To the Graduate Council:

I am submitting herewith a dissertation written by Paul Joseph Linnen entitled "Inheritance, Generation Prediction, and Interrelationships Among Quantitative Characteristics in Four Triticum aestivum L. em Thell Cultivars." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Plant and Soil Science.

Vernon H. Reich

Vernon H. Reich, Major Professor

We have read this dissertation
and recommend its acceptance:

Fred J Allen

Dennis West

B. V. Conger

Sophronia W. Ward

J. B. McLaren

Accepted for the Council:

Lew Minkel

The Graduate School

INHERITANCE, GENERATION PREDICTION, AND INTERRELATIONSHIPS AMONG QUANTITATIVE CHARACTERISTICS IN FOUR *TRITICUM AESTIVUM* L. EM THELL CULTIVARS

A Dissertation

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ABSTRACT

The soft red winter wheat cultivars 'Arthur', 'Sullivan', 'Blueboy', and 'Pioneer S76', and their F_1, reciprocal F_1, F_2, reciprocal F_2, and backcrosses of the F_1 to the parents were grown in a randomized complete block design at three locations. A genetic model was developed to estimate additive, dominance, first-order epistatic, and reciprocal effects for grain yield, primary yield components, and several morphological characteristics. For all characteristics the gene action was not all additive, and dominance and/or epistatic types of gene action were also detected.

Prediction equations were developed to use the genetic parameters to estimate parental, F_1, reciprocal F_1, F_∞, reciprocal F_∞, and backcross selfed to homozygosity (BCS_∞) values of all characteristics.

Compared to the midparent values, the F_1 hybrids tended to have a higher grain yield, weight per seed, spikes per square meter, test weight, plant height, seedling and spring vigor; a later maturity date, and a longer grain filling period.

Grain yield was positively correlated with a longer grain filling period, an increased resistance to powdery mildew, larger spike and top internode surface area, and increased seedling and spring vigor.

Compensation between the primary yield components, seeds per square meter and weight per seed, was observed. The most favorable compensation pattern in terms of high grain yield was the one that produced the highest number of seeds per square meter. This type of pattern was exhibited by the highest yielding F_1 crosses Blueboy x Pioneer S76 and reciprocal.

Such a favorable compensation pattern indicates that sink size during grain filling as measured by the number of seeds per square meter may be a favorable selection criteria.

Results indicate that selection for the improvement of wheat grain yield should be based on increasing the sink size to ensure full utilization of available assimilate sources and on increasing the source capacity especially during the grain filling period.

Using the predicted values of the F_{∞} and BCS_{∞} generation and on the basis of sink size and source capacity, the advanced generations of the Arthur x Pioneer S76 or reciprocal F_1 crosses, or the Arthur x Pioneer S76 or reciprocal backcrosses to either parent were selected as potentially favorable populations for the development of new cultivars.

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CHAPTER I

INTRODUCTION

Grain yield in wheat is the major economic product and the result of many processes preceeding it. Engledow and Wadham (1924) are credited with the first analysis of grain yield components. Grafius (1956) described the contributions of the three primary grain yield components; spikes per unit area, seeds per spike, and weight per seed; as axes of a three-dimensional space. Grain yield is the product of these three axes and can be represented by the volume of the space. Other characteristics including disease resistance (Bridgford and Hayes, 1931), spike volume (Walton, 1971), dimensions of the flag leaf (Simpson, 1968), spike and flag leaf sheath length (Hsu and Walton, 1971), days to anthesis (Walton, 1971), and grain filling period (Gebeyehou et al., 1982) have been identified as being related in some way to grain yield in wheat. Since these characters affect grain yield by altering one or more of the primary yield components, they have been called secondary yield components (Duarte and Adams, 1972).

Two different models, yield component compensation and the source-sink relationship, have been developed to elicit the interrelationships among the components of grain yield. Yield component compensation (Adams, 1967; Adams and Grafius, 1971) is viewed as a response of the developmentally flexible primary yield components to limited environmental and metabolic resources. Such compensation is exhibited by the negative correlations often found among one or more of the yield components (Grafius, 1970). The source-sink model is the result of

numerous studies on the relationship between different sources of assimilates such as leaves, and sinks or destinations of those assimilates such as an inflorescence (Quinlan and Sagar, 1962; Doodson et al., 1964; Voldeng and Simpson, 1967; Puckridge, 1969; Rawson and Hofstra, 1969; Monyo and Wittington, 1973; Cook and Evans, 1978). The results of source-sink relationship studies often suggest characteristics which could be used by the plant breeder as selection criteria for the improvement of grain yield.

To effectively use these characteristics as selection criteria, wheat breeders need to have a thorough understanding of the interrelationships that exist among these characters. It would also be useful to have a knowledge of the quantitative inheritance of these characters and to be able to predict the value of these characters in advance generations so that limited resources could be allocated to only the more promising crosses and their descendants.

The objectives of this research were (1) to estimate additive, dominance, and first-order epistatic genetic parameters for the four soft red winter wheat cultivars 'Arthur', 'Sullivan', 'Blueboy', and 'Pioneer S76' for easily measurable characters shown by previous work to be related in some manner to grain yield (2) to use the genetic parameter estimates to predict the parental, F_1, F_∞, and backcross selfed to complete homozygosity (BCS_∞) generations for grain yield, primary yield components, and secondary yield components, and (3) to evaluate the interrelationships among primary and secondary yield components and their ultimate effect on grain yield.

CHAPTER II

LITERATURE REVIEW

Source-Sink Model

Crop physiologists have studied the interrelationships among several different morphological characteristics in an attempt to identify factors which affect wheat grain yield. The results of these studies can often be interpreted in terms of the source-sink model. The source can be defined as the structure where photosynthetic assimilates are produced and the sink as the structure to which these assimilates move. It is often proposed to plant breeders that such characteristics be altered by selection in order to relax limitations and increase grain yields.

The spike and flag leaf are the most important sources of assimilates for seed growth (Quinlan and Sagar, 1962; Voldeng and Simpson, 1967; Rawson and Evans, 1971; Patrick, 1972). Estimates of their contribution to grain yield vary with the technique used, genotype, environment, and time of measurement over the grain filling period (Puckridge, 1969; Rawson and Hofstra, 1969; Evans and Rawson, 1970; Rawson and Evans, 1970; Rawson and Evans, 1971; Kaul, 1974; Bidinger et al., 1977). Shading experiments indicate that the spike and flag leaf contribute between 24-49% and 35-50% respectively to the final seed weight (Voldeng and Simpson, 1967).

The ability of a sink, such as the spike, to obtain assimilates from a source is dependent on the size of the sink, its distance from

the source, and the presence of competing sinks. Larger sinks are able to draw on assimilates from more distant sources and obtain a disproportionately greater amount than a smaller, closer sink. In general, a smaller sink must depend more heavily on assimilates from sources closer to it (Rawson and Hofstra, 1969; Patrick, 1972; Cook and Evans, 1978).

Stress applied at or immediately after anthesis may affect grain yield by decreasing the amount of seed set (Willey and Holliday, 1971; Sofield et al., 1977). The major influence of stress during the grain filling period is to decrease seed weight (Wardlaw, 1970; Willey and Holliday, 1971; Fischer and Aguilar, 1976).

To a certain extent, the change in seed size caused by environmental stress during grain filling is dependent on the pre-anthesis environment. Stress during spike development would decrease the sink size and, therefore, the demand during grain filling. This demand can usually be met by the plant even in a limited stress environment. A favorable environment during spike development would increase sink size and, hence, demand during grain filling. Under post-anthesis stress conditions, this demand might not be met and seed weight would be affected (Wardlaw, 1970; Fischer, 1975; Fischer and Aguilar, 1976; Fischer et al., 1977; Cook and Evans, 1978).

Under nonstress conditions, the pre-anthesis assimilates usually contribute less than 10% to the grain yield (Stoy, 1979). Stress caused by shading or drought may increase pre-anthesis assimilate contribution to 27% or more (Bidinger et al., 1977).

Yield Components

The contribution of the components of yield to the final grain yield can be represented geometrically as the X, Y, and Z axes of a three-dimensional space. In a general way, the axes are as follows: X, the number of fruiting bodies (pods, spikes, etc.) per unit area; Y, the number of seeds per fruiting body; and Z, the average weight of each seed (Grafius, 1956; Grafius and Wiebe, 1959). In wheat these components would be the number of spikes per unit area (X), the number of seeds per spike (Y), and the weight per seed (Z). The final grain yield per unit area is the product of X, Y, and Z; and it is represented by the volume of the space. The X, Y, and Z characteristics are called primary yield components since their product is equivalent to the final yield. Other characteristics such as leaf size or leaf number are called secondary yield components since their effect on yield can only be through one or more of the all-inclusive primary yield components (Duarte and Adams, 1972).

