.3	28.2 ± 5.1
Parental mean	23.4	73.2	101.5	17.7	30.1
L.S.D. (0.05)	7.4	14.4	24.4	0.5	9.9

† Very low spike fertility in F_1's, insufficient seed for F_2 test.
‡ One observation/plot.

PART III

COMBINING ABILITY ANALYSIS OF GRAIN PROTEIN AND OTHER TRAITS IN A DIALLEL CROSS OF WINTER WHEAT

Combining Ability Analysis of Grain Protein and Other Traits in a Diallel Cross of Winter Wheat[1]

ABSTRACT

Twelve known or suspected high protein winter wheat (*Triticum aestivum* L. em Thell) genotypes were assembled and crossed in a diallel mating system, producing 66 F_1's. These 12 parents were also crossed to a normal protein cultivar to determine their breeding potential. Combining ability analysis was conducted on the diallel F_1's for plant height, kernel weight, percent spike fertility, grain yield, and grain protein. GCA/SCA ratios indicated that additive genetic effects were more important for grain protein, plant height, kernel weight, and percent fertility. Four genotypes were identified as having good potential for high protein parents based on GCA effects and parental means. Three F_1 hybrids were identified as being most useful based on SCA effects and means for grain yield and grain protein. In the test for breeding potential, the parents were examined in terms of their behavior when crossed with an adapted, normal protein cultivar. Phenotypic correlation coefficients were calculated among the five traits for the diallel set. Significant negative associations were found between grain protein and plant height and between grain protein and kernel weight. A non-significant negative association was observed for grain yield and percent protein.

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Additional index words: *Triticum aestivum* L. em Thell, Grain yield, Combining ability.

INTRODUCTION

Both genetic and environmental influences are of concern in the development of high-protein winter wheat (Triticum aestivum L. em Thell) cultivars. Protein quantity is under genetic control but actual protein levels observed are dependent in a large part on environmental factors. Smika and Greb (15) reported that protein levels decreased with increasing soil water due to the location of N in the soil profile. They found that grain protein increased when soil NO_3-N increased. They also found that higher soil temperatures at crown depth increased the grain protein by increasing N uptake. Terman et al. (17) found that varying rates of N and moisture levels had strong effects on the yield-protein relationship. Heyne (8) reported that the environment had strong effects on selection for high protein genotypes. Miezan et al. (11) and Diehl et al. (5) found significant GxE interactions for grain protein.

Several high-protein wheat genotypes have been utilized by breeders for a number of years. 'Atlas 66' (10) has been used as a source of high protein since the mid-1950's (8). The high protein genes in Atlas 66 are from the South American cultivar 'Frondoso.' Johnson et al. (9) listed several other sources of high protein in addition to Atlas 66. These include 'Nap Hal,' 'April Bearded,' 'Aniversario,' NE542437, and SD69103. 'Flex' is a selection out of SD69103 for higher grain protein (19). 'Plainsman V' is also reported to have higher grain protein (8).

Grain protein in wheat has been studied in diallel crosses by several workers (12, 14). Mihaljev and Kovacev-Djolai (12) reported significant GCA and SCA variances for grain protein and a high GCA/SCA ratio (4.05), indicating predominantly additive genetic effects for grain protein. They studied 'Bezostaya 1' and reported that it is a poor general combiner for grain protein. Singh et al. (14) studying spring wheats, also reported a predominance of additive genetic effects for grain protein. Other workers (3, 5) have also reported that additive gene action is more important for grain protein. Bhullar (3) studied spring x winter wheat crosses and reported on the partial dominance of low protein, as did Diehl et al. (5).

Diehl et al. (5) studied crosses of Atlas 66, Nap Hal, and April Bearded and reported a negative and significant correlation between grain yield and grain protein. They suggested that Atlas 66 and Nap Hal have different genes for grain protein. Vogel et al. (18) studied protein and lysine contents of Nap Hal/Atlas 66 crosses and reported that transgressive segregates for high and low protein concentrations were obtained. They also reported that Atlas 66 and Nap Hal have different genes for high endosperm protein content.

Baker (1) reviewed diallel analysis and concluded that this technique can be used to determine the importance of specific combining ability and to predict the performance of hybrid combinations based on the performance of the parents and general combining ability effects, even though the genetic assumptions may or may not have been met. Of particular interest to the plant breeder is the genetic information that can be gained about a particular set of parents using a fixed model proposed by Griffing (7). Using a fixed model (7), the average performance of a single cross can be partitioned into GCA (main effects) and SCA (interactions) effects. The GCA effects can be used to predict the performance of a single cross hybrid if the SCA mean square is nonsignificant. In that case, the parents with highest GCA effects would produce the best hybrids. Baker (1) concluded that the estimation of GCA and

SCA mean squares and effects is the extent to which diallel analysis should be used. The information obtained can then be used to estimate hybrid performance.

Studies have been conducted to determine if hill plots can be used as effectively as row plots for evaluation of different genotypes (2, 6). Garland and Fehr (6) studied hills versus rows in soybeans and found that the coefficients of variation for hills were twice that of rows, but that the correlation between hills and rows was positive and significant for yield, height, and maturity. They concluded that there was no difference in effectiveness of selection between the two types of plots, although it was necessary to retain more hills than rows. Baker and Leisle (2) reported on hills versus row plots in wheat. They found that in some cases it may be necessary to increase the number of hills as compared to rows, but the genetic correlation between the two methods was very high (r_g=0.99). They concluded that hill plots could be very useful in genetic studies.

The objectives of the following study were 1) to obtain combining ability estimates of 12 known and/or suspected high protein winter wheat genotypes for grain protein utilizing a diallel mating design, and 2) to determine the breeding potential of these genotypes in crosses with a normal protein tester genotype.

MATERIALS AND METHODS

All the known and suspected high protein winter wheat genotypes were assembled for this study. Twelve such genotypes were obtained and these were Atlas 66 (Atl 66), Bezostaia 1 (Bezo 1), 'G.K. Protein' (GKP), Favorit/5/Cirpiz/4/Jang Kwang/2/Atl 66/Cmn/3/Velvet (F-V), GB88-13-7-B (GB88), C.I.15322/2*Osage (322-Os), OK711092-50 (OK50), Flex, Plainsman V (Pm V), 'Lancota' (Lcn), Dekalb 582 R-Line (Dk582), and Danne/Nap Hal (D-NH). Atl 66 is a soft red winter wheat from the North Carolina Exp. Stn. (10) that has been used extensively as a source of high protein. Three of the parents, Bezo 1, GKP, and F-V are of Eastern European origin and in addition to high protein content have good kernel weight values. Bezo 1 and GKP have been entries in the International Winter Wheat Performance Nursery. F-V was obtained from the High Protein-High Lysine Observation Nursery distributed by the Univ. of Nebraska. Eight lines and cultivars developed at stations in the Central Great Plains states were also used in the study, five of which are known or suspected to contain portions of alien chromosomes. GB88, 322-Os, and OK50 are presumed alien-translocation lines developed at the Okla. Agric. Exp. Stn., and Flex and Pm V are suspected but not confirmed translocation lines. GB88 is a breeding line that contains rye chromatin, presumed to be a translocation, and was developed for resistance to greenbug (Schizaphis graminum Rondani) biotype C (13). 322-Os contains Agropryon elongatum chromatin and a presumed translocation for resistance to wheat streak mosaic virus (13). OK50 is a sister line of the cultivar 'Payne' which contains the 'Teewon' (A. elongatum) translocation for leaf rust resistance (16). Flex is a germplasm line released from the South Dakota Agric. Exp. Stn. that is reported to contain a leaf rust translocation, but the pedigree of Flex is somewhat uncertain (4). Plainsman V is a cultivar released by Seed Research, Inc., Scott City, Kan., and is presumed to contain A. elongatum chromatin. Three other adapted lines were included in the study-Lcn, a cultivar released from the Neb. Agric. Exp. Stn. in 1975 that is reported to contain two of the three genes from Atl 66 for high protein, DK582, a hybrid wheat restorer breeding line, and D-NH, a breeding line developed at the Okla. Agric. Exp. Stn. by crossing a local cultivar 'Danne' with Nap Hal, a high protein and high lysine genotype obtained from the Univ. of Neb.

Ten of the 12 high protein parents have been grown in replicated tests at two locations in two years. In Table 1, grain yield is presented in kg/ha and grain protein is presented as deviations from the check cultivar 'Newton' in each environment. The data presented in Table 1 is from standard nursery plots. It is of interest to note the effects of environment on protein content with Newton, for example, which had protein values of 14.3%, 16.0%, and 17.8% in the three environments.

The 12 high protein genotypes were crossed in a diallel mating system, ignoring reciprocals, to produce 66 diallel F_1's. One normal protein cultivar adapted to the Southern Great Plains region, Newton (Ntn), a release from the Kan. Agric. Exp. Stn., was also crossed with the high protein lines and the resulting 12 F_1's were designated as "test crosses." The crosses were made in the greenhouse at Stillwater, Okla., in the spring of 1979.

