

COMBINING ABILITY ANALYSIS OF YIELD AND YIELD
COMPONENTS INVOLVING SIX WINTER WHEAT
ALIEN-TRANSLOCATION LINES

By

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CHAPTER I

INTRODUCTION

Leaf rust, stem rust, and stripe rust have long been major disease problems of wheat, (Triticum aestivum L. em. Thell.) and have caused substantial losses in yield and quality. Many of the relatives of wheat contain genes which impart resistance to these disease problems. In order to incorporate this resistance into wheat, attempts have been made to transfer specific genes from related species to wheat. With the aid of irradiation or meiotic control, several translocations between wheat chromatin and a segment of alien chromatin carrying the desired gene(s) have been successfully induced.

Because the transfer of alien genes is not a precise procedure, it is rare that a single gene transfer takes place. More often the portion of alien chromatin is sufficiently large to contain genes conditioning other effects. Many of these additional effects may be eliminated by successive generations of backcrossing to wheat. In other instances, valuable portions of wheat chromatin may be lost during the transfer process, leading to undesirable effects. The alien chromatin may, however, compensate at least in part for this loss.

At present, several alien translocation lines conditioning resistance to various pests are available for use in wheat breeding programs. Consequently, the possibility exists for the combination of two or more alien translocations into the same genotype imparting

multiple-pest resistance.

Due to the presence of additional genes, two translocations, when combined in certain genetic backgrounds, may result in an F_1 exhibiting inherent vigor. On the other hand, if two translocations, each missing portions of valuable wheat chromatin, are united, a decline in vigor of the F_1 may result. This increase or reduction in vigor may be noted by measuring agronomically and economically important characters.

The objective of this research was to study the magnitude of vigor on eight performance traits in the F_1 's and parents of a diallel cross involving six alien-translocation lines.

CHAPTER II

LITERATURE REVIEW

Several of the relatives of wheat contain genes conditioning desirable features such as disease and insect resistance. Resistance to the rusts and powdery mildew may be found in Secale, and in several of the Aegilops species. The Agropyrons are noted for resistance to all three wheat rusts, wheat streak mosaic virus, and bunt (13). The incorporation of such desirable characters into wheat would be of great potential value in breeding programs.

Wheat is an allohexaploid composed of A, B, and D genomes each containing seven pairs of chromosomes. Due to this hexaploid nature, unique opportunities exist for the introduction of desirable alien variation. According to Kimber (9), the relationship of the alien chromosome carrying the desired gene(s) to the chromosome(s) of wheat must be the basic consideration in any attempt to introduce such variation. If a normal relationship exists between the two chromosomes, the alien character may be transferred by normal hybridization. Knott (13) further adds that a diploid species carrying one of the A, B, or D genomes can either be crossed directly with common wheat or first to a tetraploid and later to a hexaploid.

Besides this normal introgression of alien genes into the wheat genome through hybridization, there are two other means of introducing alien variation. If the species is not closely related to wheat, the

transfer process can be accomplished either by irradiation or meiotic control (13). Sears (16) was the first to describe an irradiation technique used to transfer leaf rust resistance from Aegilops umbellulata to Triticum aestivum. Leaf rust resistant plants carrying an added Aegilops umbellulata isochromosome were X-rayed just prior to meiosis. The treated pollen was then used to pollinate emasculated spikes of normal 'Chinese Spring' wheat. Resistant F_1 plants were examined for the presence of a translocation between the Aegilops chromosome and a wheat chromosome. Seventeen translocations were obtained, but only one was transmitted normally through the pollen. This translocation was later named "Transfer".

Since this pioneering work by Sears, Knott (10) and several other workers have used similar techniques to successfully transfer alien genes to wheat. The success of Knott's program of transferring stem rust resistance from Agropyron elongatum was attributed to two reasons: 1. Since wheat is a allohexaploid, it can stand the loss of up to a whole chromosome without serious deleterious effects; and, 2. the added Agropyron chromatin had no serious effects except on the gametes. He also found that in families segregating for one of the translocations, resistant and susceptible sibs showed no observable difference. Both X-rays and thermal neutrons were used by Sharma and Knott (20) to translocate a segment of the Agropyron chromosome contained in a wheat-like Agropyron derivative, "Agrus", to wheat. One translocation on chromosome 7D appeared to have no detrimental effects and was normally transmitted through the gametes. This translocation is now known as "Agatha".

Not only have Aegilops and Agropyron species been used as donors

of alien material, but Secale has also been used as a source of pest resistance. Driscoll and Jensen (6) reported the translocation of a gene for wheat leaf rust resistance from a rye chromosome to wheat. It was later shown that the translocated alien segment present in this line, "Transec", occupied a terminal position and is of considerable length. The wheat chromosome involved was identified as chromosome 4A (4) and was found to involve the loss of genetically unimportant wheat chromatin (5). More recently, Sebesta and Wood (19) have successfully transferred greenbug resistance from rye to wheat through the use of X-rays.

The major advantage of induced translocations through the use of X-rays is that the procedure will work regardless of the pairing affinity of the alien chromosome with its wheat homoeologues (13). Knott (12) considered the Agropyrons the easiest to handle and the most valuable source of potentially useful genes. Usually lines can be produced in which the translocated segment is transmitted as though it were a dominant gene. He further added that the only real problem is that a segment of wheat chromosome will have been lost, and this could also be deleterious. According to Sears (17), a more desirable approach to this problem is to produce a reciprocal translocation in which the desired alien chromosome segment replaces a segment of homoeologous wheat chromosome. The alien segment may then compensate for the missing wheat segment, as well as introducing the desired alien gene.

Because transfers of this type usually involve overall phenotypic modifications or are too arbitrary, alternative procedures have been sought. According to Knott (13), Okamoto, as well as Riley and Chapman

were among the first to report that pairing of homoeologous chromosomes in wheat is genetically controlled. Several methods utilizing homoeologous crossing over to transfer alien genes to wheat chromosomes have since been reported (13).

Riley et al. (15) were the first to report a successful technique using induced homoeologous pairing to transfer yellow rust resistance from Aegilops comosa to wheat. An alien addition line containing the Aegilops comosa chromosome which was resistant to the disease was first produced. This was then crossed with Aegilops speltoides in order to suppress the activity of chromosome 5B which inhibits homoeologous pairing. The suppression of 5B activity permitted the A. comosa chromosome to recombine with its wheat homoeologue. A backcrossing program combined with selection of rust resistant plants was undertaken to develop a 42-chromosome plant which was also resistant to yellow rust.

Through the use of a deficiency for chromosome 5B, Sears (17) was able to transfer resistance to leaf rust from two different Agropyron elongatum chromosomes to wheat chromosomes, i.e., 3D in "Tap 67" (a 3D substitution line) and 7D in Agrus. For these two Agropyron chromosomes, the induction of homoeologous pairing appeared to be a much better way of effecting the transfer of the desired gene than the method utilizing ionizing radiation (18).

This method of transferring desirable characters from the relatives to wheat appears to be more precise than irradiation techniques. Such transfers may have no deleterious effects, especially if the desired alien gene is near the end of one arm, permitting transfer to the gene through exchange of only a short terminal segment (17).

According to Driscoll (2), this method of induced homoeologous pairing does have limitations. The wheat chromosome that is to be involved in the translocation would presumably have to be one of the three in the pertinent homoeologous groups. For irradiation induced transfers, any chromosome is capable of being involved in any translocation. The position of the alien gene on each of the three wheat chromosomes is also predestined, as crossing over would presumably take place between homoeologous segments of chromatin. If such positions were to coincide with wheat genes of significant value, the loss of any of these may not be tolerable. Some alien chromosomes with very limited possibilities for crossing over with their wheat homoeologues may never give rise to fully satisfactory transfers through induced pairing. Radiation induced transfers from such chromosomes might have a better chance for success (18).