Yield component compensation. Adams (1967) has cited several examples of negative correlations among the components of yield for several different crop plants. Adams feels that such negative correlations are a response to competitional forces operating on the developmentally flexible components of yield. In addition to the usual explanations of pleiotropy and linkage for genetic correlations, Adams adds the possibility of developmentally induced relationships among the components caused by competition within the plant for a limited

nutrient supply.

Adams (1967) has presented two different models to represent compensation. In one model the assimilates are supplied at a continuous rate, while in the other, they are supplied in an oscillating pattern. Under the continuous input model, the level obtained by a yield component is determined mainly by the level of any previous component. While under the oscillation model, the level which a yield component attains is mainly influenced by the position of the cycle during the development of that component. The first component in a developmental sequence may establish the metabolic input oscillation. Subsequent components may not only be affected by the phase of oscillation during their development; but they may also modify the pattern and, hence, affect later developing components.

The results of Johnson et al. (1966) were presented by Adams (1967) as an example of the occurrence of yield component compensation. Johnson et al. (1966) compared four winter wheat varieties for yield and yield components. They found a marked difference between the compensation patterns of the highest yielding cultivar, 'C.I. 13678', and the lowest yielding cultivar, 'Pawnee'. C.I. 13678 produced a greater number of seeds per spike than Pawnee, but Pawnee tended to have a higher number of spikes per plant and a higher seed weight. It appears that compensation among yield components is an inevitable situation whenever stress occurs; however, the manner in which different genotypes compensate for stress varies with some methods appearing to be more favorable than others. In this example C.I. 13678 appears

to have achieved the more optimum combination of components given the environmental stresses encountered during the study.

The Relationship Between Grain Yield and Several Other Characteristics

As several studies have shown, the components of yield are significantly correlated with the final grain yield in wheat (Bridgford and Hayes, 1931; Simpson, 1968; Hsu and Walton, 1971; Walton, 1971). Many other morphological and developmental characteristics of wheat have also been identified as being related in some way to the final grain yield. Such characteristics include the following: the level of any prevalent diseases (Bridgford and Hayes, 1931), spike volume (Walton, 1971), dimensions of the flag leaf (Simpson, 1968; Walton, 1971), spike length, flag leaf sheath length (Hsu and Walton, 1971), and days to anthesis (Walton, 1971).

Quantitative Inheritance in Wheat

The diallel (Griffing, 1956) and the generation means analysis (Hayman 1958, 1960) are the most common analyses used to investigate the inheritance of quantitative characters in wheat. Due to the difficulty of obtaining F_1 seed, experiments are usually only conducted at a single location and at low plant populations.

Significant additive genetic effects are common for wheat grain yield and yield components. Significant dominance effects are prevalent for grain yield, with estimates of the level of dominance ranging from partial to overdominance depending on the cross (Whitehouse et al., 1958; Johnson et al., 1966; Anwar and Chowdhry, 1969; Walton,

1969; Paroda and Joshi, 1970; Sun et al., 1972; Monyo and Whittington, 1973; Widner and Lebsock, 1973; Sharma and Ahmad, 1978). Some narrow sense heritability estimates for yield are 0.06 (Paroda and Joshi, 1970), 0.17 (Fonseca and Patterson, 1968), 0.26 (Kronstad and Foote, 1964), and 0.12-0.41 (Anwar and Chowdhry, 1969).

Estimates of the level of dominance for spike number range from partial to overdominance (Kronstad and Foote, 1964; Hsu and Walton, 1970; Paroda and Joshi, 1970; Monyo and Whittington, 1973). Partial dominance has been found for spikelets per spike (Rahman et al., 1978), seeds per spike (Kronstad and Foote, 1964; Johnson et al., 1966; Paroda and Joshi, 1970; Singh and Sharma, 1976), and seed weight (Johnson et al., 1966; Paroda and Joshi, 1970; Bhatt, 1972; Widner and Lebsock, 1973). Narrow sense heritability estimates presented by Fonseca and Patterson (1968) for yield components were 0.34 for spikes per plant, 0.47 for seeds per spike, and 0.15 for seed weight.

Law et al., (1978) found plant height to be positively correlated with yield. Significant additive and dominance effects and heterosis have been detected for plant height (Kronstad and Foote, 1964; Fonseca and Patterson, 1968; Anwar and Chowdhry, 1969; Bhatt, 1972; Singh and Singh, 1978). Some plant height narrow sense heritability estimates are 0.21-0.40 (Anwar and Chowdhry, 1969), 0.55 (Fonseca and Patterson, 1968), and 0.83 (Kronstad and Foote, 1964).

Significant additive effects have been demonstrated for spike length (Walton, 1969; Singh and Singh, 1978) and spike extrusion length (Walton, 1969). Significant additive and dominance effects have been

found for flag leaf area (Walton, 1969; Monyo and Whittington, 1973; McNeal and Berg, 1977), flag leaf length (Hsu and Walton, 1970), and date of anthesis (Hsu and Walton, 1970).

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CHAPTER III

MATERIALS AND METHODS

Genetic Materials

Entries consisted of the four soft red winter wheat cultivars 'Arthur', 'Sullivan', 'Blueboy', and 'Pioneer S76'; their 12 F_1 and reciprocal F_1 crosses; the 12 F_2 families derived from the F_1 crosses; and the 12 backcrosses of the F_1's to the cultivars with the cultivars always as the female parent. All the F_1 and backcross seed was produced by manual emasculation and pollination. F_2 seed was produced by natural self-pollination.

Experimental Design and Procedures

The experiment was arranged in a randomized complete block design with four replications and was conducted at: (1) Plateau Experiment Station near Crossville, (2) Tobacco Experiment Station near Greenville, and (3) Plant Sciences Field Laboratory on Government Farm Road near Knoxville during the 1981-82 winter wheat season.

The experimental unit consisted of a single row plot bordered on both sides at a distance of 30.5 cm by a single cultivar. Each plot contained 96 seeds of the appropriate entry. Plots were seeded using a manually operated single row funnel seeder, and guard rows were planted using a manually operated "planet junior" seeder. The planned plot length was 244 cm, and the actual plot length was measured after seedling emergence. Due to the limited amount of seed, all entries did not

occur in all replications but were present at least once at each location.

Plots were planted at Knoxville, Crossville, and Greenville on 24, 22, and 29 September 1981, respectively. Plots were fertilized prior to planting according to the soil tests or recommended practice at each location. The pH was adjusted to near 6.5 by the application of agricultural lime. Nitrogen was applied as a top dress in the form of ammonium nitrate at a rate of 52 kg N/ha in early March of 1982.

The characteristics studied are listed in Table 1 along with the unit- and basis- of measurement. Ten subplot samples were identified in each plot by tagging ten tillers. The average of the subplot samples were used to evaluate entries for the subplot characters listed in Table 1. Tags were occasionally lost from the samples resulting in less than ten observations per plot for some subplot characters.

Plots were harvested in Knoxville, Crossville, and Greenville on 19, 25, and 22 June 1982, respectively. A motorized cutterbar was used to cut the plants near the ground level, and subplot samples were then separated from the rest of the plot. The remaining portion of the plot was threshed using a Vogel plot thresher. The grain was stored at room temperature for several weeks before weighing to allow the moisture level to equilibrate.

Statistical Analysis

The entries were analyzed according to the genetic model developed by Moreno-Gonzalez and Dudley (1981) with the addition of reciprocal effects. By letting P_i stand for the ith parent; $F_{1(ij)}$, the cross

Table 1. The unit- and basis- of measurement of the observed and derived characters examined in this study.