The 66 diallel F_1's, 12 test cross F_1's, 12 high protein parents, one tester parent, and five check cultivars (96 total entries) were planted in the field at Stillwater, Okla., on 18 Oct., 1979. Hill plots were employed with five seeds per hill planted with a corn jabber planter. Hills were 30 cm apart in each direction. The experimental design was a randomized complete block with four replications. Standard nursery management procedures were followed during the growing season. The nursery was harvested on 25 June, 1980, by pulling all plants in individual hills. Plant height (cm), grain yield (g/plot), and grain protein (%) were measured on each plot. Grain protein percent was determined using the near infra-red technique. Kernel weight (g/1000 kernels) and percent spike fertility were calculated on an average of four spikes per hill. Spike fertility was calculated by the following formula: $[(\text{No. kernels/spike}) \div (\text{No. spikelets} \times 2)] \times 100$.

Standard analyses of variance were conducted both on the diallel F_1 set and the 96 total entries, and a combining ability analysis was then carried out on the diallel set using Griffing's Model 1, Method 4 (7). General and specific combining ability sums of squares were partitioned out of the entry sums of squares and GCA and SCA effects were estimated. Comparisons were also made between the test cross parent mean and the diallel parental means, diallel array means, and test cross means by the use of the "L.S.D."

RESULTS AND DISCUSSION

The mean squares for each trait are presented in Table 2. Entry mean squares for the diallel F_1's and the total entires for all traits were highly significant. The phenotypic correlation coefficients among the diallel F_1's are presented in Table 3. A highly significant positive relationship was found between grain yield and kernel weight (r=0.335) indicating that grain yield increased as kernel weight increased. Another significant positive relationship was found between grain yield and percent fertility (r=0.164). Negative and significant correlation coefficients were found for the association between grain protein and plant height (r=-0.182) and grain protein and kernel weight (r=-0.218). The correlation coefficient between grain yield and grain protein (r=-0.093) was negative but not significant, indicating that in this material the negative yield-protein relationship could be broken. Diehl et al. (5), also studying Atl 66 and Nap Hal, reported a significant negative association between grain protein and grain yield.

In Table 4, GCA and SCA mean squares are presented for five traits. All were highly significant, indicating the importance of both additive and non-additive genetic effects for the five traits in these crosses. The relative importance of these variances can be shown by the magnitude of the GCA/SCA ratio. The smallest GCA/SCA ratio (0.76) was found for grain yield, which indicates the importance of non-additive effects. The GCA/SCA ratio for grain protein was 2.24, indicating predominantly additive genetic effects for this character. This is in agreement with reports by other workers (3, 5, 12, 14) of the importance of additive genetic variance for grain protein. Plant height, kernel weight, and percent fertility had GCA/SCA ratios which also indicated that additive genetic effects were important for these traits.

The estimates of GCA effects and means for the 12 parents are presented in Table 5. The taller genotypes had higher positive GCA estimates for plant height and the shorter genotypes had negative estimates. The Eastern European parent lines, F-V, GKP, and Bezo 1, had the highest positive estimates for 1000-kernel weight, which were significantly different from the estimates for the other genotypes. These three genotypes had the highest values for kernel weight of all the parent lines. For grain yield, two of the adapted lines, OK50 and Dk582, had the highest estimates with 322-Os and GB88 having the greatest negative estimates. The adapted genotypes also had the highest estimates for percent fertility. The three parents with the greatest negative effects for percent fertility are three of the suspected translocation lines, Flex, GB88, and 322-Os, although the means of the parents themselves are over 100% fertility. The parent with the greatest negative estimate for percent fertility, Flex, had the highest positive estimate for grain protein. High positive estimates for grain protein were also observed for the other parents having large negative estimates for percent fertility. Atl 66 and Pm V had positive estimates for both percent fertility and grain protein, as well as grain yield, indicating that these genotypes may be most useful as high protein parents. Based on parental means for grain yield and grain protein, it appears that F-V, OK50, and Bezo 1 would also be potentially useful high protein parents, although it has been reported (12) that Bezo 1 is a poor general combiner for grain protein.

The SCA effects and means for 17 of the 66 F_1's are presented in Table 6. The first 12 entries in Table 6 correspond to the entries in the upper right quadrant of Fig. 1, which is a graph of the SCA estimates of the 66 F_1's for grain yield versus grain protein. Fig. 2 is a graph of the means of all the F_1's for grain yield versus grain protein. Identical means were observed for four F_1's. The entries in the upper right quadrant of Fig. 2 are those F_1's that had means for grain yield and grain protein equal to or greater than the F_1 mean for both traits. There are three F_1's that are common to both graphs. These are Pm V/Atl 66, F-V/Dk582, and GB88/Dk582. Since these F_1's are above average for grain yield and grain protein and exhibit positive SCA effects for both traits, they should be considered the most promising F_1's for increasing protein levels and improving grain yield.

In Table 7 the diallel parent means, diallel arrays, and the test cross means are compared with the test cross parent mean for five traits. The comparison is in the form of deviations from the test cross parent mean. For plant height, all the diallel arrays, except that of Pm V, were significantly taller than the test cross parent, Newton. Five of the test crosses were not significantly different from the test cross parent mean for plant height. For kernel weight, the test cross parent itself was rather low, thus in all cases, the test cross means were higher than the test cross parent mean.

Only one high protein parent, Lancota, was significantly higher than Newton for grain yield, while Pm V, 322-Os, and D-NH were significantly lower. In three cases, diallel array means were significantly greater than Newton. These were Dk582, Lcn, and OK50. The test cross means of Atl 66, Dk582, Lcn, and OK50 were significantly higher than the test cross parent, indicating that the potential for acceptable yields along with higher protein levels lies in the crosses with the better adapted high protein lines. None of the high protein parents, diallel arrays, or test cross means were significantly greater than the test cross parent for percent fertility, however, the test cross means for Atl 66, Dk582, GKP, and Lcn were not significantly different from the test cross parent. For grain protein, all the high protein parents were significantly higher than Newton as were all the diallel arrays except that of OK50. The test cross means of 322-Os and GB88 were significantly higher than the test cross parent, but the 322-Os test cross was also significantly lower yielding while that of GB88 was not significantly different in yield than the test cross parent mean.

The results of the diallel study indicate that several of these high protein lines would be useful as parents in a program for improving grain protein levels. Atl 66 remains as a good germplasm source for high grain protein, although there are some problems to be overcome concerning adaptation to the Great Plains and grain quality. F-V and OK50 appear to be more useful sources of higher protein in terms of their adaptation to the Central Great Plains. Pm V also appears to be a good parent for higher grain protein. The three most promising F_1's are Pm V/Atl 66, F-V/Dk582, and GB88/Dk582. It is interesting to note that Dk582 appears twice as a parent in the more promising F_1's but did not appear to be a good parent in the GCA analysis. These F_1's appear most useful since the means were above average for both protein and yield and they also had positive SCA effects for both traits.

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Table 1. Grain yield and grain protein (presented as deviations from Newton) for 10 high protein winter wheat genotypes.

Entry	1979 Lahoma Grain yield	 Grain protein	1980 Lahoma Grain yield	 Grain protein	1980 Stillwater Grain yield	 Grain protein
	kg/ha	— % —	kg/ha	— % —	kg/ha	— % —
Newton	3,676	14.3	1,465	17.8	3,132	16.0
Atl 66	2,439	3.1	934	2.3	2,943	2.2
F-V	3,044	1.7	1,848	0.6	3,804	2.3
Pm V	3,441	1.9	1,687	-0.5	3,528	1.0
GB88	2,836	1.8	2,218	-1.6	3,044	0.2
Dk582	--	---	538	0.9	2,493	1.3
GKP	--	---	1,512	0.5	3,515	-0.5
Bezo 1	3,111	-0.3	--	---	--	---
Flex	2,789	1.5	--	---	--	---
322-Os	1,962	3.1	--	---	--	---
Lcn	3,414	1.5	--	---	--	---

Table 2. Mean squares of five characters for 66 diallel winter wheat F_1's and 96 total entries.

Source		df	Mean Squares Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
Rep	a	3	89.02**	2.40	1.41	47.65	1.51**
	b	3	149.66**	7.02	10.27	84.42	0.88
Entry	a	65	192.68**	60.58**	323.89**	1,359.67**	10.42**
	b	95	249.93**	84.27**	332.68**	1,225.41**	9.94**
Error	a	195	16.68	3.87	46.87	36.40	0.36
	b	285	16.78	4.23	44.39	39.57	0.37

** Significant at the 0.01 probability level. a = Analysis of variance of 66 diallel F_1's. b = Analysis of variance of 96 total entries.

Table 3. Phenotypic linear correlation coefficients among five characters of 66 F_1's from a 12-parent winter wheat diallel cross.