Sears (17) described another technique to transfer part of an alien chromosome to wheat. This transfer may be accomplished by allowing a telocentric for one arm of the alien chromosome to combine with a wheat telocentric following misdivision of two monosomes. This transfer chromosome may be useful if the alien arm replaces a homoeologous arm or if the alien arm is not deleterious and replaces a nonessential wheat arm.

Besides being induced through irradiation or meiotic control, alien translocations occasionally arise spontaneously. Some alien translocations have been produced in this manner, including the "Agent" (22) and "Neuzucht" (24) translocations.

While the literature does not contain any information regarding the combining of two translocation lines, Knott (11) tested lines which

had a pair of Agropyron chromosomes either added to the normal chromosome complement or substituted for wheat chromosome 6A. None of the lines equaled the check cultivar for all characters, but there was no conclusive evidence for a detrimental effect of the Agropyron chromosome on any character studied. This work did not involve translocation lines containing segments of alien chromatin. Extensive reviews of the literature regarding translocation lines have recently been completed by Knott (13) and Sears (17).

If alien gene transfers are to be useful they should be relatively free from deleterious effects associated with the exchange of alien chromatin. Driscoll (3) pointed out that an alien translocation may be acceptable in some cultivars but not in others. Thus the alien translocations should be tested in a wide variety of genetic backgrounds.

Several alien translocation lines have been used successfully in the development of improved cultivars. 'Arthur 71', grown commercially in the soft red winter wheat region, contains the Transfer translocation. The Neuzucht translocation is present in the cultivars 'Aurora' and 'Kavkaz' which are grown in Eastern Russia. 'Sage' and 'Osage', grown commercially in the hard red winter wheat region, contain the Agent translocation. The "Teewon" translocation is present in the advanced breeding line OK711092A. The release of this line is pending (21).

CHAPTER III

MATERIALS AND METHODS

Materials

Six winter wheat cultivars or selections, each containing a different alien translocation were used in this study. These six cultivars are listed below along with the designation and origin of the alien segment, the translocation complex, and the chromosome arms involved.

Translocations Studied

Cultivar or Selection	Reference	Translocation Designation	Origin of Alien Gene Complex	Arms Involved	
				Alien	Wheat
Arthur 71	(16)	Transfer	<u>Aegilops umbellulata</u>	6c ^u	6B1
Sage	(22)	Agent	<u>Agropyron elongatum</u>	3Ag	3D
OK66C2108	(19)	Teewon	<u>Agropyron elongatum</u>	Unknown	
Purdue 6615D	(20)	Agatha	<u>Agropyron elongatum</u>	7el	7D1
Aurora	(24)	Neuzucht	<u>Secale cereale</u>	1R	1Bs
Winter Transec	(6)	Transec	<u>Secale cereale</u>	2R	4A

Arthur 71 and "Purdue 6615D" (6*Arthur/Agatha) are soft red winter wheats developed at Purdue Univ., Lafayette, Ind. Sage and OK66C2108 are hard red winter wheats developed at the Kansas Agric. Exp. Sta., Hays, Kansas and at Oklahoma State Univ., Stillwater, Okla., respectively. Aurora, a semi-hard red winter wheat, was developed at Krasno-

dar, USSR. "Winter Transec" is a white winter wheat developed at Cornell Univ., Ithaca, N.Y. All but Winter Transec appear to be well adapted to growing conditions in Oklahoma (21).

The 15 different F_1 's studied resulted from a diallel crossing scheme involving the six cultivars listed above. Crosses were made in the greenhouse during the 1974-75 crossing season. Reciprocal crosses were not kept separate. Crossed and parental seed were planted in flats on November 7, 1975. The seedlings were vernalized at outside temperatures for approximately six weeks.

Field Layout

The seedlings were transplanted to the field on December 19, 1975. The experiment was conducted in a randomized, complete-block design with four replications, each composed of 21 single-row plots. Alternate rows consisted of the cultivar, "Tam W-103", to reduce differential competition between genotypes. Each plot consisted of 19 plants spaced 15 cm apart. Single-row plots were spaced 30 cm apart, and all measurements with the exception of percent protein and heading date were taken on an individual plant basis. The study was conducted during the 1975-76 growing season at the Agronomy Research Station, Stillwater, Okla., on a Norge loam soil type.

A preplant application of ammonium nitrate was applied on September 4, 1975 at the rate of 30 kg/ha actual N. On February 20, 1976 and again on March 20, 1976, a topdressing of ammonium nitrate was applied at the rate of 30 kg/ha actual N.

In general, fair conditions existed throughout the growing season. Temperatures were normal for the months of January through June, how-

ever, rainfall for this same period was 127 mm below the normal 408 mm. Because of the shortage of rainfall, supplemental water was applied by sprinkler irrigation on three separate occasions.

The study was harvested on June 18 and 19 by pulling and bagging individual plants. Thirteen vigorous bordered plants from each row were evaluated.

Characters Evaluated

The number of tillers/plant, kernels/spike, kernel weight, grain yield, percent sterility, plant height, heading date, and percent grain protein were evaluated in this experiment. The measurements were made as follows.

Tiller Number

Tiller number/plant was recorded as the number of fertile spikes collected from each plant at the time of threshing and was expressed on a per plant basis.

Kernels/Spike

The number of kernels/spike was determined by selecting the three best heads from each plant. These were threshed in bulk and the seeds were counted to determine the mean number of kernels/spike.

Kernel Weight

The weight of the seeds of the three selected heads was divided by the number of seeds produced on the same three heads. This character was expressed as grams per 1000 kernels.

Grain Yield

Grain yield was taken as the weight of the threshed grain from each individual plant and was expressed as grams per plant.

Percent Sterility

This character was determined as follows: $100\% - (\text{number of seeds per spike} - \text{number of florets per spike} \times 100\%)$. Percent sterility was determined as an average of the same three main heads used to obtain the other yield components and was expressed on a per plant basis.

Plant Height

The measurement of this character was taken as the distance in centimeters from the crown (soil line) to the tip of the tallest spike, excluding awns, and was recorded on a per plant basis.

Heading Date

This character was recorded as a visual estimation of the time when 50% of the plants were fully headed. It is expressed as the number of days after March 31 and was evaluated on a per row basis.

Percent Protein

Percent protein of the grain was determined by the wheat quality lab at Oklahoma State University using an infrared analyzer. This character was determined on a per row basis.

Statistical Analysis

Standard analyses of variance were conducted on all data for the

purpose of detecting the presence or absence of significant differences among the entries for the eight previously mentioned characters. The analyses for percent protein and heading date were conducted on a row basis; the other characters on a plant basis.

Heterosis was determined for all characters with respect to both the mid-parent and high-parent values. Least Significant Differences (LSD) were used to test each hybrid-parent contrast. The standard deviation for a hybrid vs. high-parent contrast was defined as: S_d for hybrid vs. high-parent = $\sqrt{\frac{2 \text{ EMS}}{r}}$. Adjusted LSD values were used to test each hybrid vs. mid-parent contrast because hybrid means were based on only half as many observations as mid-parent values. The standard deviation for such a contrast was defined as: S_d for hybrid vs. mid-parent = $\sqrt{\frac{3 \text{ EMS}}{2r}}$ where EMS is the experimental error mean square and r represents the number of observations comprising the treatment mean. The LSD values were calculated as follows: $\text{LSD} = S_d t (\alpha, t-1)$.