Character	Unit of measurement	Basis of measurement
Grain yield per square meter	Grams/sq. meter	Plot
Weight per seed	Milligrams	Plot
Seeds per spike	Number	Subplot
Spikes per square meter	Number	Plot
Seeds per square meter	Number	Plot
Spikelets per spike	Number	Subplot
Seeds per spikelet	Number	Subplot
Test weight	Grams/liter	Plot
Days to heading	Days	Plot
Days to anthesis	Days	Plot
Days to maturity	Days	Plot
Grain filling period	Days	Plot
Percentage of powdery mildew	Percent	Plot
Spike surface area	Sq. centimeters	Subplot
Plant height	Centimeters	Plot
Top internode surface area	Sq. centimeters	Subplot
Seedling vigor	1-5 Scale	Plot
Spring vigor	1-7 Scale	Plot
Flag leaf area	Sq. centimeters	Subplot

between parent i and parent j; $F_{2(ij)}$, the self of the $F_{1(ij)}$ cross; $BC_{(i,ij)}$, the backcross of $F_{1(ij)}$ or $F_{1(ji)}$ to the ith parent; and $BC_{(j,ij)}$, the backcross of $F_{1(ij)}$ or $F_{1(ji)}$ to the jth parent then the expectations of the means of the various generations expressed in terms of the genetic parameters can be written as follows:

$$P_i = u + a_i + aa_i$$

$$F_{1(ij)} = u + 1/2(a_i + a_j) + D_{ij} + dd_{ij} + aa_{ij} + r_{ij}$$

$$F_{2(ij)} = u + 1/2(a_i + a_j) + 1/2D_{ij} + 1/4dd_{ij} + aa_{ij} + r_{ij}$$

$$BC_{(i,ij)} = u + 3/4a_i + 1/4a_j + 1/2D_{ij} + 3/8aa_i - 1/8aa_j + 3/4aa_{ij} + 1/4dd_{ij} + 1/4ad_{ij}$$

$$BC_{(j,ij)} = u + 1/4a_i + 3/4a_j + 1/2D_{ij} - 1/8aa_i + 3/8aa_j + 3/4aa_{ij} + 1/4dd_{ij} - 1/4ad_{ij}$$

where u is the overall mean, a_i is the additive effect of cultivar P_i, D_{ij} is the mixed dominance effect of the P_i x P_j cross, aa_i is the additive by additive effect of cultivar P_i, aa_{ij} is the specific additive by additive effect of the P_i x P_j cross, dd_{ij} is the dominance by dominance effect of the P_i x P_j cross, ad_{ij} is the additive by dominance effect of the P_i x P_j cross, and r_{ij} is the reciprocal effect of the P_i x P_j cross.

An analysis of variance was used to remove replication effects and to test the significance of the genetic effects. The locations and cultivars used in this study were considered to be a fixed set (Eisenhart, 1947), and all F-tests were made with the three-way interaction of location x replication x entry as the error term. Data on spring vigor was only available from the Crossville location.

Measurements on flag leaf area were not taken on all entries at all locations resulting in a loss of the estimate of location by entry interaction for these characters.

The estimated genetic effects were used to calculate the predicted parental, F_1, F_∞, and BC selfed to homozygosity values (BCS_∞) for each character using the least squares genetic parameter estimates. The parental predicted values were calculated using the above expectation for the parental mean. The F_1, F_∞, and BCS_∞ were calculated as follows:

$$F_{1(i,j)} = u + 1/2(a_i + a_j) + D_{ij} + dd_{ij} + aa_{ij} + 1/2r_{ij}$$

$$F_{1(j,i)} = u + 1/2(a_i + a_j) + D_{ij} + dd_{ij} + aa_{ij} - 1/2r_{ij}$$

$$F_{\infty(i,j)} = u + 1/2(a_i + a_j) + aa_{ij} + 1/2r_{ij}$$

$$F_{\infty(j,i)} = u + 1/2(a_i + a_j) + aa_{ij} - 1/2r_{ij}$$

$$BCS_{\infty(i,ij)} = u + 3/4a_i + 1/4a_j + 3/8aa_i - 1/8aa_j + 3/4aa_{ij}$$

$$BCS_{\infty(j,ij)} = u + 1/4a_i + 3/4a_j - 1/8aa_i + 3/8aa_j + 3/4aa_{ij}$$

Percentage of heterosis was calculated on a midparent basis as $[(F_1 - (\text{midparent value}))\,100\,] / (\text{midparent value})$. Percentage of inbreeding was calculated as $[\,(F_1 - F_2)\,100\,] / F_1$. Following transformation to a logarithmic scale, the relationship among yield and the primary yield components; weight per seed, seeds per spike, and spikes per square meter; was investigated by a path coefficient analysis (Li, 1956). The least squares means for grain yield and the primary yield components for the parental and F_1 generations were standardized using the formula $[x_i - (\Sigma x_i / n)] / [(\Sigma x_i^2 - (\Sigma x_i)^2 / n)) / (n - 1)]$ where x_i is a least squares mean, and n is the number of least squares means.

Following this transformation, the standardized traits will be on the same scale with a mean of zero and a standard deviation of one. Standardized least squares means were used to further clarify the relationship among entries and the characteristics of each entry. Standardized least squares means of the F_1 generation were used to examine compensation patterns and source-sink relationships. Simple product moment correlations were used to determine the associations among yield and primary yield components and the associations among the secondary yield components and the primary yield components.

CHAPTER IV

RESULTS

The mean squares for the characteristics investigated are listed in Tables 2 through 5 . Location effects, where estimable, were significant at the 0.01 level for all characteristics. Highly significant differences among entries were detected for all characters. Additive effects were highly significant for all characteristics with the exception of grain yield which was nonsignificant. Dominance effects were highly significant for all characters except for seeds per spike which was nonsignificant.

One or more of the epistatic effects were significant at least at the 0.05 level for all characters with the exception of test weight. Reciprocal effects were significant at the 0.01 level for spikes per square meter, test weight, days to heading, days to anthesis, days to maturity, and seedling vigor. Reciprocal effects were significant at the 0.05 level for seeds per spikelet and percentage of powdery mildew.

Where estimated, the location x entry interactions were highly significant for all characters except for seeds per spike, spikes per square meter, and spike surface area which were significant at the 0.05 level, and seeds per spikelet, plant height, top internode surface area and seedling vigor which were nonsignificant. The variation due to location by additive, dominance, or epistatic genetic effects was in general much smaller than the genetic effects alone. When the location by genetic effects were significant, they were only significant at the

Table 2. Mean squares for grain yield per square meter and the primary yield components: weight per seed, seeds per spike, spikes per square meter, and seeds per square meter.

Source of variation	df	Mean squares				
		Yield	Wt./seed	Seeds/spike	Spikes/sq. m	Seeds/sq. m
		g/sq. m	mg	no.		
Location	2	707799.1**	1643.03**	273.92**	325983.1**	441661003**
Entry	39	7553.7**	80.81**	174.27**	14929.5**	13933216**
Additive effects	3	3765.3	20.19**	627.11**	75710.6**	7549862**
Dominance effects	6	22852.8**	479.85**	664.74**	21170.3**	49807479**
Add x Add (lines)	4	15464.6**	28.20**	20.97	21075.9**	30491552**
Add x Add (specific)	2	14836.6**	0.77	62.46**	10896.5*	16013138**
Dom x Dom	6	3875.6*	5.00	24.31*	4773.6	4732652*
Add x Dom	6	1076.8	5.95*	42.05**	3634.9	2338524
Reciprocal	6	3054.8	2.32	18.40	7742.6**	3897304
Residual	6	1281.7	3.23	13.32	5220.0	1277920
Loc x Entry	78	2127.6**	4.29**	12.25*	3699.3*	2764153**
Loc x Add	6	655.3	3.37	9.36	2262.6	612287
Loc x Dom	12	1970.4	3.79	8.48	3592.2	3334876*
Loc x (Add x Add) (lines)	8	1086.5	4.31	6.61	2208.3	1868488
Loc x (Add x Add) (specific)	4	4407.8*	1.87	18.19	6387.1*	5994850*
Loc x (Dom x Dom)	12	1630.5	3.69	9.24	2953.6	2965479
Loc x (Add x Dom)	12	1202.3	3.68	18.83*	2281.1	1336172
Loc x Reciprocal	12	1080.4	4.32	8.60	2746.5	1181848
Loc x Residual	12	2081.4	2.86	0.00	2177.0	2533017
Error	289	1499.2	2.76	8.82	2646.5	1854298

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

Table 3. Means squares for the secondary yield components: spikelets per spike, seeds per spikelet, test weight, days to heading, days to anthesis, and days to maturity.