Character	Plant height	Kernel weight	Grain yield	Percent fertility
Kernel weight	0.077			
Grain yield	0.121	0.335**		
Percent fertility	0.004	0.003	0.164*	
Grain protein	-0.182*	-0.218**	-0.093	0.053

*, ** Significant at the 0.05 and 0.01 levels of probability, respectively.

Table 4. Mean squares and GCA/SCA ratios for five characters from a 12-parent winter wheat diallel cross.

Character	Mean Squares GCA	 SCA	 Error	GCA/SCA ratio
Plant height	936.52**	41.15**	16.68	7.52
Kernel weight	254.95**	20.99**	3.87	2.93
Grain yield	760.10**	235.04**	46.87	0.76
Percent fertility	6,235.60**	366.43**	36.40	3.76
Grain protein	41.70**	4.05**	0.36	2.24

** Significant at the 0.01 probability level. Degrees of freedom for GCA, SCA, and error mean squares are 11, 54, and 195, respectively.

Table 5. Estimates of GCA effects and parental means for five characters from a 12-parent winter wheat diallel cross.

Parent	Plant height		Kernel weight		Grain yield		Percent fertility		Grain protein	
	GCA effect	Mean	GCA effect	Mean	GCA effect	Mean	GCA effect	Mean	GCA effect	Mean
	cm		g/1,000 kernels		g/hill		%			
Atl 66	6.62	114.5	-0.25	27.8	1.50	25.8	4.88	133.5	0.29	17.9
F-V	-5.51	97.5	4.70	41.2	-1.28	36.6	-6.61	96.8	0.61	17.7
Dk582	5.54	117.5	-2.88	26.8	5.15	33.5	15.69	137.0	-0.65	17.2
Pm V	-7.81	85.0	-1.56	28.6	0.70	24.8	12.32	137.0	0.32	16.6
GKP	-6.61	92.5	3.00	35.0	0.40	27.6	-1.36	103.2	-0.02	16.6
322-Os	0.99	110.5	-1.87	27.5	-8.31	24.3	-8.54	117.4	0.95	16.6
Flex	2.87	109.5	0.99	28.1	-2.34	29.6	-27.30	104.7	1.87	15.6
Len	1.54	113.0	-0.13	33.3	1.30	45.9	10.29	138.0	-0.67	15.6
Bezo 1	-0.58	99.0	3.23	37.4	0.23	36.0	-2.51	100.9	-1.11	15.3
OK50	-3.01	94.0	-1.32	26.5	8.50	36.4	12.07	120.5	-1.55	15.1
D-NH	5.14	111.5	-3.37	18.1	-0.45	14.1	3.65	121.6	-1.03	15.1
GB88	0.82	113.0	-0.54	33.7	-5.40	41.1	-12.58	109.6	0.99	15.0
Mean		104.8		30.3		31.3		118.3		16.2
L.S.D. (0.05)		5.7		2.8		9.6		8.5		0.8
SE	0.91		0.44		1.53		1.35		0.13	

Table 6. Estimates of SCA effects and means for 17 F_1's from a 12-parent winter wheat diallel cross.

Entry	Plant height		Kernel weight		Grain yield		Percent fertility		Grain protein	
	SCA effect	Mean	SCA effect	Mean	SCA effect	Mean	SCA effect	Mean	SCA effect	Mean
	cm		g/1,000 kernels		g/hill		%			
1 GB88/Atl 66	5.22	125.3	1.15	36.4	0.18	33.3	3.80	106.4	0.65	17.8
2 Pm V/Atl 66	-0.91	110.5	0.90	35.1	4.32	43.6	0.11	127.6	0.10	16.5
3 OK50/Atl 66	0.79	117.0	0.33	34.8	12.85	59.9	1.66	128.9	0.86	15.4
4 F-V/D-NH	4.77	117.0	-0.22	37.1	9.06	44.4	5.57	112.9	0.17	15.6
5 F-V/Dk582	0.87	113.5	1.77	39.6	4.37	45.8	1.10	120.5	0.02	15.8
6 Bezo 1/F-V	-4.01	102.5	0.33	44.2	2.54	38.1	-5.07	96.1	0.39	15.7
7 GB88/Dk582	6.54	125.5	2.16	34.7	1.29	38.1	-6.46	107.0	0.42	16.6
8 Lcn/Dk582	-0.18	119.5	-0.64	32.3	5.41	48.9	-0.80	135.5	0.46	15.0
9 Bezo 1/Dk582	1.41	119.0	1.56	37.8	7.96	50.4	1.41	124.9	0.06	14.1
10 D-NH/GKP	-1.64	109.5	1.16	36.8	5.04	42.0	-3.55	109.0	0.31	15.1
11 OK50/322-Os	1.92	112.5	1.73	34.5	4.43	41.7	2.16	116.0	0.43	15.7
12 Lcn/GB88	-0.96	114.0	1.97	37.3	3.87	36.8	2.00	110.0	0.84	17.0
13 Flex/Atl 66	-2.58	119.5	-1.68	35.1	11.12	47.3	14.82	102.7	-0.78	17.2
14 Atl 66/Dk582	-0.26	124.5	-0.91	32.0	-5.34	38.4	-6.34	124.5	0.79	16.3
15 GB88/F-V	0.59	108.5	0.40	40.6	8.86	39.2	15.05	106.2	-1.47	16.0
16 GKP/322-Os	1.52	108.5	2.36	39.5	17.85	47.0	1.76	102.2	-0.72	16.0
17 Lcn/Flex	0.99	118.0	-1.74	35.1	1.62	37.6	5.99	99.3	-0.81	16.2
F_1 Mean		112.6		36.0		37.0		110.3		15.8
L.S.D. (0.05)		5.7		2.8		9.6		8.5		0.8
SE a ($\hat{s}_{ij} - \hat{s}_{ik}$)	2.74		1.32		4.59		4.05		0.40	
SE b ($\hat{s}_{ij} - \hat{s}_{kl}$)	2.58		1.24		4.33		3.82		0.38	

SE a is for comparison of F_1's having one parent in common; SE b is for comparison of F_1's having no parent in common.

Table 7. Comparisons of winter wheat parental, diallel array, and test cross means with test cross parental mean (presented as deviations from the test cross parental mean).

Parent	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	— cm —	g/1,000 kernels	g/hill	——— %	———
Atl 66					
Parent	13.0*	0.6	-9.0	-2.7	3.9*
Diallel array	17.1*	8.6*	3.6	-21.5*	2.1*
Test cross	11.5*	7.4*	15.8*	-6.3	0.7
F-V					
Parent	-4.0	14.0*	1.8	-39.4*	3.7*
Diallel array	6.1*	13.1*	1.1	-31.9*	2.4*
Test cross	3.0	12.6*	7.1	-18.9*	0.5
Dk582					
Parent	16.0*	-0.4	-1.3	0.8	3.2*
Diallel array	16.1*	6.2*	6.9*	-11.6*	1.2*
Test cross	14.5*	7.9*	11.8*	0.9	0.3
Pm V					
Parent	-16.5*	1.4	-10.0*	0.8	2.6*
Diallel array	4.0	7.4*	2.9	-14.7*	2.1*
Test cross	-2.0	3.1*	-3.3	-10.5*	0.6
GKP					
Parent	-9.0*	7.8*	-7.2	-33.0*	2.6*
Diallel array	5.1*	11.5*	2.6	-27.1*	1.8*
Test cross	5.5	8.6*	5.2	-8.7	-0.1
322-Os					
Parent	9.0*	0.3	-10.5*	-18.8*	2.6*
Diallel array	12.0*	7.1*	-5.3	-33.7*	2.7*
Test cross	8.0*	4.7*	-10.3*	-21.4*	1.6*
Flex					
Parent	8.0*	0.9	-5.2	-31.5*	1.6*
Diallel array	13.7*	9.7*	0.1	-50.7*	3.5*
Test cross	10.0*	5.1*	6.0	-19.7*	0.2
Lcn					
Parent	11.5*	6.1*	11.1*	1.8	1.6*
Diallel array	12.5*	8.7*	3.4*	-16.6*	1.2*
Test cross	12.5*	6.6*	17.2*	-7.3	0.1
Bezo 1					
Parent	-2.5	10.2*	1.2	-35.3*	1.3*
Diallel array	10.6*	11.7*	2.5	-28.2*	0.8*
Test cross	5.5	9.1*	5.3	-15.6*	-0.8
OK50					
Parent	-7.5*	-0.7	1.6	-15.7*	1.1*
Diallel array	8.4*	7.6*	10.0*	-14.9*	0.4
Test cross	2.5	7.0*	9.5*	-10.2*	-0.3
D-NH					
Parent	10.0*	-9.1*	-20.7*	-14.6*	1.1*
Diallel array	15.8*	5.7*	1.8	-22.6*	0.9*
Test cross	13.0*	4.8*	2.4	-23.1*	-0.1
GB88					
Parent	11.5*	6.5*	6.3	-26.6*	1.0*
Diallel array	11.8*	8.3*	-2.7	-37.3*	2.7*
Test cross	8.0*	10.8*	-0.5	-39.0*	1.6*
Test cross parental mean	101.5	27.2	34.8	136.2	14.0

* Significant at the 0.05 probability level.