Combining Ability Analysis

Combining ability analyses were conducted using F_1 and parental data for all eight characters according to the procedure outlined by Griffing (7) which he has designated as method 2, model 1. Under this model, the genotypes and blocks are regarded as fixed effects. Inferences, therefore, are restricted to the genotypes entering the diallel cross, since the experimental material was not a random sample of a definable larger population. Griffing's analysis provides for the partitioning of the sum of squares due to genotypes into general combining ability (GCA) and specific combining ability (SCA) sum of

squares associated with $p-1$ and $\left[p(p-1) \right] / 2$ degrees of freedom, respectively, where p represents the number of parents involved in the diallel cross. Under this model, the tests of significance for GCA and SCA are: MS_{GCA} / MS_E and MS_{SCA} / MS_E where MS_{GCA} and MS_{SCA} are the mean squares associated with GCA and SCA, respectively, and MS_E is the error mean square. The variance components for GCA and SCA were calculated according to the procedures outlined by Griffing (7).

CHAPTER IV

EXPERIMENTAL RESULTS

General Considerations

There were no serious problems with disease or insects, however, severe stunting and leaf injury were observed in the Sage/OK66C2108 hybrid. This damage was apparently due to hybrid necrosis, a genetic defect, as described by Hermesen (8). After heading, an abnormal amount of sterility was observed in four hybrids, Arthur 71/Aurora, Arthur 71/Winter Transec, Purdue 6615D/Aurora, and Purdue 6615D/Winter Transec. The low performance of these hybrids, with respect to grain yield, is indicative of the adverse effects brought about by hybrid necrosis and high levels of sterility.

Analysis of Variance

Mean squares from the analyses of variance of the eight measured traits are represented in Tables I and II. Since heading date and percent protein were measured on a per row basis as opposed to a per plant basis, their mean squares are presented separately. Highly significant entry (genotype) mean squares were obtained for all eight characters. Mean squares for replications were highly significant for five of the eight traits studied. Though the mean squares for replications has no genetical interpretation, these results do indicate that

blocking of replications was effective in removing some of the nonessential variation from treatment effects for those five characters, thus increasing the precision of their analysis. All characters measured on a per plant basis (Table I) exhibited a significant to highly significant differences between replication by entry mean square and residual mean square. This indicates that experimental error for these traits contains variation in addition to that among subsamples (residual).

Comparisons Among Means

The means for each trait are presented in Table III. In this and subsequent tables, the names of four parents have been abbreviated as follows: Arthur 71 = Atr71, OK66C2108 = 2108, Purdue 6615D = 6615D, and Winter Transec = W.Trans. Abbreviations for Sage and Aurora were not necessary. All means with the exception of those for heading date and percent protein were based on 52 observations. The means describing heading date and percent protein were based on four observations (one observation/entry/replication).

The performance of the hybrids in relation to their respective mid-parent and high-parent values are illustrated in Table IV. Parental and hybrid means, ranked in order of performance, along with hybrid deviations may be found in the Appendix (Tables X through XVII) for each character separately.

As shown in Table III, the means for tiller number ranged from 6.0 for Winter Transec to 17.1 for OK66C2108/Purdue 6615D. The parent with the highest tiller number was Purdue 6615D with 13.2. The overall means for F_1 's and parents were 12.7 and 10.5, respectively.

TABLE I

MEAN SQUARES FOR SIX TRAITS FROM THE ANALYSIS OF VARIANCE
OF F_1 HYBRIDS AND PARENTS

Source of Variation	df	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield	Percent Sterility	Plant Height
Replication	3	8.9	505.0**	177.5**	61.5	350.3	486.7**
Entry	20	322.7**	4462.5**	1372.8**	475.8**	22574.9**	2036.7**
Rep x Entry	60	20.8*	70.9**	40.0**	25.1**	218.8**	84.9**
Residual	1008	14.5	41.7	19.5	13.8	136.2	33.1
Corrected Total	1091	20.4	125.7	45.9	23.0	552.7	73.9

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

TABLE II

MEAN SQUARES FOR HEADING DATE AND PERCENT PROTEIN
FROM THE ANALYSIS OF VARIANCE OF
F₁ HYBRIDS AND PARENTS

Source of Variation	df	Heading Date	Percent Protein
Replication	3	25.2**	0.7**
Entry	20	238.9**	7.7**
Error	60	3.9	0.1

** Significant at the 0.01 level of probability

Eleven of the 15 F_1 's exhibited significant positive mid-parent heterosis, while four had significantly more tillers than their respective high-parents. No F_1 produced significantly few tillers than its mid-parent or high-parent (Table IV).

The number of kernels/spike ranged from 40.2 to 10.4 for OK66C2108/Aurora and Purdue 6615D/Winter Transec, respectively (Table III). OK66C2108 was the parent with the greatest number of kernels/spike with a mean of 38.8, while Arthur 71 was the parent with the lowest value of this trait with a mean of 23.1. The overall parental mean was 32.0, while the overall F_1 mean was 27.2. The average of all F_1 's expressed as a percent of the overall parental mean was 85%, which is rather low. As shown in Table IV, three hybrids exhibited significant positive mid-parent and/or high-parent heterosis for this trait. However, eight hybrids had a significantly smaller number of kernels/spike than both their mid-parents and high-parents. Five of these hybrids had Arthur 71 as a parent. One additional hybrid was significantly lower than its high-parent but not its mid-parent.

The overall F_1 mean for kernel weight was 33.0 g and the overall parental mean was 28.0 g (Table III). Means for this trait ranged from 40.3 g for Arthur 71/Aurora to 19.4 g for Winter Transec. Aurora was the highest parent with a kernel weight of 32.8 g. Sage/OK66C2108 was the only hybrid which did not significantly exceed its mid-parent value (Table IV). This was the hybrid in which hybrid necrosis was observed. Eight hybrids had significant positive high-parent heterosis. No significant deviations toward lighter kernel weight were observed.

OK66C2108/Purdue 6615D was the highest yielding entry with a mean yield of 14.1 g, while Purdue 6615D/Winter Transec was the lowest

TABLE III
MEANS FOR EIGHT CHARACTERS FROM A SIX-PARENT
DIALLEL CROSS OF WINTER WHEAT
ALIEN-TRANSLOCATION LINES

Entry	Tiller Number (no./plant)	Kernels/ Spike (no.)	Kernel Weight (g/1000 seed)	Grain Yield (g/plant)
<u>F₁ Hybrids</u>				
Atr71/Sage	15.3	24.3	32.4	9.3
Atr71/2108	14.5	24.5	34.8	9.2
Atr71/6615D	13.5	21.4	34.3	7.3
Atr71/Aurora	12.5	15.7	40.3	5.8
Atr71/W.Trans	11.7	16.1	31.7	4.2
Sage/2108	10.9	29.8	25.6	6.2
Sage/6615D	15.6	30.1	34.8	11.8
Sage/Aurora	11.6	35.0	36.4	11.9
Sage/W.Trans	10.0	40.1	26.6	8.0
2108/6615D	17.1	32.5	36.7	14.1
2108/Aurora	12.2	40.2	35.3	13.3
2108/W.Trans	11.1	39.7	26.3	7.4
6615D/Aurora	12.4	11.7	39.7	4.5
6615D/W.Trans	13.1	10.4	29.0	2.9
Aurora/W.Trans	9.5	34.4	30.8	7.5
Overall F ₁ Mean (\bar{F}_1)	12.7	27.1	33.0	8.2
<u>Parents</u>				
Atr71	12.4	23.1	31.7	7.2
Sage	11.4	33.1	27.2	7.6
2108	11.5	38.8	26.2	7.7
6615D	13.2	30.0	30.5	9.1
Aurora	8.3	34.1	32.8	8.2
W.Trans	6.0	32.8	19.4	3.3
Overall Parental (\bar{P}) Mean	10.5	32.0	28.0	7.2
$\bar{F}_1/\bar{P}\%$	121	85	118	115