Source of variation	df	Mean squares					
		Spikelets /spike	Seeds/ spikelet	Test wt.	Days to heading	Days to anthesis	Days to maturity
		---------no.--------		g/L	---------- days ----------		
Location	2	420.760**	1.463**	212.09**	5850.51**	5179.15**	1257.28**
Entry	39	2.864**	0.484**	71.11**	22.05**	18.62**	13.72**
Additive effects	3	27.103**	1.184**	504.30**	238.66**	199.87**	68.26**
Dominance effects	6	1.372**	2.264**	156.65**	4.08**	4.74**	24.08**
Add x Add (lines)	4	1.642**	0.019	3.50	7.12**	7.74**	19.69**
Add x Add (specific)	2	2.037**	0.137**	3.62	3.38*	4.87**	5.65*
Dom x Dom	6	1.270**	0.042	7.89	0.89	0.53	1.19
Add x Dom	6	0.503	0.086**	3.09	0.48	0.32	1.06
Reciprocal	6	0.331	0.064*	13.41**	5.12**	3.27**	7.47**
Residual	6	0.107	0.040	21.83**	6.77**	5.77**	6.22**
Loc x Entry	78	0.695**	0.032	9.69**	1.85**	1.71**	2.93**
Loc x Add	6	0.793*	0.034	4.92	1.15	0.53	1.50
Loc x Dom	12	0.493	0.033	5.44	0.56	0.46	2.42
Loc x (Add x Add) (lines)	8	0.819*	0.045	4.68	0.89	0.95	1.32
Loc x (Add x Add) (specific)	4	0.020	0.040	2.36	0.03	0.16	3.45
Loc x (Dom x Dom)	12	0.391	0.032	6.98	0.52	0.52	3.06
Loc x (Add x Dom)	12	0.341	0.044	2.80	0.77	1.44	1.96
Loc x Reciprocal	12	0.402	0.031	8.01*	1.21	1.47	2.32
Loc x Residual	12	0.222	0.000	2.82	1.37	1.06	2.04
Error	289	0.329	0.029	4.17	1.11	1.04	1.79

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

Table 4. Mean squares for the secondary yield components: grain filling period, percentage of powdery mildew, spike surface area, plant height, top internode surface area, and seedling vigor.

Source of variation	df	Mean squares					
		Grain filling period	Powdery mildew	Spike surface area	Plant height	Top internode surface area	Seedling vigor
		days	%	sq. cm	cm.	sq. cm	rate
Location	2	1507.89**	57080.7**	46.31**	8137.4**	566.8**	18.76**
Entry	39	12.73**	798.9**	44.60**	251.4**	141.3**	2.91**
Additive effects	3	59.30**	8437.0**	11.79**	432.9**	798.0**	9.09**
Dominance effects	6	36.06**	160.5	20.97**	682.7**	281.4**	2.34**
Add x Add (lines)	4	12.43**	561.6**	5.22	510.4**	75.0*	10.22**
Add x Add (specific)	2	0.23	69.6	10.94*	116.6**	45.1	1.71**
Dom x Dom	6	2.16	74.8	4.34	43.5*	83.5**	0.40
Add x Dom	6	0.73	66.7	2.03	26.7	37.2	0.82*
Reciprocal	6	2.42	165.2*	3.27	11.9	35.9	2.38**
Residual	6	2.59	122.8	0.00	24.1	22.1	1.13**
Loc x Entry	78	4.44**	262.2**	3.72*	16.2	36.0	0.41
Loc x Add	6	0.75	60.2	2.03	10.5	29.3	0.60
Loc x Dom	12	2.63	85.0	2.47	9.7	41.0	0.28
Loc x (Add x Add) (lines)	8	1.93	107.1	1.34	10.3	31.2	0.47
Loc x (Add x Add) (specific)	4	3.98	80.0	5.48	7.7	74.1*	0.19
Loc x (Dom x Dom)	12	3.31	82.3	2.55	9.5	44.0	0.24
Loc x (Add x Dom)	12	1.72	26.2	4.11	21.3	52.9*	0.39
Loc x Reciprocal	12	3.78*	126.8	2.32	13.1	11.2	0.34
Loc x Residual	12	2.45	50.7	0.00	3.2	11.5	0.28
Error	289	1.94	76.5	1.25	15.5	28.0	0.32

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

Table 5. Mean squares for the secondary yield components: spring vigor, and flag leaf area.

Source of variation	df	Spring vigor	df	Flag leaf area
		rate		sq cm
Location	0		2	59.21**
Entry	39	1.981**	39	69.01**
Additive effects	3	4.795**	3	714.35**
Dominance effects	6	3.214**	6	31.40**
Add x Add (lines)	4	4.555**	4	22.73*
Add x Add (specific)	2	0.308	2	9.36
Dom x Dom	6	0.831	6	8.76
Add x Dom	6	0.429	6	5.92
Reciprocal	6	1.246	6	14.45
Residual	6	1.618*	6	12.61
Error	97	0.607	209	8.86

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

0.05 level. The location x reciprocal interaction was significant at the 0.05 level for test weight and grain filling period.

The residual and location by residual sources of variation provide estimates of the lack of fit due to higher order epistatic effects and/or linkage and due to higher order location x epistatic effects and/or location x linkage interactions, respectively (Gardner and Ebberhart, 1966). Where estimated, the location x residual interactions were nonsignificant for all characteristics. Residual effects were significant for test weight, days to heading, days to anthesis, days to maturity, seedling and spring vigor. The coefficient of determination with and without reciprocal effects in the model along with the difference between the two coefficients is listed in Table 6 for each characteristic studied. The difference between the two coefficients indicates the amount of the variation in the model including residual effects that is due to higher order epistatic effects and/or linkage.

The observed least squares means and predicted values for the parental and F_1 generations are listed in Tables 7 through 13. An examination of the standard errors for each character of the F_1 generation reveals that the standard errors are actually smaller for the predicted values than for the observed least squares means. A comparison of the standard errors for observed least squares means and predicted values for the parental generation indicates that the standard errors are often identical or nearly so.

Table 6. The coefficient of determination for the model with and without the residual effects and the difference between the two.

	Coefficient of determination		
	With	Without	Difference
Grain yield per square meter	0.831	0.818	0.013
Weight per seed	0.907	0.901	0.006
Seeds per spike	0.776	0.772	0.004
Spikes per square meter	0.686	0.662	0.024
Seeds per square meter	0.770	0.754	0.016
Spikelets per spike	0.924	0.921	0.003
Seeds per spikelet	0.753	0.750	0.003
Test weight	0.775#	0.745	0.030
Days to heading	0.978#	0.974	0.004
Days to anthesis	0.977#	0.973	0.004
Days to maturity	0.879#	0.864	0.015
Grain filling period	0.887	0.878	0.009
Percentage of powdery mildew	0.899	0.893	0.006
Spike surface area	0.758	0.758	0.000
Plant height	0.866	0.861	0.005
Top internode surface area	0.576	0.562	0.014
Seedling vigor	0.684#	0.649	0.035
Spring vigor	0.620#	0.557	0.063
Flag leaf area	0.615	0.599	0.016

Significant residual effect at the 0.05 level.

Table 7. Least squares means and standard errors† of the observed and predicted values for grain yield per square meter, weight per seed, and seeds per head for the parental and F_1 generation.

Entry#	Yield		Wt./seed		Seeds/spike	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	g/sq. m		mg		no.	
Parents						
A	209.0(11.2)	212.2(11.2)	24.29(0.48)	24.33(0.48)	30.51(0.86)	30.39(0.83)
S	176.2(11.2)	176.6(11.2)	23.99(0.48)	24.00(0.48)	28.40(0.86)	28.37(0.84)
B	152.7(11.2)	153.0(11.2)	23.92(0.48)	23.93(0.48)	34.50(0.86)	34.47(0.84)
P	198.9(11.2)	199.8(11.2)	23.41(0.48)	23.44(0.48)	35.90(0.86)	36.02(0.84)
F_1						
A x S	249.5(11.8)	248.3(08.7)	25.73(0.51)	25.65(0.37)	30.15(0.91)	29.57(0.65)
S x A	240.7(11.2)	242.9(08.5)	25.35(0.48)	25.43(0.37)	28.30(0.86)	28.81(0.64)
A x B	246.3(13.0)	236.8(09.5)	31.05(0.56)	30.86(0.41)	27.05(1.00)	28.16(0.71)
B x A	236.2(12.4)	234.5(09.7)	30.51(0.53)	30.72(0.40)	28.54(0.95)	28.30(0.70)
A x P	224.5(13.0)	225.8(09.8)	32.29(0.56)	31.82(0.42)	22.96(1.00)	23.23(0.73)
P x A	234.2(13.0)	234.3(09.7)	31.21(0.56)	31.72(0.42)	22.59(1.00)	22.49(0.73)
S x B	229.8(11.2)	230.5(08.6)	31.13(0.48)	31.07(0.37)	24.71(0.86)	25.17(0.64)
B x S	234.5(11.8)	234.1(08.8)	31.22(0.51)	31.27(0.37)	25.98(0.91)	25.50(0.65)
S x P	210.0(13.0)	216.4(09.3)	32.23(0.56)	32.83(0.40)	21.58(1.00)	21.38(0.69)
P x S	233.6(11.2)	227.4(08.8)	33.48(0.48)	33.02(0.37)	21.67(0.86)	21.77(0.65)
B x P	296.9(15.9)	289.2(10.9)	25.44(0.68)	25.44(0.47)	39.08(1.22)	38.77(0.81)
P x B	279.6(12.4)	285.4(10.1)	25.87(0.53)	25.84(0.43)	38.13(0.95)	38.43(0.75)
LSD##	70.9		3.04		5.44	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 8. Least squares means and standard errors† of the observed and predicted values for spikes per square meter, seeds per square meter, and spikelets per spike for the parental and F_1 generation.