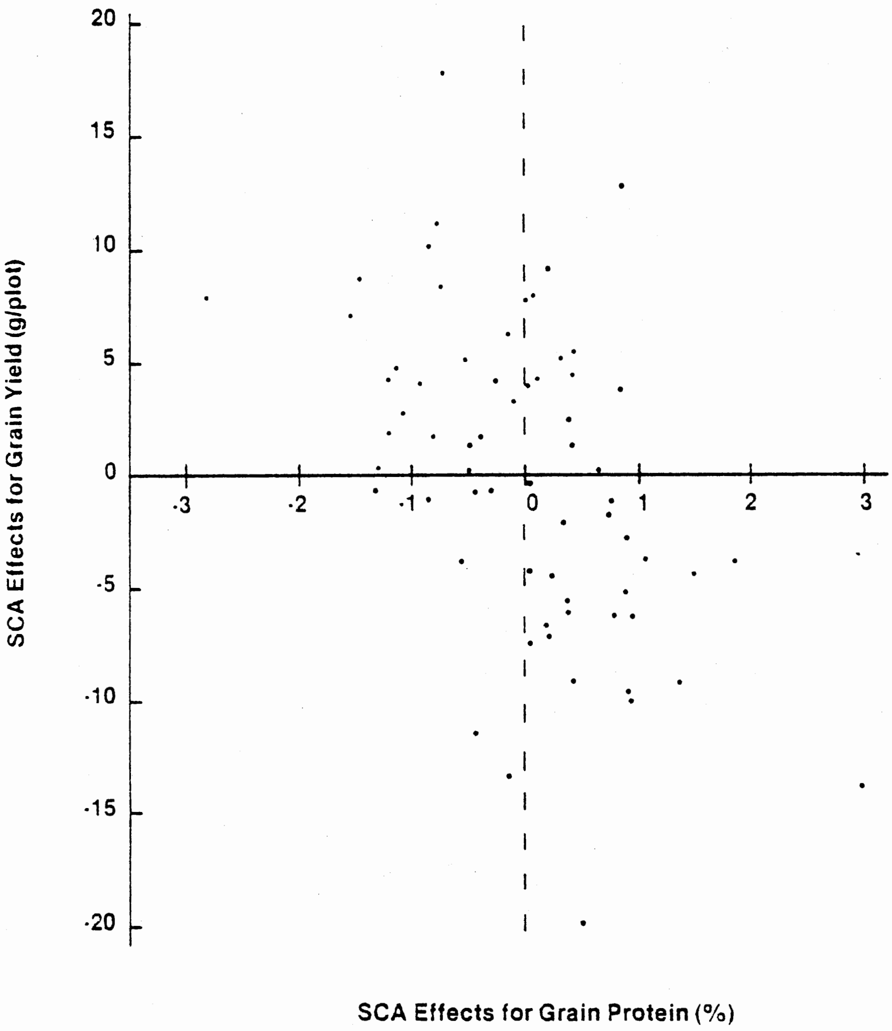

Fig. 1. SCA effects for grain yield vs. protein for 66 winter wheat diallel F_1's.

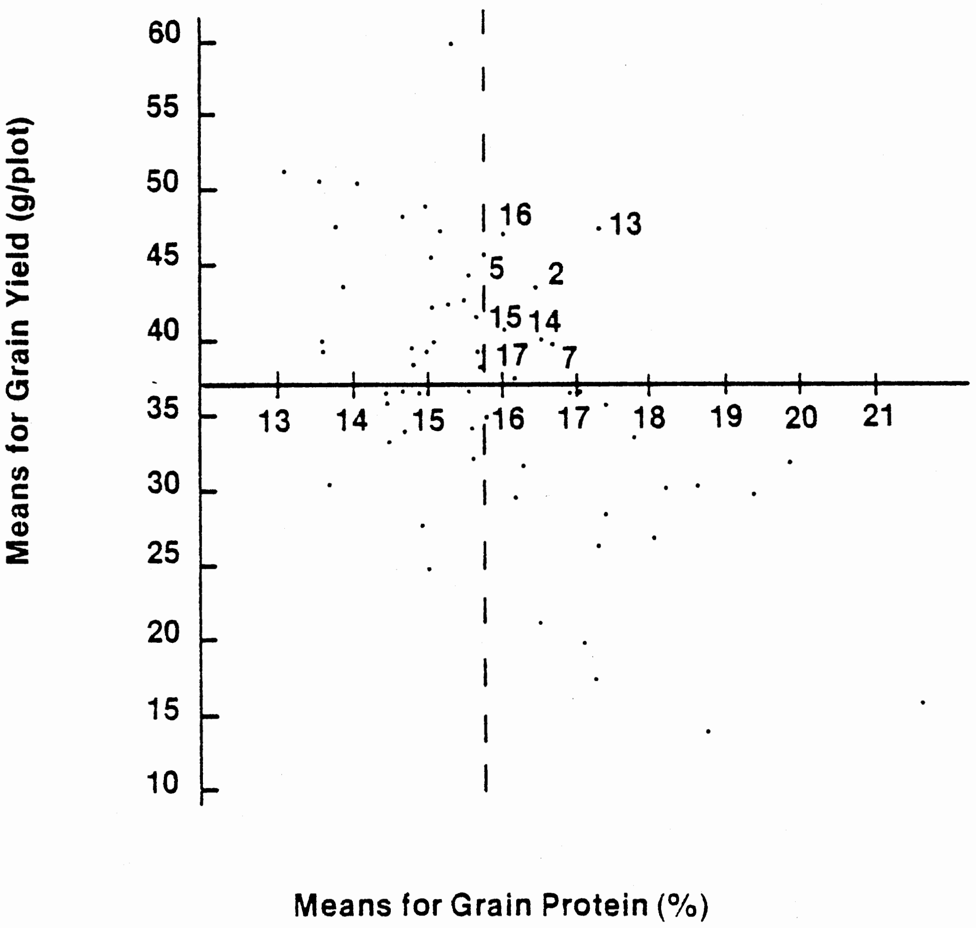

Fig. 2. Means for grain yield vs. protein for 66 winter wheat diallel F_1's.

PART IV

APPENDIX

(Tables 1 through 12)

Table 1. Response of grain protein and grain yield to high and low selection for grain protein in four grids in six winter wheat crosses.

		Grain protein			Grain yield		
		Prot. Sel. Group			Prot. Sel. Group		
Cross	Grid	High	Low	Diff.	High	Low	Diff.
		g			%		
Atl 66/Flex	A	18.0	17.1	0.9***	30.3	32.9	-2.6
	B	18.0	17.3	0.7***	27.5	30.5	-3.0
	C	18.2	17.0	1.2***	26.6	27.1	-0.5
	D	18.4	17.1	1.3***	26.2	29.1	-2.9
Over grids		18.2	17.1	1.1***	27.6	29.9	-2.3
Flex/D-NH	A	16.6	15.7	0.9**	24.0	33.2	-9.2**
	B	16.7	15.7	1.0**	25.5	27.6	-2.1
	C	17.3	15.5	1.8***	23.2	31.2	-8.0**
	D	16.7	16.4	0.3	30.8	25.0	5.8**
Over grids		16.8	15.8	1.0***	25.9	29.3	-3.4**
Atl 66/D-NH	A	18.0	17.1	0.9**	18.9	22.9	-4.0
	B	17.2	16.4	0.8**	29.2	29.1	0.1
	C	17.3	16.8	0.5*	23.7	24.1	-0.4
	D	18.0	16.5	1.5***	26.1	27.3	-1.2
Over grids		17.6	16.7	0.9***	24.5	25.9	-1.4
KS73114/Flex	A	15.4	15.3	0.1	29.6	32.6	-3.0
	B	14.9	14.0	0.9**	31.8	30.4	1.4
	C	16.0	15.1	0.9**	31.3	27.7	3.6**
	D	14.9	14.6	0.3	32.9	34.0	-1.1
Over grids		15.3	14.8	0.5***	31.4	31.1	0.3
KS73114/Atl 66	A	16.9	15.3	1.6***	36.2	37.1	-0.9
	B	16.2	15.8	0.4*	31.3	33.0	-1.7
	C	16.4	15.5	0.9***	36.0	37.9	-1.9
	D	16.9	15.4	1.5***	33.7	35.6	-1.9
Over grids		16.6	15.5	1.1***	34.3	35.9	-1.6*
KS73114/D-NH	A	15.6	14.0	1.6***	23.3	26.1	-2.8*
	B	15.5	14.7	0.8***	25.7	23.9	1.8
	C	15.0	14.2	0.8***	29.6	24.6	5.0
	D	15.4	15.3	0.1	25.1	22.3	2.8*
Over grids		15.4	14.5	0.9***	25.9	24.2	1.7*

*, **, *** Significant at the 0.1, 0.01, and 0.001 levels of probability, respectively.