TABLE III (CONTINUED)

Entry	Percent Sterility (%)	Plant Height (cm)	Heading Date ¹	Percent Protein (%)
<u>F₁ Hybrids</u>				
Atr71/Sage	17.2	71.4	38.3	14.6
Atr71/2108	23.2	76.1	34.5	15.2
Atr71/6615D	25.7	65.0	31.5	16.0
Atr71/Aurora	54.6	70.7	32.0	17.2
Atr71/W.Trans	48.3	76.6	40.8	17.9
Sage/2108	10.4	72.5	44.0	13.8
Sage/6615D	10.4	73.4	29.5	14.5
Sage/Aurora	8.3	77.1	32.0	14.3
Sage/W.Trans	4.5	89.0	48.5	16.0
2108/6615D	10.1	80.3	30.0	14.4
2108/Aurora	5.0	77.4	28.8	14.1
2108/W.Trans	7.5	85.9	48.8	16.8
6615D/Aurora	68.1	70.4	30.5	18.6
6615D/W.Trans	69.5	78.2	36.0	18.6
Aurora/W.Trans	11.6	80.6	43.5	15.1
Overall F ₁ Mean(\bar{F}_1)	25.0	76.3	36.6	15.7
<u>Parents</u>				
Atr71	17.2	66.4	30.8	15.1
Sage	1.6	72.8	45.3	14.4
2108	3.5	77.5	42.8	14.5
6615D	7.3	69.4	30.3	14.5
Aurora	18.6	69.0	39.5	15.7
W.Trans	18.0	83.8	55.3	16.3
Overall Parental (\bar{P}) Mean	11.0	73.1	40.6	15.0
$\bar{F}_1/\bar{P}_1\%$	227	104	90	104

¹ Number of days after March 31

TABLE IV
MEAN PERFORMANCE OF HYBRIDS EXPRESSED AS PERCENT OF
MID-PARENT (MP) AND HIGH-PARENT (HP) VALUES

F ₁ Hybrids	Tiller Number		Kernels/Spike		Kernel Weight		Grain Yield	
	%MP	%HP	%MP	%HP	%MP	%HP	%MP	%HP
Atr71/Sage	128**	123**	86**	73**	110**	102	125**	122
Atr71/2108	121**	117**	79**	63**	120**	110**	124*	120
Atr71/6615D	105	102	81**	71**	110**	108*	89	80
Atr71/Aurora	120	100	55**	46**	125**	123**	75*	71*
Atr71/W.Trans	127**	94	57**	49**	124**	100	80	58**
Sage/2108	95	95	83**	77**	96	94	81	81
Sage/6615D	127**	118**	96	91	121**	114**	142**	131**
Sage/Aurora	117*	101	104	103	121**	111**	151**	146**
Sage/W.Trans	113	86	122**	121**	114**	98	146**	104
2108/6615D	138**	129**	95	84**	133**	124**	168**	155**
2108/Aurora	123**	106	110*	104	120**	108*	168**	163**
2108/W.Trans	127**	97	111**	102	115**	100	134*	96
6615D/Aurora	115*	94	36**	34**	125**	121**	53**	50**
6615D/W.Trans	135**	99	33**	32**	116**	95	48**	32**
Aurora/W.Trans	132**	114	103	101	118**	94	131*	92

TABLE IV (CONTINUED)

F ₁ Hybrids	Percent Sterility		Plant Height		Heading Date		Percent Protein	
	%MP	%HP ¹	%MP	%HP ²	%MP	%HP ³	%MP	%HP
Atr71/Sage	183**	100	102	98	101	85**	98	95**
Atr71/2108	224**	135**	106	98	94	81**	102	99
Atr71/6615D	210**	150**	96	94*	103	102	107**	104*
Atr/Aurora	305**	294**	104	102	91*	81**	111**	110**
Atr71/W.Trans	274**	269**	102	91**	95	74**	108**	105**
Sage/2108	411*	300*	96	94**	100	97	95**	95**
Sage/6615D	236*	144	103	101	78**	65**	100	100
Sage/Aurora	82	44**	109**	106**	76**	71**	95**	91**
Sage/W.Trans	46*	25**	114**	106**	97	88**	104**	98
2108/6615D	189	139	109**	104	82**	70**	99	99
2108/Aurora	46*	27**	106**	100	70**	67**	94**	90**
2108/W.Trans	69	42**	107**	103**	99	88**	102	97*
6615D/Aurora	526**	366**	102	101	87**	77**	123**	119**
6615D/W.Trans	550**	387**	102	93	84**	65**	121**	114**
Aurora/W.Trans	63**	62*	106**	96	92**	79**	95**	93**

¹HP = most sterile parent, ²HP = tallest parent, and ³HP = later parent

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

with 2.9 g (Table III). The overall parental mean was 7.2 g and the overall F_1 mean was 8.2 g. Winter Transec was the lowest yielding parent with a mean of 3.3 g, indicating its general lack of adaptation to the environmental conditions encountered in this study. Four hybrids yielded significantly greater and four yielded significantly less than their respective high-parents. Three hybrids were significantly lower than their mid-parents for grain yield with nine hybrids yielding significantly greater than their mid-parents (Table IV). OK66C2108/Aurora, OK66C2108/Purdue 6615D, Sage/Aurora, and Sage/Purdue 6615D, the highest yield in hybrids in this test exceeded their high-parent values by 63, 55, 46 and 31% respectively.

Percent sterility ranged from 1.6% for Sage to 69.5% for Purdue 6615D/Winter Transec (Table III). The hybrid with the lowest percent sterility was Sage/Winter Transec with 4.5%. Four hybrids, (Arthur 71/Winter Transec, Arthur 71/Aurora, Purdue 6615D/Winter Transec, and Purdue 6615D/Aurora) exhibited a much higher mean percent sterility than any of the other hybrids or parents. The possible reasons for this elevated sterility and its implications in breeding programs will be considered in the following chapter. The overall means for sterility were 25.0% and 11.0% for F_1 's and parents, respectively. Only three hybrids had significantly lower percent sterility than their mid-parent values (Table IV).

The highest parental mean for plant height was 83.8 cm for Winter Transec (Table III) while Sage/Winter Transec was the tallest hybrid with a mean plant height of 89.0 cm. Arthur 71/Purdue 6615D was the shortest entry with a mean of 65.0 cm. The overall F_1 mean was 76.3 cm while the overall parental mean was 73.1 cm. As shown in Table IV,

three hybrids were significantly shorter than their tallest parent, while none was significantly shorter than its mid-parent. Three hybrids were significantly taller than their tallest parent.

Means for heading date ranged from an earliest of 28.8 days for the OK66C2108/Aurora hybrid to a latest of 55.3 days for Winter Transec (Table III). Purdue 6615D was the earliest parent with a heading value of 30.3 days. In general, F_1 's were earlier than the parent with means of 36.6 days for the F_1 's and 40.6 days for the parents. Eight hybrids were significantly earlier than their respective mid-parents and high-parents, but no hybrid was significantly later in heading than its mid-parent or high-parent.