Entry#	Spikes/sq. m		Seeds/sq. m		Spikelets/spike	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	no.					
Parents						
A	278.2(14.8)	284.1(14.8)	8382(393)	8492(392)	17.05(0.17)	17.01(0.16)
S	253.8(14.8)	254.5(14.9)	7190(393)	7198(395)	17.76(0.17)	17.76(0.16)
B	176.3(14.8)	177.0(14.9)	6126(393)	6134(395)	18.86(0.17)	18.85(0.16)
P	223.4(14.8)	223.4(14.9)	8132(393)	8165(393)	18.55(0.17)	18.53(0.16)
F_1						
A x S	320.8(15.7)	327.5(11.6)	9589(415)	9555(307)	17.28(0.18)	17.41(0.13)
S x A	335.9(14.8)	331.3(11.4)	9363(393)	9429(300)	17.61(0.17)	17.48(0.12)
A x B	286.7(17.2)	267.7(12.7)	7739(456)	7476(335)	18.58(0.19)	18.59(0.14)
B x A	269.7(16.5)	265.4(12.5)	7603(436)	7427(331)	18.71(0.18)	18.70(0.14)
A x P	304.0(17.2)	303.1(13.0)	6856(456)	6947(342)	17.73(0.19)	17.83(0.14)
P x A	321.5(17.2)	322.9(12.9)	7337(456)	7299(342)	18.06(0.19)	17.94(0.14)
S x B	297.0(14.8)	292.7(11.4)	7294(393)	7301(300)	18.82(0.17)	18.75(0.12)
B x S	284.3(15.7)	289.4(11.6)	7292(415)	7302(307)	18.57(0.18)	18.65(0.13)
S x P	308.5(17.2)	310.9(12.4)	6495(456)	6497(327)	18.10(0.19)	18.22(0.14)
P x S	321.5(14.8)	318.4(11.6)	6891(393)	6836(307)	18.30(0.17)	18.21(0.13)
B x P	283.0(21.2)	284.0(14.5)	11156(560)	11015(383)	19.14(0.24)	19.13(0.16)
P x B	279.1(16.5)	278.7(13.3)	10574(436)	10709(351)	19.05(0.18)	19.06(0.15)
LSD##	94.2		2493		1.05	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (p), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 9. Least squares means and standard errors† of the observed and predicted values for seeds per spikelet, test weight, and days to heading for the parental and F_1 generation.

Entry#	Seeds/spikelet		Test wt.		Days to heading	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	no.		g/L		days	
Parents						
A	1.799(0.049)	1.795(0.048)	50.42(0.59)	50.57(0.61)	39.92(0.30)	39.85(0.32)
S	1.605(0.049)	1.604(0.048)	52.57(0.59)	52.57(0.61)	38.67(0.30)	38.66(0.32)
B	1.836(0.049)	1.835(0.048)	43.82(0.59)	43.84(0.61)	44.25(0.30)	44.25(0.32)
P	1.942(0.049)	1.948(0.048)	50.37(0.59)	50.49(0.61)	40.67(0.30)	40.60(0.32)
F_1						
A x S	1.755(0.052)	1.710(0.037)	52.48(0.62)	52.52(0.47)	38.41(0.32)	38.63(0.25)
S x A	1.619(0.049)	1.660(0.036)	52.62(0.59)	52.55(0.46)	38.83(0.30)	38.63(0.24)
A x B	1.471(0.057)	1.521(0.041)	52.88(0.68)	52.81(0.52)	41.44(0.35)	41.76(0.27)
B x A	1.526(0.055)	1.523(0.040)	53.00(0.65)	52.39(0.51)	41.65(0.34)	41.83(0.27)
A x P	1.294(0.057)	1.287(0.042)	53.95(0.68)	53.04(0.53)	39.44(0.35)	39.86(0.28)
P x A	1.221(0.057)	1.238(0.042)	52.33(0.68)	53.41(0.53)	39.89(0.35)	39.36(0.28)
S x B	1.321(0.049)	1.349(0.036)	53.20(0.59)	53.17(0.46)	40.83(0.30)	41.03(0.24)
B x S	1.403(0.052)	1.374(0.037)	53.33(0.62)	53.41(0.47)	41.43(0.32)	41.22(0.25)
S x P	1.127(0.057)	1.143(0.040)	54.39(0.68)	54.58(0.50)	38.89(0.35)	39.01(0.27)
P x S	1.183(0.049)	1.168(0.037)	54.93(0.59)	54.77(0.47)	39.08(0.30)	38.99(0.25)
B x P	2.060(0.070)	2.037(0.047)	47.67(0.84)	48.14(0.59)	41.77(0.43)	41.47(0.31)
P x B	2.004(0.055)	2.024(0.043)	48.98(0.65)	48.63(0.54)	41.15(0.34)	41.32(0.28)
LSD##	0.312		3.74		1.93	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 10. Least squares means and standard errors† of the observed and predicted values for days to anthesis, days to maturity, and grain filling period for the parental and F_1 generation .

Entry#	Days to anthesis		Days to maturity		Grain filling period	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	days					
Parents						
A	44.08(0.29)	44.00(0.30)	71.75(0.39)	71.70(0.39)	27.67(0.40)	27.71(0.40)
S	43.42(0.29)	43.41(0.31)	70.67(0.39)	70.66(0.40)	27.25(0.40)	27.25(0.41)
B	48.33(0.29)	48.33(0.31)	72.00(0.39)	72.00(0.40)	23.67(0.40)	23.67(0.41)
P	44.83(0.29)	44.75(0.31)	69.25(0.39)	69.20(0.40)	24.42(0.40)	24.46(0.40)
F_1						
A x S	42.62(0.31)	42.84(0.24)	71.24(0.41)	71.39(0.31)	28.62(0.42)	28.56(0.32)
S x A	43.08(0.29)	42.87(0.23)	71.58(0.39)	71.42(0.30)	28.50(0.40)	28.55(0.31)
A x B	45.69(0.34)	45.89(0.26)	73.61(0.45)	73.87(0.34)	27.92(0.47)	28.00(0.34)
B x A	45.83(0.33)	45.99(0.26)	73.60(0.43)	73.85(0.33)	27.77(0.45)	27.86(0.34)
A x P	43.69(0.34)	44.07(0.27)	72.61(0.45)	72.75(0.34)	28.92(0.47)	28.68(0.35)
P x A	44.25(0.34)	43.73(0.27)	72.39(0.45)	72.19(0.34)	28.14(0.47)	28.46(0.35)
S x B	44.83(0.29)	45.06(0.23)	73.58(0.39)	73.31(0.30)	28.75(0.40)	28.25(0.31)
B x S	45.42(0.31)	45.18(0.24)	73.15(0.41)	73.51(0.31)	27.73(0.42)	28.33(0.32)
S x P	43.36(0.34)	43.46(0.25)	72.61(0.45)	72.45(0.33)	29.26(0.47)	29.00(0.34)
P x S	43.58(0.29)	43.50(0.24)	71.92(0.39)	72.09(0.31)	28.33(0.40)	28.58(0.32)
B x P	45.72(0.42)	45.70(0.30)	73.13(0.55)	73.36(0.39)	27.41(0.57)	27.66(0.39)
P x B	45.47(0.33)	45.49(0.27)	72.79(0.43)	72.81(0.35)	27.32(0.45)	27.32(0.36)
LSD##	1.68		2.45		2.55	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 11. Least squares means and standard errors† of the observed and predicted values for percentage of powdery mildew, spike surface area, and plant height for the parental and F_1 generation.