Table 2. Mean squares of four characters of winter wheat for 21 diallel F_1's and 48 total entries from a seven-parent diallel cross.

			Mean squares			
Source		df	Kernel weight	Grain yield	Percent fertility	Grain protein
Rep	a	5	7.97	44.95	341.89**	0.99**
	b	5	19.79**	17.33	531.30**	2.87**
Entry	a	20	79.11**	523.29**	3,407.04**	17.30**
	b	47	153.38**	522.87**	3,329.00**	19.89**
Error	a	100	3.49	33.87	103.60	0.27
	b	235	4.92	45.09	75.55	0.30

** Significant at the 0.01 probability level. a = Analysis of variance of 21 diallel F_1's. b = Analysis of variance of 48 total entries.

Table 3. Means of six characters for parents, 21 diallel F_1's, and 14 test cross F_1's of a seven-parent diallel winter wheat cross.

Entry	Heading date	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	after 3/31	- cm -	g/1,000 kernels	g/hill	——— % ———	
Diallel parents						
Atl 66	42.17	117.33	29.78	31.60	139.58	18.3
F-V	35.83	97.33	42.28	32.78	96.73	17.6
Pm V	33.50	84.50	29.42	31.88	145.47	17.2
322-Os	35.83	110.33	26.93	26.06	124.18	16.4
Flex	43.67	112.50	28.90	32.50	94.32	16.1
D-NH	38.17	109.33	16.48	16.72	137.65	15.4
GB88	33.33	110.67	34.32	40.02	116.92	15.1
Mean	37.50	106.00	29.73	30.22	122.12	16.6
Diallel F_1's						
Atl 66/D-NH	36.33	125.67	34.37	44.42	119.70	15.7
Atl 66/F-V	36.67	113.33	41.85	34.69	108.62	17.4
Atl 66/Flex	42.33	119.00	34.07	41.62	107.73	17.7
Atl 66/Pm V	35.50	111.00	35.68	44.00	136.07	16.3
GB88/Atl 66	36.00	116.67	38.27	34.35	105.48	16.9
322-Os/Atl 66	41.17	117.67	29.85	10.99	93.27	19.8
F-V/D-NH	34.33	112.00	36.90	35.07	112.42	15.8
F-V/322-Os	36.33	109.83	41.13	36.53	93.82	18.4
Flex/F-V	36.67	110.67	42.20	32.01	82.28	18.6
GB88/F-V	34.00	104.67	40.57	41.75	103.00	16.4
Pm V/F-V	35.33	95.67	37.05	41.40	135.57	16.4
Pm V/D-NH	32.50	108.67	33.05	38.05	140.85	14.9
Pm V/Flex	37.17	108.33	40.27	29.81	77.98	19.9
Pm V/GB88	33.50	101.67	36.45	40.09	121.23	17.5
Pm V/322-Os	35.00	107.33	34.35	32.76	133.97	16.0
D-NH/322-Os	35.17	116.67	30.48	16.54	86.20	16.9
Flex/322-Os	39.33	115.83	35.15	39.82	101.03	16.9
GB88/322-Os	34.00	114.00	37.93	29.22	84.45	19.0
Flex/D-NH	42.17	115.33	34.18	29.32	75.95	18.5
Flex/GB88	36.17	113.33	31.17	13.82	45.43	21.6
D-NH/GB88	33.17	115.67	34.70	34.23	115.48	15.3
Mean	36.33	112.05	36.17	33.36	103.83	17.4
Test cross parents						
TX562	39.67	94.00	26.27	38.50	161.15	14.4
Ntn	38.33	97.00	28.68	44.30	144.30	13.7
Mean	39.00	95.5	27.48	41.4	152.73	14.1
Test cross F_1's						
Ntn/Atl 66	38.83	115.00	34.42	48.13	131.93	15.7
Ntn/F-V	36.00	105.33	37.95	43.49	115.35	15.1
Ntn/Pm V	37.00	94.00	33.18	39.25	141.95	15.2
Ntn/322-Os	38.50	111.00	30.32	37.21	133.48	14.5
Ntn/Flex	41.67	112.33	32.37	46.74	118.88	14.7
Ntn/D-NH	35.17	114.50	31.90	42.70	121.45	13.9
Ntn/GB88	35.50	110.00	38.67	41.16	102.08	16.3
Atl 66/TX562	39.33	116.33	34.80	54.64	143.75	14.8
TX562/F-V	36.17	99.67	37.03	46.30	125.97	14.6
TX562/Pm V	35.33	96.17	29.92	44.23	152.20	14.9
322-Os/TX562	37.67	106.33	35.23	31.66	123.20	15.0
TX562/Flex	40.67	107.00	41.87	38.71	85.28	16.2
D-NH/TX562	34.67	111.17	31.53	46.57	132.65	13.6
TX562/GB88	35.67	109.33	35.22	42.52	126.67	13.9
Mean	37.30	107.73	34.60	43.09	125.35	14.9

Table 4. Comparison of parental, diallel, and test cross array means for six characters from a seven-parent winter wheat diallel cross.

Parent	Heading date	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	days after 3/31	— cm —	g/1,000 kernels	g/hill	%	
Atl 66						
Parental mean	42.2	117.3	29.8	31.6	139.6	18.3
Diallel array mean	38.2	117.2	35.3	31.9	108.7	17.5
Test cross array mean	39.0	115.4	34.5	50.3	135.9	15.4
F-V						
Parental mean	35.8	97.3	42.3	32.8	96.7	17.6
Diallel array mean	35.6	107.1	40.1	37.1	106.5	17.2
Test cross array mean	36.1	102.5	37.5	44.9	120.7	14.8
Pm V						
Parental mean	33.5	84.5	29.4	31.9	145.5	17.2
Diallel array mean	34.9	106.2	36.1	38.6	126.0	16.8
Test cross array mean	36.2	95.1	31.6	41.7	147.1	15.0
322-Os						
Parental mean	35.8	110.3	26.9	26.1	124.2	16.4
Diallel array mean	36.4	113.2	35.3	29.2	99.3	17.6
Test cross mean	38.2	109.4	32.0	35.4	130.1	14.6
Flex						
Parental mean	43.7	112.5	28.9	32.5	94.3	16.1
Diallel array mean	39.2	113.7	36.4	32.2	84.5	18.8
Test cross array mean	41.2	109.7	37.1	42.7	102.1	15.4
D-NH						
Parental mean	38.2	109.3	16.5	16.7	137.7	15.4
Diallel array mean	35.9	115.6	34.2	34.5	110.0	16.2
Test cross mean	35.0	113.4	31.8	44.0	125.2	13.8
GB88						
Parental mean	33.3	110.7	34.3	40.0	116.9	15.1
Diallel array mean	34.4	110.7	35.7	31.3	95.3	17.9
Test Cross array mean	35.6	109.7	36.9	41.8	114.4	15.1
Test cross parent mean	39.0	95.5	27.5	41.4	152.7	14.1
L.S.D. (0.05)						
Parental vs. Diallel array	1.0	3.1	1.9	5.7	7.4	0.5
Parent vs. Test cross array	1.2	3.5	2.2	6.6	8.5	0.5
Diallel vs. Test cross array	0.8	2.3	1.4	4.3	5.6	0.4

Table 5. Means and standard deviations for kernels/spike for F_2's and parents from a seven-parent winter wheat diallel cross.

Entry	Stillwater	Lahoma	Avg.
	number		
$\underline{F_2}$			
D-NH/Pm V	34.6 ± 6.6	37.6 ± 9.7	36.1 ± 8.3
F-V/D-NH	35.0 ± 6.7	34.5 ± 7.8	34.7 ± 7.3
D-NH/Atl 66	36.1 ± 6.5	32.5 ± 6.8	34.3 ± 6.7
Pm V/Atl 66	36.7 ± 8.8	30.4 ± 6.7	33.5 ± 7.8
F-V/Pm V	33.4 ± 5.3	32.6 ± 7.2	33.0 ± 6.3
F-V/Atl 66	35.5 ± 7.5	29.5 ± 5.8	32.5 ± 6.7
GB88/Pm V	30.7 ± 6.5	33.3 ± 5.8	32.0 ± 6.2
Flex/D-NH	30.7 ± 9.1	31.5 ± 9.3	31.1 ± 9.2
GB88/D-NH	30.6 ± 7.0	31.0 ± 5.5	30.8 ± 6.3
322-Os/D-NH	32.4 ± 6.1	28.0 ± 9.3	30.2 ± 7.9
Pm V/Flex	28.2 ± 5.1	31.7 ± 6.6	29.9 ± 5.9
GB88/F-V	28.6 ± 4.8	30.9 ± 6.1	29.7 ± 5.5
322-Os/Atl 66	32.9 ± 6.3	25.9 ± 5.4	29.4 ± 5.9
GB88/Atl 66	29.2 ± 4.3	29.0 ± 8.3	29.1 ± 6.6
322-Os/Pm V	31.9 ± 4.5	25.4 ± 8.4	28.6 ± 6.7
322-Os/F-V	27.3 ± 8.2	27.3 ± 6.9	27.3 ± 7.6
Flex/Atl 66	30.3 ± 5.1	24.2 ± 4.3	27.2 ± 4.7
F-V/Flex	25.3 ± 6.8	25.9 ± 4.7	25.6 ± 5.8
322-Os/Flex	27.6 ± 5.9	23.0 ± 6.6	25.3 ± 6.3
Mean	31.4	29.7	30.5
<u>Parents</u>			
D-NH	39.6 ± 7.1	34.1 ± 10.2	36.8 ± 8.8
Atl 66	38.0 ± 7.2	30.8 ± 9.4	34.4 ± 8.4
Pm V	31.0 ± 5.7	30.6 ± 5.3	30.8 ± 5.5
GB88	28.6 ± 5.3	27.7 ± 4.9	28.2 ± 5.1
F-V	26.6 ± 5.5	28.1 ± 5.5	27.3 ± 5.5
322-Os	29.6 ± 6.0	24.9 ± 7.2	27.2 ± 6.6
Flex	26.6 ± 6.0	25.7 ± 5.7	26.2 ± 5.2
Mean	31.4	28.8	30.1
L.S.D. (0.05)	14.8	13.7	9.9