The mean values for percent protein ranged from 18.6% to 13.8% for Purdue 6615D/Winter Transec and Sage/OK66C2108, respectively (Table III). The overall F_1 mean was 15.7%, while the overall parental mean was 15.1%. Four hybrids (Arthur 71/Aurora, Arthur 71/Winter Transec, Purdue 6615D/Aurora, and Purdue 6615D/Winter Transec) were higher than expected in percent protein values. These four hybrids exceeded their respective high-parents for percent protein by values significant at the 0.01 probability level. These same hybrids also showed high levels of sterility. Five hybrids were significantly higher in protein than their high-parents and six were higher than their mid-parents (Table IV). Four hybrids were significantly lower in protein than their respective mid-parent values (Table IV).

Diallel Analysis for General and Specific Combining Ability

All data were subjected to diallel analyses for general combining ability (GCA) and specific combining ability (SCA) for each of the

eight characters. The mean squares from the analyses of variance are presented in Table V. Highly significant GCA and SCA variances were observed for all characters.

In order to obtain estimates of additive and nonadditive genetic effects, the variance components for GCA, which is associated with additive genetic effects, and SCA, which is associated with nonadditive effects including genotype by environment interactions, were calculated. Although estimates of variance components for GCA and SCA effects are valid only with random models, estimates of these components were made from the fixed model used in this study. This was done to provide some information on the relative magnitudes of the components while recognizing at the same time that severe restrictions are placed on the interpretations of these estimates. These components, along with the ratios of GCA to SCA for each trait are presented in Table VI. The GCA components were 1.62 to 3.09 times greater than the SCA components for tiller number, kernel weight, plant height, and heading date, indicating that additive genetic effects were more important than nonadditive effects for these traits. On the other hand, the ratios of GCA to SCA were less than unity for kernels/spike, grain yield, percent sterility, and percent protein which indicates that these traits are influenced to a greater degree by dominance, epistasis and/or genotype by environment interactions.

Since the GCA variances were significant for all traits (Table IV), GCA effects for the individual parents could be estimated for all eight characters studied. Those estimates and their respective standard errors, are illustrated in Table VII. The GCA effects as expected closely agreed in rank with the parental means for all characters.

TABLE V
 MEAN SQUARES FOR GENERAL COMBINING ABILITY, SPECIFIC
 COMBINING ABILITY, AND ERROR FOR EIGHT CHARACTERS

Trait	GCA ¹	SCA	Error
Tiller Number	65.81**	11.71**	1.60
Kernels/Spike	652.15**	240.34**	5.46
Kernel Weight	283.34**	46.34**	3.07
Grain Yield	52.21**	30.05**	1.93
Percent Sterility	2382.55**	1521.14**	16.83
Plant Height	475.74**	50.33**	6.53
Heading Date	760.31**	65.03**	3.90
Percent Protein	14.09**	5.55**	0.13

** Significant of the .01 level of probability.

¹The degrees of freedom for GCA, SCA, and Error Mean squares are 5, 15, and 60, respectively.

This indicates that selection of parents for use in a breeding program to improve those traits may be based largely on phenotypic performance of the parents themselves and also suggests the presence of considerable additive effects.

The parents, Sage and OK66C2108 had significant positive effects for kernels/spike and heading date. These parents also exhibited the greatest amount of negative GCA effects for sterility (low percent sterility). Winter Transec had significant negative GCA effects for tiller number, kernel weight, and grain yield. This parent had greater positive effects for plant height and heading date, indicating that it contributes toward taller stature and later maturity in its hybrids. Arthur 71 and Purdue 6615D exhibited the greatest positive GCA effects for sterility (high percent sterility). Aurora had the greatest positive effects for percent protein. In general, OK66C2108 had the greatest positive effects for yield and its components while Winter Transec had the greatest negative effects indicating these to be the best and poorest of the six parents respectively.

The SCA effects for grain yield and the components of yield are illustrated in Table VIII along with their respective standard errors. Sage/OK66C2108 showed significant negative effects for all four characters (two of which were significant) illustrated in this table indicating that this hybrid did not perform as well as expected on the basis of the GCA effects of its two parents. Purdue 6615D/Aurora had significant negative SCA effects for kernels/spike and grain yield. Four hybrids (Sage/Purdue 6615D, Sage/Aurora, OK66C2108/Purdue 6615D, and OK66C2108/Aurora) had positive effects for grain yield and its components. However many of these effects were not significantly different

TABLE VI
ESTIMATES OF VARIANCE COMPONENTS FOR GENERAL AND
SPECIFIC COMBINING ABILITY EFFECTS
FOR EIGHT CHARACTERS

Trait	GCA Component	SCA Component	GCA/SCA
Tiller Number	16.05	9.57	1.68
Kernels/Spike	161.67	234.88	0.69
Kernel Weight	70.07	43.27	1.62
Grain Yield	13.57	28.12	0.48
Percent Sterility	591.43	1504.31	0.39
Plant Height	117.30	43.80	2.68
Heading Date	189.10	61.13	3.09
Percent Protein	3.49	5.42	0.64

TABLE VII
ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS
OF SIX PARENTS FOR EIGHT CHARACTERS

Parent	Tiller Number	Kernels/ Spike	Kernel Weight	Grain Yield	Percent Sterility	Plant Height	Heading Date	Percent Protein
Atr71	0.98	-6.38	2.01	-0.65	7.06	-4.39	-3.20	0.27
Sage	0.20	3.28	-1.35	0.87	-11.60	0.15	2.33	-0.82
2108	0.51	5.64	-1.20	1.26	-10.46	2.42	0.90	-0.80
6615D	1.69	-4.16	1.82	0.41	6.45	-2.70	-5.76	0.28
Aurora	-1.23	0.73	3.41	0.48	4.75	-1.71	-2.29	0.26
W.Trans	-2.15	0.89	-4.69	-2.37	3.80	6.23	7.99	0.81
Std. Error	0.63	1.17	0.88	0.69	2.05	1.28	0.18	0.99

from zero. The specific effects for grain yield of these four hybrids are in close agreement with the rank of the F_1 means. OK66C2108/Purdue 6615D, and OK66C2108/Aurora displayed the greatest specific effects for grain yield, while Sage/OK66C2108, Purdue 6615D/Aurora, Purdue 6615D/Winter Transec and OK66C2108/Winter Transec had the greatest negative effects.

The SCA effects for percent sterility, plant height, heading date, and percent protein are present in Table IX. The most striking effects are those for percent sterility. Arthur 71/Aurora, Purdue 6615D/Aurora, Purdue 6615D/Winter Transec and Sage/OK66C2108 showed the greatest positive SCA effects for this character (high sterility). Three of these hybrids displayed the highest mean percent sterility. As illustrated in Table VIII, Purdue 6615D/Aurora and Purdue 6615D/Winter Transec also displayed negative effects for yield. Sage/OK66C2108 also exhibited considerable positive effects for sterility and a negative (though nonsignificant) effect for grain yield; however, this association may have been confounded with the high incidence of hybrid necrosis observed in the entry. None of the SCA effects were significant for plant height. Significant positive SCA effects for heading date were exhibited by OK66C2108/Winter Transec and Aurora/Winter Transec while significant negative effects were shown by Sage/Aurora and OK66C2108/Aurora. Significant SCA effects in the positive direction for percent protein were indicated by Arthur 71/Aurora, Sage/Winter Transec, and Purdue 6615D/Aurora. Significant negative effects were only exhibited by Aurora/Winter Transec.