Entry#	Powdery mildew		Spike surface area		Plant height	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	%		sq. cm		cm	
Parents						
A	23.23(2.52)	22.68(2.50)	19.96(0.46)	19.91(0.44)	82.97(1.14)	82.99(1.12)
S	20.13(2.52)	20.10(2.52)	19.04(0.46)	19.03(0.45)	80.86(1.14)	80.85(1.13)
B	42.58(2.52)	42.56(2.52)	26.43(0.46)	26.42(0.45)	83.50(1.14)	83.49(1.13)
P	10.79(2.52)	10.56(2.51)	23.95(0.46)	23.94(0.44)	75.35(1.14)	75.39(1.12)
F_1						
A x S	18.03(2.67)	20.99(1.96)	20.35(0.49)	20.31(0.35)	86.83(1.20)	87.27(0.88)
S x A	25.29(2.52)	22.41(1.92)	19.92(0.46)	19.95(0.34)	88.26(1.14)	87.88(0.86)
A x B	38.92(2.93)	40.82(2.14)	23.79(0.54)	23.99(0.38)	95.05(1.32)	94.68(0.96)
B x A	39.74(2.80)	40.36(2.12)	24.50(0.51)	24.36(0.37)	94.54(1.26)	95.21(0.95)
A x P	19.20(2.930	19.93(2.19)	22.74(0.54)	23.18(0.39)	89.41(1.32)	89.03(0.98)
P x A	18.31(2.93)	16.94(2.18)	23.88(0.54)	23.49(0.39)	88.70(1.32)	89.10(0.98)
S x B	38.73(2.52)	39.23(1.92)	23.34(0.46)	23.09(0.34)	93.24(1.14)	93.37(0.86)
B x S	38.53(2.67)	37.97(1.96)	22.62(0.49)	22.90(0.35)	93.39(1.20)	93.22(0.88)
S x P	21.20(2.93)	19.65(2.09)	23.68(0.54)	23.80(0.37)	93.08(1.32)	92.26(0.93)
P x S	15.87(2.52)	17.30(1.97)	23.80(0.46)	23.73(0.35)	92.18(1.14)	92.71(0.88)
B x P	27.74(3.60)	31.24(2.45)	26.86(0.66)	27.13(0.43)	90.62(1.62)	88.97(1.09)
P x B	34.68(2.80)	32.07(2.24)	27.25(0.51)	27.14(0.40)	87.77(1.26)	88.74(1.00)
LSD##	16.01		2.92		7.22	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 12. Least squares means and standard errors† of the observed and predicted values for top internode surface area, and seedling vigor for the parental and F_1 generation.

Entry#	Top internode surface area		Seedling vigor	
	Observed	Predicted	Observed	Predicted
	sq. cm		rate	
Parents				
A	56.03(1.53)	55.89(1.50)	2.92(0.16)	2.92(0.17)
S	49.61(1.53)	49.60(1.51)	2.08(0.16)	2.08(0.17)
B	58.58(1.53)	58.57(1.51)	2.75(0.16)	2.75(0.17)
P	55.15(1.53)	55.14(1.50)	1.17(0.16)	1.15(0.17)
F_1				
A x S	57.39(1.62)	57.11(1.17)	2.69(0.17)	2.75(0.13)
S x A	55.79(1.53)	56.00(1.15)	2.75(0.16)	2.70(0.13)
A x B	63.95(1.77)	63.86(1.28)	3.34(0.19)	3.32(0.14)
B x A	64.00(1.70)	64.50(1.26)	2.99(0.18)	3.04(0.14)
A x P	60.30(1.77)	60.95(1.31)	2.79(0.19)	2.71(0.15)
P x A	61.72(1.77)	60.95(1.30)	2.34(0.19)	2.43(0.14)
S x B	59.97(1.53)	59.37(1.15)	3.08(0.16)	3.31(0.13)
B x S	59.24(1.62)	59.71(1.17)	3.44(0.17)	3.19(0.13)
S x P	62.47(1.77)	61.74(1.25)	2.23(0.19)	2.39(0.14)
P x S	62.08(1.53)	62.50(1.17)	2.42(0.16)	2.31(0.13)
B x P	64.90(2.19)	64.63(1.46)	3.01(0.23)	2.91(0.16)
P x B	62.93(1.70)	63.42(1.34)	2.35(0.18)	2.50(0.15)
LSD##	9.69		1.04	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 13. Least squares means and standard errors† of the observed and predicted values for spring vigor, and flag leaf area for the parental and F_1 generation.

Entry#	Spring vigor		Flag leaf area	
	Observed	Predicted	Observed	Predicted
	rate		sq. cm	
Parents				
A	3.50(0.39)	3.45(0.41)	18.23(1.24)	18.18(1.25)
S	3.00(0.39)	3.00(0.41)	17.91(1.24)	17.85(1.25)
B	4.00(0.39)	4.00(0.41)	26.86(1.14)	26.84(1.15)
P	2.25(0.39)	2.20(0.41)	21.44(1.36)	21.41(1.36)
F_1				
A x S	4.75(0.39)	4.62(0.31)	17.52(1.24)	17.74(0.95)
S x A	4.50(0.39)	4.62(0.31)	18.31(1.24)	18.00(0.94)
A x B	5.15(0.45)	5.44(0.35)	22.70(1.14)	24.17(0.91)
B x A	5.15(0.45)	5.01(0.35)	24.96(1.24)	24.48(0.92)
A x P	5.48(0.45)	4.73(0.35)	22.72(1.36)	23.79(1.07)
P x A	3.48(0.45)	4.15(0.35)	24.63(1.52)	23.08(1.11)
S x B	4.50(0.39)	4.96(0.31)	23.72(1.24)	23.84(0.90)
B x S	5.25(0.39)	4.79(0.31)	23.01(1.00)	23.03(0.81)
S x P	4.15(0.45)	4.27(0.34)	20.96(1.23)	22.07(0.92)
P x S	4.25(0.39)	4.17(0.32)	23.56(1.14)	22.54(0.89)
B x P	5.13(0.56)	4.94(0.40)	28.61(1.23)	29.46(0.91)
P x B	4.48(0.45)	4.66(0.37)	29.83(1.14)	29.11(0.88)
LSD##	2.56		6.97	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

The estimates of the genetic parameters can also be employed to predict the average performance of populations not included in an analysis (Gardner and Eberhart, 1966). Tables 14 through 20 list the observed least squares means for the F_2 generation and the predicted performance of the F_∞ resulting from selfing the F_2 to complete homozygosity. The standard errors of the predicted F_∞ are much higher than those of the F_2 generation; however, they do provide some indication of the predicted performance following selfing to homozygosity.

A comparison of the different hybrids across characters indicates that the F_∞ populations recovered from the F_1 Sullivan x Blueboy or its reciprocal, or the F_1 Arthur x Pioneer S76 or its reciprocal may be useful sources of new cultivars due to their high predicted performance for certain agronomically desirable characteristics. Compared to the other populations, the F_∞ derived from the F_1 of Sullivan x Blueboy (or reciprocal) is predicted to have a high grain yield, seed weight, number of seeds per spike, and seeds per spikelet; and it is predicted to have a long grain filling period, large spike, and high spring vigor. The F_∞ mean of Arthur x Pioneer S76 (or reciprocal) was comparatively higher for grain yield, seeds per spike, spikes per square meter, seeds per square meter, and spikelets per spike. The population is also expected to be late maturing with a long grain filling period, to have a long spike with a large surface area, to have large plants with large stems and flag leaf, and to have high seedling and spring vigor.

Considering only additive genetic effects Bailey (1976) presented

Table 14. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for grain yield per square meter, weight per seed, and seeds per spike.

Entry#	Yield		Wt./seed		Seeds/spike	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	g/sq. m		mg		no.	
A x S	224.6(11.2)	116.6(45.3)	24.21(0.48)	20.70(1.94)	30.58(0.86)	26.77(3.38)
S x A	212.8(11.2)	111.2(45.3)	23.71(0.48)	20.48(1.94)	29.30(0.86)	26.00(3.38)
A x B	253.1(11.2)	211.5(44.8)	26.37(0.48)	24.37(1.91)	29.20(0.86)	21.23(3.34)
B x A	214.9(11.2)	198.5(44.8)	26.10(0.48)	24.19(1.92)	31.65(0.86)	22.24(3.34)
A x P	213.3(11.2)	236.6(42.4)	25.54(0.48)	20.01(1.81)	30.95(0.86)	36.01(3.16)
P x A	236.1(11.2)	245.2(42.2)	25.93(0.48)	19.01(1.80)	27.45(0.86)	35.28(3,15)
S x B	243.6(11.2)	256.4(50.1)	27.26(0.48)	28.45(2.14)	30.72(0.86)	36.98(3.74)
B x S	247.4(11.2)	260.0(50.0)	28.04(0.48)	28.65(2.13)	30.15(0.86)	37.31(3.73)
S x P	252.0(11.2)	162.8(57.4)	27.61(0.48)	22.99(2.45)	27.13(0.86)	28.12(4.28)
P x S	274.3(11.2)	173.7(57.5)	27.11(0.48)	23.18(2.45)	28.97(0.86)	28.51(4.29)
B x P	234.5(11.2)	110.9(49.6)	23.03(0.48)	19.19(2.12)	34.80(0.86)	29.06(3.70)
P x B	232.4(11.2)	107.0(49.6)	24.05(0.48)	19.59(2.12)	34.27(0.86)	28.72(3.70)
LSD##	70.9		3.04		5.44	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 15. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for spikes per square meter, seeds per square meter, and spikelets per spike.