Table 6. Means and standard deviations for kernel weight for F_2's and parents from a seven-parent winter wheat diallel cross.

Entry	Stillwater	Lahoma	Avg.
	g/1,000 kernels		
F_2			
GB88/F-V	34.6 ± 3.5	28.6 ± 4.3	31.6 ± 3.9
Pm V/Flex	33.6 ± 5.2	27.7 ± 5.1	30.6 ± 5.2
F-V/Flex	32.8 ± 5.0	27.8 ± 3.7	30.3 ± 4.4
F-V/Pm V	34.4 ± 3.8	24.0 ± 3.8	29.2 ± 3.8
GB88/D-NH	30.8 ± 3.8	27.5 ± 2.7	29.2 ± 3.3
F-V/Atl 66	32.1 ± 7.4	26.1 ± 4.6	29.1 ± 6.2
322-Os/Pm V	32.9 ± 4.1	24.7 ± 5.2	28.8 ± 4.7
GB88/Atl 66	32.8 ± 4.2	24.8 ± 3.7	28.8 ± 4.0
322-Os/F-V	32.0 ± 5.9	25.1 ± 5.9	28.6 ± 5.9
322-Os/Flex	31.6 ± 4.8	24.2 ± 4.3	27.9 ± 4.5
Flex/Atl 66	29.9 ± 4.1	25.6 ± 3.2	27.8 ± 3.7
GB88/Pm V	27.8 ± 3.4	25.3 ± 3.7	26.6 ± 3.6
D-NH/Atl 66	30.4 ± 5.4	21.1 ± 4.3	25.8 ± 4.9
Pm V/Atl 66	29.5 ± 5.5	21.6 ± 4.8	25.6 ± 5.2
D-NH/Pm V	29.6 ± 3.4	21.2 ± 3.8	25.4 ± 3.7
F-V/D-NH	26.9 ± 7.0	23.5 ± 4.2	25.2 ± 5.8
322-Os/Atl 66	29.0 ± 4.7	21.3 ± 4.7	25.1 ± 4.7
Flex/D-NH	27.3 ± 5.4	21.6 ± 4.7	24.4 ± 5.1
322-Os/D-NH	26.7 ± 4.9	18.9 ± 5.0	22.8 ± 5.0
Mean	30.8	24.2	27.5
Parents			
F-V	38.3 ± 6.6	27.1 ± 5.5	32.7 ± 6.1
GB88	33.0 ± 2.1	28.5 ± 2.6	30.8 ± 2.4
Pm V	25.2 ± 3.1	20.1 ± 3.4	22.6 ± 3.3
Flex	25.4 ± 3.2	19.1 ± 3.5	22.3 ± 3.3
322-Os	23.9 ± 2.0	19.6 ± 2.4	21.7 ± 2.2
Atl 66	24.5 ± 5.6	17.5 ± 3.9	21.0 ± 4.8
D-NH	14.1 ± 3.0	11.6 ± 2.6	12.8 ± 2.8
Mean	26.3	20.5	23.4
L.S.D. (0.05)	12.2	8.7	7.4

Table 7. Means for grain yield for F_2's and parents from a seven-parent diallel winter wheat cross.

Entry	Stillwater	Lahoma	Avg.
	g/plot		
F_2			
F-V/Pm V	143.7	90.6	117.1
Pm V/Flex	122.9	101.1	112.0
GB88/F-V	128.6	85.3	107.0
F-V/Flex	122.0	85.5	103.7
Flex/Atl 66	125.6	75.7	100.6
D-NH/Pm V	117.2	76.1	96.6
GB88/Pm V	107.6	81.5	94.5
Pm V/Atl 66	127.2	55.3	91.3
GB88/D-NH	100.7	78.0	89.4
GB88/Atl 66	107.9	68.8	88.3
F-V/Atl 66	123.2	46.8	85.0
322-Os/Pm V	108.0	57.9	82.9
322-Os/Flex	99.7	55.6	77.7
Flex/D-NH	93.8	52.3	73.0
322-Os/F-V	99.6	45.4	72.5
D-Nh/Atl 66	103.8	38.9	71.4
322-Os/Atl 66	104.5	37.5	71.0
F-V/D-NH	82.0	59.3	70.6
322-Os/D-NH	90.8	38.8	64.8
Mean	111.0	64.8	87.9
Parents			
GB88	133.0	100.0	116.5
F-V	106.6	66.4	86.5
Flex	93.3	53.9	73.6
Pm V	86.1	57.9	72.0
322-Os	87.8	47.6	67.7
Atl 66	99.8	15.9	57.9
D-NH	57.5	18.5	38.0
Mean	94.9	51.5	73.2
L.S.D. (0.05)	24.3	16.4	14.4

Table 8. Means and standard deviations for percent fertility for F_2's and parents from a seven-parent winter wheat diallel cross.

Entry	Stillwater	Lahoma	Avg.
		%	
F_2			
D-NH/Pm V	121.1 ± 14.4	119.3 ± 21.3	120.2 ± 18.2
Pm V/Atl 66	123.6 ± 20.9	104.2 ± 18.4	113.9 ± 19.7
F-V/Pm V	116.1 ± 16.0	111.3 ± 20.8	113.7 ± 18.5
F-V/D-NH	105.3 ± 16.4	109.5 ± 20.3	107.4 ± 18.4
D-NH/Atl 66	107.6 ± 13.8	102.7 ± 18.5	105.2 ± 16.3
Pm V/Flex	104.1 ± 12.3	105.0 ± 18.7	104.5 ± 15.9
GB88/Pm V	103.2 ± 14.6	105.2 ± 15.8	104.2 ± 15.2
F-V/Atl 66	109.0 ± 15.5	94.0 ± 16.1	101.5 ± 15.8
GB88/D-NH	102.9 ± 18.3	96.6 ± 13.3	99.7 ± 16.0
322-Os/Pm V	107.9 ± 13.9	88.7 ± 23.9	98.3 ± 19.5
GB88/F-V	95.3 ± 11.1	101.1 ± 14.8	98.2 ± 13.1
GB88/Atl 66	95.4 ± 12.5	95.6 ± 21.0	95.5 ± 17.3
322-Os/Atl 66	103.0 ± 17.1	82.0 ± 17.8	92.5 ± 17.5
322-Os/D-NH	96.9 ± 16.0	87.0 ± 24.0	91.9 ± 20.4
322-Os/F-V	91.6 ± 21.1	92.3 ± 16.0	91.9 ± 18.8
Flex/Atl 66	95.2 ± 14.7	87.2 ± 11.5	91.2 ± 13.2
Flex/D-NH	88.4 ± 19.6	93.6 ± 18.3	91.0 ± 19.0
F-V/Flex	84.1 ± 18.8	87.3 ± 11.4	85.7 ± 15.6
322-Os/Flex	86.3 ± 12.5	78.2 ± 18.1	82.3 ± 15.6
Mean	101.9	96.9	99.4
Parents			
Pm V	127.8 ± 13.5	115.2 ± 19.2	121.5 ± 16.6
D-NH	113.5 ± 15.9	101.6 ± 25.9	107.6 ± 21.5
Atl 66	118.4 ± 18.6	93.7 ± 20.5	106.0 ± 19.6
GB88	103.4 ± 12.1	93.7 ± 12.0	98.5 ± 12.1
322-Os	105.1 ± 15.0	88.1 ± 19.8	96.6 ± 17.6
F-V	91.6 ± 11.8	97.3 ± 13.1	94.4 ± 12.5
Flex	84.4 ± 13.7	87.0 ± 12.1	85.7 ± 12.9
Mean	106.3	96.7	101.5
L.S.D. (0.05)	37.0	33.1	24.4

Table 9. Means for percent protein for F_2's and parents from a seven-parent winter wheat diallel cross.