TABLE VIII
ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR
TILLER NUMBER, KERNELS/SPIKE, KERNEL
WEIGHT, AND GRAIN YIELD

		Atr71	Sage	2108	6615D	Aurora	W.Trans
Atr71	a	-1.60	2.03	0.93	-1.25	0.67	-0.78
	b	7.43	-1.12	-3.25	3.47	-7.09	0.56
	c	-3.88	0.17	2.50	-1.11	3.35	-1.03
	d	0.62	1.12	0.70	-0.41	-1.94	-0.90
Sage	a		-1.04	-1.89	1.66	0.51	-1.27
	b		-1.91	-7.56	2.54	2.48	5.57
	c		-1.70	-3.40	2.75	2.78	0.60
	d		-2.04	-3.82	2.63	2.61	0.50
2108	a			-1.65	2.77	0.82	-0.98
	b			-0.94	2.59	5.37	3.79
	c			-2.93	4.54	1.56	-2.27
	d			-2.76	4.46	3.64	-2.22
6615D	a				-2.23	-0.16	-0.79
	b				9.79	-13.39	-5.00
	c				-4.68	2.89	-4.39
	d				0.31	-4.27	-2.72
Aurora	a					-1.31	-0.53
	b					4.15	8.48
	c					-5.55	-5.03
	d					-0.74	0.70
W.Trans	a						4.35
	b						13.40
	c						13.32
	d						4.83

a = Tiller Number, b = Kernels/Spike, c = Kernel Weight, and d = Grain Yield. Standard Errors for a, b, c, and d are 1.67, 3.09, 2.32 and 1.84, respectively.

TABLE IX
ESTIMATES OF SPECIFIC COMBINING ABILITY EFFECTS FOR
STERILITY, HEIGHT, HEADING DATE,
AND PERCENT PROTEIN

		Atr71	Sage	2108	6615D	Aurora	W.Trans
Atr71	a	-17.91	-0.76	5.59	-8.77	21.81	-1.48
	b	-0.17	0.18	2.70	-3.29	1.38	-0.80
	c	-0.58	1.39	-0.96	2.73	-0.24	-2.34
	d	-0.72	0.33	0.20	-0.10	1.19	-0.24
Sage	a		3.80	11.48	-5.38	-5.80	-4.86
	b		-2.90	-5.45	0.59	3.29	4.29
	c		2.86	3.01	-4.80	-5.77	3.31
	d		0.56	-0.09	-0.52	-0.64	1.02
2108	a			3.41	-6.83	-10.23	-3.42
	b			-2.76	5.19	1.29	-0.97
	c			3.17	-2.89	-7.61	5.28
	d			0.57	-0.63	-0.86	0.81
6615D	a				-26.60	35.92	11.66
	b				-0.58	-0.56	-1.35
	c				4.04	0.83	0.09
	d				-1.61	2.51	0.35
Aurora	a					-11.88	-29.82
	b					-3.02	-2.38
	c					6.36	6.43
	d					-0.37	-1.83
W.Trans	a						27.92
	b						1.21
	c						-12.77
	d						-0.11

a = Sterility, b = Height, c = Heading Date, and d = Percent Protein. Standard Errors for a, b, c, and d are 5.42, 3.38, 2.61 and 0.48, respectively.

CHAPTER V

DISCUSSION

The ratios of variance components indicate that a large portion of the genetic variation (especially for tiller number, kernel weight, plant height, and heading date) could be accounted for by variation due to GCA. According to Sprague and Tatum (23) GCA provides a measure of additive gene action. Brown et al (1) and Kronstad and Foote (14) found that most of the total genetic variability for a number of characters studied in wheat crosses was due to additive effects of genes. The results of the present study, with regard to GCA, are in good agreement with those of previous workers.

Kernels/spike, percent sterility, percent protein and grain yield showed larger components for SCA than for GCA. Kernels/spike is related to percent sterility and some of the hybrids showed unusually high amounts of sterility which could account for the large SCA component. Grain yield is a complex trait, the major components of which are tiller number, kernels/spike, and kernel weight. The interaction of these three traits could account in part for the high SCA estimates for grain yield. The occurrence of significant SCA effects for all traits in this study suggests that the genetic variation present for each trait was also due in part to nonadditive effects; dominance, epistasis, and/or genotype by environment interactions.

The GCA effects for all traits (including kernels/spike, grain

yield, and percent sterility) indicated Sage and OK66C2108 were the better parents of the six lines studied, while Aurora and Purdue 6615D appeared to be adequate. On the other hand, Arthur 71 and Winter Transec seem to be the least favorable parents in this set. Some combinations of these translocations resulted in heterosis for grain yield, while other combinations resulted in high sterility accompanied by low yield. The four high yielding hybrids, OK66C2108/Purdue 6615D, OK66C-2108/Aurora, Sage/Aurora, and Sage/Purdue 6615D, had low levels of sterility. Good agreement between actual yield of these hybrids and the SCA effects for yield was observed.

As illustrated in Appendix Tables X to XVII the best hybrid exceeded the best parent for grain yield, tiller number, kernels/spike, and kernel weight. The parents Sage and OK66C2108 displayed the lowest percent sterility, followed by the Sage/Winter Transec hybrid. Six hybrids had higher levels of sterility than Aurora, the most sterile of the parental lines. Four hybrids in particular had very high levels of sterility ranging from 69.5 to 48.3%. These were Purdue 6615D/Winter Transec, Purdue 6615D/Aurora, Arthur 71/Aurora, and Arthur 71/Winter Transec, respectively. These four hybrids also had the lowest values for kernels/spike among all parents and hybrids studied and were the lowest yielding of the hybrids.

Four hybrids had higher percent protein than Winter Transec, the highest percent sterility and fewest kernels/spike. A possible explanation is that the plant produces a certain protein to carbohydrate ratio for grain production and if a reduced number of sinks (i.e., kernels) are available, the normal protein produced is deposited in a reduced number of kernels, thus, increasing the protein content of

those kernels.

The relationship among the characters of grain yield, percent sterility, kernels/spike, and percent protein, as observed for the four highest and four lowest yielding hybrids, are listed below. The higher

High-Yielding vs. Low-Yielding Hybrids

F ₁ Hybrid	Grain Yield	Percent Sterility	Kernels/ Spike	Percent Protein
	(g/plant)	(%)	(no.)	(%)
<u>High-Yielding Group</u>				
2108/6615D	14.1	10.1	32.5	14.4
2108/Aurora	13.3	5.0	40.2	14.1
Sage/Aurora	11.9	8.3	35.0	14.3
Sage/6615D	11.8	10.4	30.1	14.5
<u>Low-Yielding Group</u>				
Atr71/Aurora	5.8	54.6	15.7	17.2
6615D/Aurora	4.5	68.1	11.7	18.6
Atr71/W.Trans	4.2	48.3	16.1	17.1
6615D/W.Trans	2.9	69.5	10.4	18.8

yielding hybrids displayed low sterility, high kernels/spike values, and normal percent protein values while the lower yielding hybrids exhibited the reverse. Two of the parents associated with the high yielding hybrids were also present in combinations which resulted in low yield and high sterility, i.e., Purdue 6615D and Aurora. When compared with the other parents, these parents were the highest yielding, however, Aurora displayed the highest sterility.