Entry#	Spikes/sq. m		Seeds/sq. m		Spikelets/spike	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	no.					
A x S	299.3(14.8)	229.6(60.2)	9128(393)	5933(1591)	17.81(0.17)	17.90(0.66)
S x A	301.2(14.8)	233.4(60.2)	8881(393)	5807(1591)	17.75(0.17)	17.94(0.66)
A x B	322.6(14.8)	353.9(59.6)	9446(393)	8204(1574)	17.97(0.17)	15.31(0.66)
B x A	250.4(14.8)	329.5(59.6)	7975(393)	7754(1574)	18.30(0.17)	15.43(0.66)
A x P	261.4(14.8)	312.4(56.3)	8121(393)	10750(1487)	18.40(0.17)	20.18(0.62)
P x A	334.8(14.8)	332.2(56.1)	9008(393)	11102(1483)	18.45(0.17)	20.29(0.61)
S x B	283.5(14.8)	195.0(66.6)	8778(393)	8391(1759)	18.88(0.17)	19.30(0.73)
B x S	280.1(14.8)	191.7(66.4)	8541(393)	8392(1753)	18.81(0.17)	19.20(0.73)
S x P	332.2(14.8)	252.7(76.2)	8998(393)	7097(1013)	18.60(0.17)	17.87(0.83)
P x S	348.1(14.8)	260.2(76.4)	10022(393)	7436(1017)	18.34(0.17)	17.86(0.84)
B x P	289.4(14.8)	248.5(65.9)	10028(393)	7332(1740)	18.68(0.17)	18.75(0.72)
P x B	274.5(14.8)	243.2(65.9)	9392(393)	7026(1740)	18.51(0.17)	18.67(0.72)
LSD##	94.2		2493		1.05	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 16. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for seeds per spikelet, test weight, and days to heading.

Entry#	Seeds/spikelet		Test wt.		Days to heading	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	no.		g/L		days	
A x S	1.725(0.049)	1.494(0.193)	51.53(0.59)	49.66(2.46)	39.00(0.30)	40.46(1.29)
S x A	1.660(0.049)	1.445(0.193)	51.45(0.59)	49.68(2.46)	38.58(0.30)	40.46(1.29)
A x B	1.632(0.049)	1.537(0.191)	52.22(0.59)	50.77(2.43)	39.67(0.30)	38.67(1.28)
B x A	1.773(0.049)	1.589(0.191)	47.84(0.59)	49.57(2.43)	41.83(0.30)	39.32(1.28)
A x P	1.686(0.049)	1.781(0.181)	49.83(0.59)	45.17(2.30)	41.83(0.30)	41.91(1.21)
P x A	1.518(0.049)	1.732(0.180)	52.10(0.59)	45.53(2.29)	39.75(0.30)	41.41(1.20)
S x B	1.632(0.049)	1.895(0.214)	50.40(0.59)	46.96(2.72)	41.25(0.30)	42.91(1.43)
B x S	1.609(0.049)	1.920(0.213)	51.03(0.59)	47.20(2.71)	41.42(0.30)	43.10(1.42)
S x P	1.469(0.049)	1.453(0.245)	53.13(0.59)	47.62(3.11)	39.75(0.30)	40.64(1.64)
P x S	1.541(0.049)	1.478(0.245)	53.22(0.59)	47.81(3.12)	39.75(0.30)	40.63(1.64)
B x P	1.866(0.049)	1.643(0.212)	46.59(0.59)	42.70(2.69)	42.17(0.30)	43.66(1.41)
P x B	1.858(0.049)	1.630(0.212)	47.33(0.59)	43.18(2.69)	42.08(0.30)	43.51(1.41)
LSD##	0.312		3.74		1.93	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 17. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for days to anthesis, days to maturity, and grain filling period.

Entry#	Days to anthesis		Days to maturity		Grain filling period	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	days					
A x S	43.33(0.29)	44.64(1.24)	71.17(0.39)	69.98(1.60)	27.83(0.40)	25.34(1.63)
S x A	43.00(0.29)	44.67(1.24)	70.92(0.39)	70.00(1.60)	27.92(0.40)	25.34(1.63)
A x B	44.08(0.29)	44.10(1.22)	71.83(0.39)	70.19(1.58)	27.75(0.40)	26.08(1.62)
B x A	45.92(0.29)	44.64(1.22)	73.75(0.39)	70.72(1.58)	27.83(0.40)	26.08(1.62)
A x P	46.08(0.29)	46.86(1.16)	73.75(0.39)	75.09(1.49)	27.67(0.40)	28.23(1.53)
P x A	44.50(0.29)	46.52(1.15)	71.92(0.39)	74.53(1.49)	27.42(0.40)	28.01(1.52)
S x B	45.58(0.29)	47.12(1.37)	73.25(0.39)	74.42(1.77)	27.67(0.40)	27.30(1.81)
B x S	45.58(0.29)	47.24(1.36)	74.25(0.39)	74.62(1.76)	28.67(0.40)	27.34(1.80)
S x P	44.33(0.29)	46.22(1.56)	72.17(0.39)	72.64(2.02)	27.83(0.40)	26.42(2.07)
P x S	44.42(0.29)	46.27(1.57)	71.67(0.39)	72.27(2.03)	27.25(0.40)	26.00(2.07)
B x P	46.67(0.29)	48.40(1.35)	74.08(0.39)	72.27(1.75)	27.42(0.40)	23.87(1.79)
P x B	46.17(0.29)	48.19(1.35)	72.50(0.39)	71.72(1.75)	26.33(0.40)	23.53(1.79)
LSD##	1.68		2.45		2.55	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 18. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for powdery mildew, spike surface area, and plant height.

Entry#	Powdery mildew		Spike surface area		Plant height	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	%		sq. cm		cm	
A x S	24.31(2.52)	26.55(10.17)	20.19(0.46)	19.15(1.80)	83.71(1.14)	83.73(4.54)
S x A	22.79(2.52)	27.97(10.17)	19.17(0.46)	18.79(1.80)	84.77(1.14)	84.34(4.54)
A x B	29.04(2.25)	19.26(10.06)	22.46(0.46)	17.78(1.78)	88.79(1.14)	76.07(4.49)
B x A	35.58(2.25)	21.32(10.06)	23.45(0.46)	18.20(1.78)	92.71(1.14)	77.06(4.49)
A x P	30.60(2.25)	40.75(9.51)	22.86(0.46)	25.32(1.68)	91.02(1.14)	94.75(4.25)
P x A	20.27(2.25)	37.77(9.47)	22.66(0.46)	25.63(1.68)	91.01(1.14)	94.82(4.23)
S x B	34.02(2.25)	28.25(11.24)	23.12(0.46)	24.04(1.99)	94.61(1.14)	90.00(5.02)
B x S	31.87(2.25)	26.99(11.21)	23.02(0.46)	23.85(1.98)	93.24(1.14)	89.86(5.00)
S x P	26.35(2.25)	57.23(12.87)	22.44(0.46)	20.48(2.28)	89.11(1.14)	87.95(5.75)
P x S	21.48(2.25)	54.88(12.89)	22.09(0.46)	20.41(2.28)	92.07(1.14)	88.39(5.76)
B x P	35.35(2.25)	25.60(11.12)	24.68(0.46)	22.21(1.97)	90.59(1.14)	80.27(4.97)
P x B	33.92(2.25)	26.43(11.12)	24.47(0.46)	22.22(1.97)	91.65(1.14)	80.04(4.97)
LSD##	16.01		2.92		7.22	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 19. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for top internode surface area, and seedling vigor.

Entry#	Top internode surface area		Seedling vigor	
	Observed	Predicted	Observed	Predicted
	-------- sq. cm --------		--------- rate --------	
A x S	57.33(1.53)	54.45(6.07)	2.75(0.16)	2.08(0.67)
S x A	54.44(1.53)	53.35(6.07)	2.50(0.16)	2.03(0.67)
A x B	59.40(1.53)	40.69(6.01)	2.92(0.16)	1.27(0.67)
B x A	63.97(1.53)	41.97(6.01)	2.17(0.16)	0.99(0.67)
A x P	62.17(1.53)	71.72(5.68)	3.67(0.16)	5.18(0.63)
P x A	59.92(1.53)	71.71(5.66)	3.00(0.16)	4.89(0.63)
S x B	59.54(1.53)	57.55(6.71)	3.58(0.16)	2.59(0.75)
B x S	61.56(1.53)	57.89(6.69)	2.75(0.16)	2.46(0.74)
S x P	57.48(1.53)	50.16(7.69)	3.17(0.16)	4.26(0.85)
P x S	60.69(1.53)	50.92(7.70)	2.75(0.16)	4.19(0.86)
B x P	62.55(1.53)	48.74(6.64)	3.58(0.16)	4.08(0.74)
P x B	59.82(1.53)	47.53(6.64)	2.67(0.16)	3.68(0.74)
LSD##	9.69		1.04	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 20. Least squares means and standard errors† of the observed (F_2) and predicted (F_∞) values for spring vigor, and flag leaf area.