Entry	Stillwater	Lahoma	Avg.
		%	
F_2			
322-Os/Atl 66	18.0	19.6	18.8
F-V/Flex	18.5	17.9	18.2
322-Os/Pm V	17.8	18.3	18.0
322-Os/Flex	17.7	18.3	18.0
Flex/Atl 66	17.6	18.3	18.0
F-V/Atl 66	17.5	18.4	17.9
322-Os/F-V	17.3	18.5	17.9
GB88/Atl 66	17.9	17.9	17.9
GB88/Pm V	17.7	17.6	17.6
Pm V/Atl 66	16.8	18.3	17.5
Pm V/Flex	17.4	17.3	17.3
Flex/D-NH	16.2	18.5	17.3
F-V/Pm V	16.8	17.7	17.3
F-V/D-NH	16.6	17.3	16.9
GB88/F-V	16.3	17.3	16.8
D-NH/Atl 66	16.0	17.5	16.7
GB88/D-NH	16.2	17.1	16.6
322-Os/D-NH	15.4	17.7	16.5
D-NH/Pm V	15.1	17.1	16.1
Mean	17.0	17.9	17.4
Parents			
Atl 66	18.4	21.1	19.7
Flex	17.8	19.2	18.5
F-V	18.0	17.9	17.9
Pm V	17.4	18.5	17.9
D-NH	17.0	17.9	17.4
322-Os	17.1	17.0	17.0
GB88	15.2	15.5	15.3
Mean	17.3	18.2	17.7
L.S.D. (0.05)	0.7	0.7	0.5

Table 10. Means of five characters for parents, 66 diallel F_1's, and 12 test cross F_1's from a 12-parent winter wheat diallel cross.

Entry	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	– cm –	g/1,000 kernels	g/hill	%	
Diallel F_1's					
Flex/Atl 66	119.5	35.1	47.3	102.7	17.2
D-NH/Atl 66	125.0	35.0	24.7	113.0	15.0
GB88/Atl 66	125.3	36.4	33.3	106.4	17.8
322-Os/Atl 66	121.5	30.4	28.0	105.3	17.4
Pm V/Atl 66	110.5	35.1	43.6	127.6	16.5
F-V/Atl 66	108.5	41.9	17.3	99.9	17.2
OK50/Atl 66	117.0	34.8	59.9	128.9	15.4
Lcn/Atl 66	121.0	34.1	48.2	121.9	14.7
Atl 66/GKP	114.0	39.3	38.2	120.0	15.7
Atl 66/Dk582	124.5	32.0	38.4	124.5	16.3
Bezo 1/Atl 66	118.0	39.5	43.5	111.9	13.9
Flex/F-V	111.5	41.9	29.6	71.3	19.4
F-V/D-NH	117.0	37.1	44.4	112.9	15.6
GB88/F-V	108.5	40.6	39.2	106.2	16.0
322-Os/F-V	110.5	40.4	35.4	95.2	17.4
F-V/Pm V	101.0	34.9	36.8	119.9	15.5
F-V/OK50	106.5	37.6	39.8	119.1	15.1
Lcn/F-V	111.5	43.4	42.2	112.1	15.3
F-V/GKP	92.5	41.4	26.1	94.1	17.3
F-V/Dk582	113.5	39.6	45.8	120.5	15.8
Bezo 1/F-V	102.5	44.2	38.1	96.1	15.7
Flex/Dk582	119.5	32.3	39.1	113.3	15.7
D-NH/Dk582	117.0	25.8	30.3	122.2	13.7
GB88/Dk582	125.5	34.7	38.1	107.0	16.6
322-Os/Dk582	118.0	28.8	29.6	125.9	16.2
Pm V/Dk582	108.5	31.1	42.6	140.5	15.5
OK50/Dk582	114.0	34.7	50.6	132.2	13.6
Lcn/Dk582	119.5	32.3	48.9	135.5	15.0
GKP/Dk582	115.0	38.0	45.3	123.8	15.1
Bezo 1/Dk582	119.0	37.8	50.4	124.9	14.1
Flex/Pm V	105.5	39.3	31.6	69.0	19.9
Flex/D-NH	120.5	33.3	29.9	80.6	18.2
GB88/Pm V	104.0	34.5	36.5	117.9	16.9
Pm V/322-Os	104.5	34.6	26.6	104.1	18.0
OK50/Pm V	97.5	33.5	39.1	132.7	14.8
Lcn/Pm V	106.5	35.8	39.1	137.3	15.0
Pm V/GKP	103.0	32.5	31.6	125.1	16.3
Bezo 1/GKP	102.5	41.9	31.9	95.7	15.6
Flex/GKP	112.5	44.2	30.0	73.8	18.6
D-NH/GKP	109.5	36.8	42.0	109.0	15.1
GB88/GKP	102.5	35.8	33.9	105.3	15.6
GKP/322-Os	108.5	39.5	47.0	102.2	16.0
OK50/GKP	104.0	38.6	47.4	125.5	13.8
Lcn/GKP	108.5	38.0	38.1	125.2	14.8
Bezo 1/GKP	102.5	41.9	31.9	95.7	15.6
Flex/322-Os	109.0	34.1	34.4	99.6	15.8
322-Os/D-NH	119.0	29.1	27.2	105.0	14.9
322-Os/GB88	113.5	37.3	13.7	72.8	18.7
OK50/322-Os	112.5	34.5	41.7	116.0	15.7
322-Os/Lcn	115.0	31.7	21.0	111.2	16.5
322-Os/Bezo 1	116.5	36.9	19.8	90.6	17.1
Flex/D-NH	120.5	33.3	29.9	80.6	18.2
Flex/GB88	116.5	31.5	15.4	41.2	21.6
OK50/Flex	116.5	36.4	47.2	98.2	15.2
Lcn/Flex	118.0	35.1	37.6	99.3	16.2
Bezo 1/Flex	118.3	42.6	42.0	91.4	15.1
Lcn/D-NH	120.5	32.7	36.2	126.9	14.9
Lcn/GB88	114.0	37.3	36.8	110.0	17.0
Lcn/OK50	106.0	34.0	39.3	127.3	13.6
Lcn/Bezo 1	113.5	40.2	33.1	109.5	14.5
Bezo 1/D-NH	115.5	36.4	35.7	113.4	14.5
Bezo 1/GB88	110.5	38.2	36.3	101.9	14.5
OK50/Bezo 1	109.5	35.0	39.7	121.0	13.6
OK50/D-NH	116.0	30.7	51.3	125.2	13.1
OK50/GB88	109.0	32.9	36.4	107.8	14.7
GB88/D-NH	117.5	31.4	33.8	111.1	14.7
Mean	112.6	36.0	37.0	110.3	15.8

Table 10. Continued.

Entry	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	— cm —	g/1,000 kernels	g/hill	——— % ———	
Diallel parents					
Atl 66	114.5	27.8	25.8	133.5	17.9
F-V	97.5	41.2	36.6	96.8	17.7
Dk582	117.5	26.8	33.5	137.0	17.2
Pm V	85.0	28.6	24.8	137.0	16.6
GKP	92.5	35.0	27.6	103.2	16.6
322-Os	110.5	27.5	24.3	117.4	16.6
Flex	109.5	28.1	29.6	104.7	15.6
Lcn	113.0	33.3	45.9	138.0	15.6
Bezo 1	99.0	37.4	36.0	100.9	15.3
OK50	94.0	26.5	36.4	120.5	15.1
D-NH	111.5	18.1	14.1	121.6	15.1
GB88	113.0	33.7	41.1	109.6	15.0
Mean	104.8	30.3	31.3	118.3	16.2
Test cross F_1's					
Ntn/Atl 66	113.0	34.6	50.6	129.9	14.7
F-V/Ntn	104.5	39.8	41.9	117.3	14.5
Ntn/Dk582	116.0	35.1	46.6	137.1	14.3
Ntn/Pm V	99.5	30.3	31.5	125.7	14.6
Ntn/GKP	107.0	35.8	40.0	127.5	13.9
322-Os/Ntn	109.5	31.9	24.5	114.8	15.6
Ntn/Flex	111.5	32.3	40.8	116.5	14.2
Ntn/Lcn	114.0	33.8	52.0	128.9	14.1
Ntn/Bezo 1	107.0	36.3	40.1	120.6	13.2
Ntn/OK50	104.0	34.2	44.3	126.0	13.7
Ntn/D-NH	114.5	32.0	37.2	113.1	13.9
Ntn/GB88	109.5	38.0	34.3	97.2	15.6
Mean	109.2	34.5	40.3	121.2	14.4
Test cross parent					
Ntn	101.5	27.2	34.8	136.2	14.0

Table 11. Comparison of parental, diallel array, and test cross means for five characters of a 12-parent winter wheat diallel cross.