If the chromosomes involved in these translocations are considered, it should be noted that those F₁'s which exhibited positive heterosis for yield contained either the 3Ag-3D translocation of Sage or the unknown Agropyron translocation of OK66C2108. When either of these translocation stocks were crossed with any of the other translocation

lines used in this study, considerable heterosis for yield was imparted to the F_1 . Those F_1 's which did not have either Sage or OK66C2108 as a parent did not exhibit this positive heterosis (except for Aurora/Winter Transec). From this evidence it can be deduced that either the portions of alien chromatin contained in those two translocations compensated for any loss of valuable wheat chromatin, or that these two translocation lines contained some added genes for vigor that, when combined with other translocations, imparted vigor to the F_1 .

The four F_1 's which showed low yield and high sterility contained one of the two rye translocations, either Aurora (1R-1Bs) or Winter Transec (2R-4A). According to Sears (17), certain rye chromosomes may not pair with wheat as readily as Agropyron chromosomes, and sterility may be due to the lack of pairing which results in chromosome imbalance. If this be the case, the hybrid combination of Aurora/Winter Transec, containing both rye translocations, should be the most sterile of all the hybrids studied. However, this F_1 did not show a significant decrease in yield below Aurora, the higher yielding of its parents. It was significantly higher yielding than Winter Transec. The hybrid had significantly less sterility than either parent.

The extra vigor for yield apparently imparted by Sage and OK66C-2108 may have been due to the particular alien translocations involved in these lines. It should be noted, however, that of the six translocation lines examined in this study, these two were developed specifically for the Southern Great Plains region, within which this study was conducted. Their prepotency for yield may be due to their background genotypes rather than the particular alien gene complex involved. In order to make a definitive study of the effects of combining alien

translocation lines, each translocation should be in a common genetic background which could be accomplished by backcrossing each line to one adapted cultivar. This has been started at the Okla. Agric. Exp. Sta.

Wheat breeding programs in the Hard Red Winter Wheat area have progressed to the point that more attention is now being given to the development of cultivars having multiple pest resistance. Because many of the pest-resistant sources now available are alien translocation lines, it is important to know something about the possible beneficial and/or detrimental effects when different alien translocations are combined in a single genotype.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The F_1 's and parents of a diallel cross among six alien translocation lines of winter wheat were studied to determine the effects on eight performance traits when two different alien gene complexes were combined in two-way combinations. The six parents and 15 F_1 's were grown in a space-planted nursery on the Agronomy Research Station, Stillwater, Okla. during the 1975-76 growing season. The experiment was conducted in a randomized, complete-block design with four replications. Thirteen vigorous, bordered plants from each single-row plot were evaluated. Measurements were taken on tiller number, kernels/spike, kernel weight, grain yield, percent sterility, plant height, heading date, and percent protein. All data were subjected to a standard analysis of variance, as well as Griffing's analysis of variance for GCA and SCA. Hybrid-parent contrasts were also examined for each trait.

SCA and GCA variances were statistically significant for all eight characters. The GCA components were larger than those for SCA for tiller number, kernel weight, plant height, and heading date indicating that additive gene effects were more important for those traits than were nonadditive gene effects. On the other hand, SCA components were larger for kernels/spike, grain yield, percent sterility, and percent protein, indicating that (in this particular set of geno-

types) nonadditive gene effects for those traits were more important than additive effects.

The combining ability data for yield and yield components indicated that Sage and OK66C2108 were the better parents in the set; whereas Arthur 71 and Winter Transec were the least so. Four hybrids, OK66C-2108/Purdue 6615D, OK66C2108/Aurora, Sage/Aurora, and Sage/Purdue 6615D showed high positive heterosis for grain yield. Four hybrids, Arthur 71/Aurora, Purdue 6615D/Aurora, Arthur 71/Winter Transec, and Purdue 6615D/Winter Transec exhibited unexpectedly high levels of sterility, low values for kernels/spike, and low grain yields.

Aurora and Purdue 6615D were involved, as parents, in the four highest yielding, as well as the four lowest yielding hybrids. This indicates that specific combinations of alien translocation lines could do very well, whereas others could do very poorly. This situation would have important implications in wheat breeding programs for multiple-pest resistance because many of the present sources of pest resistance exist in alien translocation lines.

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APPENDIX

TABLE X
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR TILLER NUMBER

F ₁ Hybrid or Parent	Rank (High to Low)	Tiller Number	Hybrid Deviations	
			Mid-Parent	High-Parent
2108/6615D	1	17.1	4.7**	3.8**
Sage/6615D	2	15.6	3.3**	2.4**
Atr71/Sage	3	16.3	3.8	2.9**
Atr71/2108	4	14.5	2.6**	2.1*
Atr71/6615D	5	13.5	0.7	0.3
6615D	6	13.2	---	---
6615D/W.Trans	7	13.1	3.4**	-0.2
Atr71/Aurora	8	12.5	2.1	0.1
Atr71	9	12.4	---	---
6615D/Aurora	10	12.4	1.6**	-0.9
2108/Aurora	11	12.2	2.3	0.7
Atr71/W.Trans	12	11.7	2.5**	-0.7
Sage/Aurora	13	11.6	1.7*	0.1
2108	14	11.5	---	---
Sage	15	11.4	---	---
2108/W.Trans	16	11.1	2.4**	-0.4
Sage/2108	17	10.9	-0.6	-0.6
Sage/W.Trans	18	9.9	1.4	-1.6
Aurora/W.Trans	19	9.5	2.3**	1.2
Aurora	20	8.3	---	---
W.Trans	21	6.0	---	---

*,** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE XI
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR KERNELS/SPIKE

F ₁ Hybrid or Parent	Rank (High to Low)	Kernels/ Spike	Hybrid Deviations	
			Mid-Parent	High-Parent
2108/Aurora	1	40.2	3.8*	1.4
Sage/W.Trans	2	40.1	7.2**	7.0**
2108/W.Trans	3	39.7	3.9	0.9
2108	4	38.8	---	---
Sage/Aurora	5	35.0	1.4	0.9
Aurora/W.Trans	6	34.4	1.0	0.3
Aurora	7	34.1	---	---
Sage	8	33.1	---	---
W.Trans	9	32.8	---	---
2108/6615D	10	32.5	-1.8	-6.3**
Sage/6615D	11	30.1	-1.4	-3.0
6615D	12	29.9	---	---
Sage/2108	13	29.8	-6.1**	-9.0**
Atr71/2108	14	24.5	-6.5	-14.3**
Atr71/Sage	15	24.3	-3.9**	-8.9**
Atr71	16	23.1	---	---
Atr71/6615D	17	21.4	-5.1**	-8.5**
Atr71/W.Trans	18	16.1	-11.9**	-16.7**
Atr71/Aurora	19	15.7	-12.9**	-18.4**
6615D/Aurora	20	11.7	-20.4**	-22.4**
6615D/W.Trans	21	10.4	-21.0**	-22.4**

*, ** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE XII
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR KERNEL WEIGHT

F ₁ Hybrid or Parent	Rank (High to Low)	Kernel Weight	Hybrid Deviations	
			Mid-Parent	High-Parent
Atr71/Aurora	1	40.3	8.1**	7.5**
6615D/Aurora	2	39.7	8.0**	6.9**
2108/6615D	3	37.7	9.4**	7.2**
Sage/Aurora	4	36.4	6.4**	3.6**
2108/Aurora	5	35.3	5.8**	2.5*
Atr71/2108	6	34.8	5.9**	3.2**
Sage/6615D	7	34.8	5.9**	4.3**
Atr71/6615D	8	34.3	3.5**	2.6*
Aurora	9	32.8	---	---
Atr71/Sage	10	32.4	3.0**	0.7
Atr71/W.Trans	11	31.7	6.2**	0.0
Atr71	12	31.7	---	---
Aurora/W.Trans	13	30.8	4.7**	-2.0
6615D	14	30.5	---	---
6615D/W.Trans	15	29.0	4.0**	-1.5
Sage	16	27.2	---	---
Sage/W.Trans	17	26.6	3.3**	-0.6
2108/W.Trans	18	26.3	3.5**	0.1
2108	19	26.2	---	---
Sage/2108	20	25.6	-1.1	-1.6
W.Trans	21	19.4	---	---

* , ** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE XIII
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR GRAIN YIELD

F ₁ Hybrid or Parent	Rank (High to Low)	Grain Yield	Hybrid Deviations	
			Mid-Parent	High-Parent
2108/6615D	1	14.1	5.7**	5.0**
2108/Aurora	2	13.3	5.4**	5.2**
Sage/Aurora	3	11.9	4.0**	3.7**
Sage/6615D	4	11.8	3.5**	2.8**
Atr71/Sage	5	9.3	1.8*	1.6
Atr71/2108	6	9.2	1.8*	1.6
6615D	7	9.1	---	---
Aurora	8	8.2	---	---
Sage/W.Trans	9	8.0	2.5**	0.3
2108	10	7.7	---	---
Sage	11	7.6	---	---
Aurora/W.Trans	12	7.5	1.8*	-0.7
2108/W.Trans	13	7.4	1.9*	-0.3
Atr71/6615D	14	7.3	-0.9	-1.8
Atr71	15	7.2	---	---
Sage/2108	16	6.2	-1.4	-1.4
Atr71/Aurora	17	5.8	-1.9*	-2.4*
6615D/Aurora	18	4.5	-4.1**	-4.5**
Atr71/W.Trans	19	4.2	-1.1	-3.0**
W.Trans	20	3.3	---	---
6615D/W.Trans	21	2.9	-3.2**	-6.1**

*,** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE XIV
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR PERCENT STERILITY

F ₁ Hybrid or Parent	Rank (Low to High)	Percent Sterility	Hybrid Deviations	
			Mid-Parent	High-Parent
Sage	1	1.6	---	---
2108	2	3.5	---	---
Sage/W.Trans	3	4.5	-5.3*	-13.4**
2108/Aurora	4	5.0	-6.0*	-13.6**
6615D	5	7.3	---	---
2108/W.Trans	6	7.5	-3.2	-10.5**
Sage/Aurora	7	8.3	-1.8	-10.3**
2108/6615D	8	10.1	4.8	2.9
Sage/2108	9	10.4	7.9**	6.9
Sage/6615D	10	10.4	6.0*	3.2
Aurora/W.Trans	11	11.6	-6.7**	-7.0*
Atr71/Sage	12	17.2	7.8**	0.0
Atr71	13	17.2	---	---
W.Trans	14	18.0	---	---
Aurora	15	18.6	---	---
Atr71/2108	16	23.2	12.8**	6.0*
Atr71/6615D	17	25.7	13.5**	8.5**
Atr71/W.Trans	18	48.3	30.7**	30.3**
Atr71/Aurora	19	54.6	36.7**	36.0**
6615D/Aurora	20	68.1	55.2**	49.5**
6615D/W.Trans	21	69.5	56.9**	51.5**

*,** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively,

TABLE XV
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR PLANT HEIGHT

F ₁ Hybrid or Parent	Rank (Tall to Short)	Plant Height	Hybrid Deviation	
			Mid-Parent	High-Parent
Sage/W.Trans	1	89.0	10.7**	5.2**
2108/W.Trans	2	85.9	5.3**	8.4**
W.Trans	3	83.8	----	----
Aurora/W.Trans	4	80.6	4.2**	-3.2
2108/6615D	5	80.3	6.9**	2.8
6615D/W.Trans	6	78.2	1.6	-5.6
2108	7	77.5	----	----
2108/Aurora	8	77.4	4.2**	-0.1
Sage/Aurora	9	77.1	6.2**	4.3
Atr71/W.Trans	10	76.6	1.6	-7.1**
Atr71/2108	11	76.1	4.2	-1.4
Sage/6615D	12	73.4	2.3	0.6
Sage	13	72.8	----	----
Sage/2108	14	72.5	-3.0	-5.0**
Atr71/Sage	15	71.4	1.7	-1.5
Atr71/Aurora	16	70.7	3.0	1.7
6615D/Aurora	17	70.4	1.2	1.0
6615D	18	69.4	----	----
Aurora	19	69.0	----	----
Atr71	20	66.4	----	----
Atr71/6615D	21	65.0	-2.9	-4.4*

*, ** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively.

TABLE XVI
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR HEADING DATE

F ₁ Hybrid or Parent	Rank (Early to Late)	Heading Date ¹	Hybrid-Deviation	
			Mid-Parent	High-Parent
2108/Aurora	1	28.8	-12.4**	-14.0**
Sage/6615D	2	29.5	-8.3**	-15.8**
2108/6615D	3	30.0	-6.5**	-12.8**
6615D	4	30.3	----	----
6615D/Aurora	5	30.5	-4.4**	-9.0**
Atr71	6	30.8	----	----
Atr71/6615D	7	31.5	1.0	0.8
Atr71/Aurora	8	32.0	-3.1*	-7.5**
Sage/Aurora	9	32.0	-10.4**	-13.3**
Atr71/2108	10	34.5	-2.3	-8.3**
6615D/W.Trans	11	36.0	-6.8**	-19.3**
Atr71/Sage	12	38.3	0.3	-7.0**
Aurora	13	39.5	----	----
Atr71/W.Trans	14	40.8	-2.3	-14.5**
2108	15	42.8	----	----
Aurora/W.Trans	16	43.5	-3.9**	-11.8**
Sage/2108	17	44.0	0.0	-1.3
Sage	18	45.3	----	----
Sage/W.Trans	19	48.5	-1.8	-6.8**
2108/W.Trans	20	48.8	-0.3	-6.5**
W.Trans	21	55.3	----	----

¹Days after March 31

*,** Hybrid-parent contrast is significant at 0.05 and 0.01 levels of probability, respectively.

TABLE XVII
PARENTAL AND F₁ RANKED MEANS AND HYBRID-PARENT
DEVIATIONS FOR PERCENT PROTEIN

F ₁ Hybrid or Parent	Rank (High to Low)	Percent Protein	Hybrid Deviations	
			Mid-Parent	High-Parent
6615D/W.Trans	1	18.6	3.2**	2.3**
6615D/Aurora	2	18.6	3.5**	2.9**
Atr71/Aurora	3	17.2	1.7**	1.6**
Atr71/W.Trans	4	17.1	1.3**	0.8**
W.Trans	5	16.3	---	---
Sage/W.Trans	6	16.0	0.6**	-0.3
Atr71/6615D	7	16.0	1.1**	0.6*
2108/W.Trans	8	15.8	0.4	-0.6*
Aurora	9	15.7	---	---
Atr71	10	15.3	---	---
Atr71/2108	11	15.2	0.3	-0.2
Aurora/W.Trans	12	15.1	-0.9**	-1.2**
Atr71/Sage	13	14.6	-0.3	-0.7**
2108	14	14.5	---	---
Sage/6615D	15	14.5	0.0	0.0
6615D	16	14.5	---	---
Sage	17	14.4	---	---
2108/6615D	18	14.4	-0.1	-0.1
Sage/Aurora	19	14.3	-0.7**	-1.4**
2108/Aurora	20	14.1	-1.0**	-1.6**
Sabe/2108	21	13.8	-0.7**	-0.7**

*,** Hybrid-parent contrast is significant at the 0.05 and 0.01 levels of probability, respectively.

VITA

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