Parent	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	— cm —	g/1,000	g/hill	——— %	———
Atl 66					
Parental mean	114.5	27.8	25.8	133.5	17.9
Diallel array mean	118.6	35.8	38.4	114.7	16.1
Test cross mean	113.0	34.6	50.6	129.9	14.7
F-V					
Parental mean	97.5	41.2	36.6	96.8	17.7
Diallel array mean	107.6	40.3	35.9	104.3	16.4
Test cross mean	104.5	39.8	41.9	117.3	14.5
Dk582					
Parental mean	117.5	26.8	33.5	137.0	17.2
Diallel array mean	117.6	33.4	41.7	124.6	15.2
Test cross mean	116.0	35.1	46.6	137.1	14.3
Pm V					
Parental Mean	85.0	28.6	24.8	137.0	16.6
Diallel array mean	105.5	34.6	37.7	121.5	16.1
Test cross mean	99.5	30.3	31.5	125.7	14.6
GKP					
Parental mean	92.5	35.0	27.6	103.2	16.6
Diallel array mean	106.6	38.7	37.4	109.1	15.8
Test cross array	107.0	35.8	40.0	127.5	13.9
322-Os					
Parental mean	110.5	27.5	24.3	117.4	16.6
Diallel array mean	113.5	34.3	29.5	102.5	16.7
Test cross mean	109.5	31.9	24.5	114.8	15.6
Flex					
Parental mean	109.5	28.1	29.6	104.7	15.6
diallel array mean	115.2	36.9	34.9	85.5	17.5
Test cross mean	111.5	32.3	40.8	116.5	14.2
Lcn					
Parental mean	113.0	33.3	45.9	138.0	15.6
Diallel array mean	114.0	35.9	38.2	119.6	15.2
Test cross mean	114.0	33.8	52.0	128.9	14.1
Bezo 1					
Parental mean	99.0	37.4	36.0	100.9	15.3
Diallel array mean	112.1	38.9	37.3	108.0	14.8
Test cross mean	107.0	36.3	40.1	120.6	13.2
OK50					
Parental Mean	94.0	26.5	36.4	120.5	15.1
Diallel array mean	109.9	34.8	44.8	121.3	14.4
Test cross mean	104.0	34.2	44.3	126.0	13.7
D-NH					
Parental mean	111.5	18.1	14.1	121.6	15.1
Diallel array mean	117.3	32.9	36.6	113.6	14.9
Test cross mean	114.5	32.0	37.2	113.1	13.9
GB88					
Parental mean	113.0	33.7	41.1	109.6	15.0
Diallel array mean	113.3	35.5	32.1	98.9	16.7
Test cross mean	109.5	38.0	34.3	97.2	15.6
Test cross parental mean	101.5	27.2	34.8	136.2	14.0
L.S.D. (0.05)					
Parental vs. Diallel array $\bar{x}$	4.2	2.1	6.8	6.4	0.6
Parental vs. Test cross $\bar{x}$	5.7	2.9	9.2	8.7	0.8
Diallel array vs. Test cross $\bar{x}$	4.2	2.1	6.8	6.4	0.6

Table 12. Estimates of SCA effects for five characters for 66 F_1's from a 12-parent winter wheat diallel cross.

Entry	Plant height	Kernel weight	Grain yield	Percent fertility	Grain protein
	– cm –	g/1,000 kernels	g/hill	%	
Flex/Atl 66	-2.58	-1.68	11.12	14.82	-0.78
D-NH/Atl 66	0.64	2.66	-13.37	-5.85	-0.13
GB88/Atl 66	5.22	1.15	0.18	3.30	0.65
322-Os/Atl 66	1.29	-3.47	-2.19	-1.31	0.32
Pm V/Atl 66	-0.91	0.90	4.32	0.11	0.10
F-V/Atl 66	-5.21	1.46	-19.97	-8.69	0.50
OK50/Atl 66	0.79	0.33	12.85	1.66	0.86
Lcn/Atl 66	0.24	-1.50	8.40	-3.59	-0.74
Atl 66/GKP	1.39	0.54	-0.70	6.16	-0.42
Atl 66/Dk582	-0.26	-0.91	-5.34	-6.34	0.79
Bezo 1/Atl 66	-0.61	0.52	4.70	-0.77	-1.15
Flex/F-V	1.54	0.20	-3.80	-5.08	1.05
F-V/D-NH	4.77	-0.22	9.06	5.57	0.17
GB88/F-V	0.59	0.40	8.86	15.05	-1.47
322-Os/F-V	2.42	1.53	7.94	0.01	0.00
F-V/Pm V	1.72	-4.25	0.37	3.91	-1.27
F-V/OK50	2.42	-1.80	-4.46	3.36	0.21
Lcn/F-V	2.37	2.87	5.13	-1.92	-0.51
F-V/GKP	-7.98	-2.29	-10.04	-8.24	0.91
F-V/Dk582	0.87	1.77	4.37	1.10	0.02
Bezo 1/F-V	-4.01	0.33	2.54	-5.07	0.39
Flex/Dk582	-1.51	-1.82	-0.78	14.56	-1.31
D-NH/Dk582	-6.28	-3.96	-11.47	-7.43	-0.44
GB88/Dk582	6.54	2.16	1.29	-6.46	0.42
322-Os/Dk582	-1.13	-2.41	-4.25	8.41	0.06
Pm V/Dk582	-1.33	-0.47	-0.32	2.23	0.04
OK50/Dk582	-1.13	2.91	-0.06	-5.90	0.00
Lcn/Dk582	-0.18	-0.64	5.41	-0.80	0.46
GKP/Dk582	3.50	1.81	3.19	-0.78	-0.10
Bezo 1/Dk582	1.41	1.56	7.96	1.41	0.06
Flex/Pm V	-2.16	3.89	-3.83	-26.33	1.85
Flex/D-NH	2.57	2.77	10.18	4.20	-0.85
GB88/Pm V	-1.61	0.59	4.16	7.90	-0.25
Pm V/322-Os	-1.28	2.05	-2.81	-9.94	0.39
OK50/Pm V	-4.28	0.37	-7.15	-1.97	0.21
Lcn/Pm V	0.17	1.46	0.01	4.43	-0.51
Pm V/GKP	4.82	-4.90	-6.57	3.83	0.19
Bezo 1/GKP	2.79	-2.41	1.64	11.63	-0.40
Flex/GKP	3.64	4.20	-5.11	-7.36	0.38
D-NH/GKP	-1.64	1.16	5.04	-3.55	0.31
GB88/GKP	-4.31	-2.64	1.88	8.90	-1.21
GKP/322-Os	1.52	2.36	17.85	1.76	-0.72
OK50/GKP	1.02	0.91	1.44	4.53	-0.48
Lcn/GKP	0.97	-0.90	-0.61	6.00	-0.30
Bezo 1/GKP	-2.93	-0.25	-6.37	-10.75	0.94
Flex/322-Os	-7.46	-1.03	7.97	25.17	-2.83
322-Os/D-NH	0.27	-1.67	-1.06	-0.40	-0.86
322-Os/GB88	-0.91	3.68	-9.63	-16.37	0.92
OK50/322-Os	1.92	1.73	4.43	2.16	0.43
322-Os/Lcn	-0.13	-2.28	-9.06	-0.34	0.41
322-Os/Bezo 1	3.49	-0.49	-9.19	-8.65	1.38
Flex/D-NH	-0.11	-0.28	-4.40	-6.07	1.49
Flex/GB88	0.22	-4.91	-13.87	-29.24	2.95
OK50/Flex	4.04	0.77	4.02	3.14	-0.94
Lcn/Flex	0.99	-1.74	1.62	5.99	-0.81
Bezo 1/Flex	3.39	2.40	7.06	10.90	-1.55
Lcn/D-NH	1.22	0.17	-1.73	2.67	0.74
Lcn/GB88	-0.96	1.97	3.87	2.00	0.84
Lcn/OK50	-5.13	-0.53	-7.51	-5.35	0.03
Lcn/Bezo 1	-0.06	1.12	-5.53	-8.59	0.39
Bezo 1/D-NH	-1.65	0.59	-1.10	1.98	0.78
Bezo 1/GB88	-2.31	-0.50	4.37	6.71	-1.22
OK50/Bezo 1	0.49	-2.87	-6.08	1.20	0.38
OK50/D-NH	1.27	-0.57	6.24	-0.33	-0.14
OK50/GB88	-1.41	-1.25	-3.72	-2.00	-0.56
GB88/D-NH	-1.06	-0.65	2.61	9.71	-1.07
SE a ($\hat{s}_{ij} - \hat{s}_{ik}$)	2.74	1.32	4.59	4.05	0.40
SE b ($\hat{s}_{ij} - \hat{s}_{kl}$)	2.58	1.24	4.33	3.82	0.38

SE a is for comparison of F_1's having one parent in common; SE b is for comparison of F_1's having no parent in common.

VITA

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