Entry#	Spring vigor		Flag leaf area	
	Observed	Predicted	Observed	Predicted
	rate		sq. cm	
A x S	4.25(0.39)	1.78(1.73)	19.43(1.15)	21.50(4.68)
S x A	4.50(0.39)	1.78(1.73)	19.68(1.14)	21.76(4.68)
A x B	4.75(0.39)	0.89(1.66)	22.32(1.24)	16.39(4.58)
B x A	3.75(0.39)	0.60(1.66)	25.42(1.14)	17.74(4.56)
A x P	5.00(0.39)	4.98(0.60)	26.01(1.08)	31.82(4.97)
P x A	4.50(0.39)	4.40(0.57)	22.56(1.15)	31.11(4.96)
S x B	6.00(0.39)	5.83(1.87)	25.16(1.24)	25.55(4.94)
B x S	4.50(0.39)	5.66(1.85)	22.96(1.14)	24.75(4.89)
S x P	4.75(0.39)	6.08(2.21)	22.28(1.24)	25.17(5.03)
P x S	4.50(0.39)	5.99(2.22)	21.68(1.14)	25.65(5.03)
B x P	4.75(0.39)	4.66(1.80)	27.79(1.15)	23.52(4.47)
P x B	4.25(0.39)	4.38(1.80)	25.43(1.06)	23.17(4.46)
LSD##	2.56		6.97	

† Listed in parentheses.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

evidence to show that it is advantageous to backcross one or more times to the superior parent before selfing to develop new cultivars. Tables 21 through 27 list the observed backcross least squares means and the predicted mean of a population (BCS_{∞}) resulting from selfing the backcross to complete homozygosity for the characteristics investigated. The equations employed to determine the BCS_{∞} populations in this study consider both additive and additive by additive genetic effects. Comparing the parental performance in Tables 7 through 13 with the predicted BCS_{∞} values in Tables 21 through 27 shows that, in general, BCS_{∞} values were higher for backcrosses made to the higher parent when compared to a backcross to the other lower parent.

Percentage heterosis on the midparent basis and percentage inbreeding from the F_1 to the F_2 generation for the characters studied are listed in Tables 28 through 30. An examination of percentage heterosis indicates that compared to the midparent value, the F_1 hybrids tended to have a higher grain yield, weight per seed, and test weight; to have a higher number of spikes per square meter; to reach heading and anthesis earlier and maturity later thereby resulting in a longer grain filling period; to have a taller plant height, a larger top internode surface area; and to have a higher seedling and spring vigor. The percentage heterosis for seeds per spike is negative and significant at 0.01 level for the Arthur x Blueboy, Arthur x Pioneer S76, Sullivan x Blueboy, Sullivan x Pioneer S76 F_1 hybrids and reciprocals; it is nonsignificant for Arthur x Sullivan and reciprocal;

Table 21. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for yield per square meter, weight per seed, and seeds per spike.

Entry#	Yield		Wt./seed		Seeds/spike	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	g/sq. m		mg		no.	
ASA	259.7(11.8)	142.9(34.4)	25.20(0.51)	21.57(1.47)	31.33(0.91)	27.64(2.57)
ABA	262.7(11.8)	214.2(34.1)	26.86(0.51)	24.34(1.46)	30.47(0.91)	23.39(2.54)
APA	256.3(18.4)	235.3(32.1)	26.18(0.79)	21.16(1.37)	29.42(1.41)	33.63(2.39)
SAS	231.5(12.4)	125.1(34.6)	24.77(0.53)	21.40(1.47)	28.74(0.95)	26.63(2.58)
SBS	230.9(13.0)	240.7(38.0)	26.66(0.56)	27.42(1.62)	26.64(1.00)	34.19(2.84)
SPS	260.1(20.6)	167.4(43.5)	26.33(0.88)	23.38(1.86)	32.46(1.58)	27.37(3.25)
BAB	208.4(11.2)	184.6(34.2)	25.40(0.48)	24.14(1.46)	34.17(0.86)	25.43(2.55)
BSB	208.4(13.0)	229.0(38.0)	26.23(0.56)	27.38(1.62)	30.73(1.00)	37.24(2.84)
BPB	240.3(14.0)	114.9(37.7)	24.57(0.60)	20.59(1.61)	37.32(1.08)	30.09(2.81)
PAP	209.2(13.0)	229.1(32.2)	27.83(0.56)	20.72(1.37)	29.19(1.00)	36.44(2.40)
PSP	268.9(13.0)	179.1(43.5)	28.64(0.56)	23.10(1.86)	27.06(1.00)	31.20(3.24)
PBP	253.1(13.0)	137.5(37.7)	24.75(0.56)	20.34(1.61)	35.80(1.00)	30.86(2.81)
LSD##	70.9		3.04		5.44	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76(P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 22. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for spikes per square meter, seeds per square meter, and spikelets per spike.

Entry#	Spikes/sq. m		Seeds/sq. m		Spikelets/spike	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	no.					
ASA	329.7(15.7)	248.4(45.7)	10206(415)	6687(1208)	17.42(0.18)	17.59(0.50)
ABA	318.5(15.7)	340.7(45.3)	9593(415)	8402(1196)	18.27(0.18)	15.55(0.50)
APA	334.2(24.5)	320.4(42.6)	9683(648)	10358(1126)	17.43(0.27)	19.24(0.47)
SAS	322.0(16.5)	233.6(45.9)	9183(436)	6040(1214)	17.74(0.18)	17.97(0.50)
SBS	321.5(17.2)	218.3(50.5)	8537(456)	8226(1335)	18.52(0.19)	18.74(0.55)
SPS	298.6(27.4)	259.9(57.8)	9736(725)	7128(1528)	18.87(0.31)	17.74(0.63)
BAB	238.2(14.9)	287.2(45.5)	8076(393)	7223(1201)	19.10(0.17)	16.47(0.50)
BSB	253.0(17.2)	179.6(50.5)	7767(456)	7694(1335)	18.78(0.19)	19.29(0.55)
BPB	247.3(18.6)	222.8(50.1)	9253(493)	6664(1323)	18.66(0.21)	18.78(0.55)
PAP	255.2(17.2)	290.0(42.7)	7360(456)	10195(1129)	17.88(0.19)	20.00(0.47)
PSP	347.1(17.2)	244.3(57.8)	9263(456)	7612(1526)	18.25(0.19)	18.13(0.63)
PBP	272.9(17.2)	246.0(50.0)	9871(456)	7680(1321)	18.57(0.19)	18.62(0.55)
LSD##	94.2		2493		1.05	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 23. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for seeds per spikelet, test weight, and days to heading.

Entry#	Seeds/spikelet		Test/wt.		Days to heading	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	no.		g/L		days	
ASA	1.810(0.052)	1.575(0.147)	52.18(0.62)	49.64(1.87)	38.93(0.32)	40.46(0.98)
ABA	1.671(0.052)	1.616(0.145)	51.52(0.62)	51.11(1.85)	40.63(0.32)	38.66(0.97)
APA	1.691(0.081)	1.747(0.137)	53.68(0.97)	46.67(1.74)	39.60(0.50)	41.11(0.91)
SAS	1.635(0.054)	1.479(0.148)	52.13(0.65)	50.65(1.87)	38.01(0.34)	39.87(0.99)
SBS	1.470(0.057)	1.803(0.162)	53.75(0.68)	49.55(2.06)	39.44(0.35)	41.23(1.08)
SPS	1.737(0.091)	1.457(0.186)	54.01(1.09)	49.19(2.36)	39.33(0.56)	39.90(1.24)
BAB	1.796(0.049)	1.636(0.146)	47.29(0.59)	47.75(1.85)	42.42(0.30)	40.85(0.98)
BSB	1.637(0.057)	1.918(0.162)	48.05(0.68)	45.18(2.06)	42.44(0.35)	44.02(1.08)
BPB	1.949(0.062)	1.672(0.161)	46.61(0.74)	42.33(2.04)	42.99(0.38)	44.20(1.08)
PAP	1.651(0.057)	1.824(0.137)	53.57(0.68)	46.63(1.74)	40.00(0.35)	41.49(0.92)
PSP	1.496(0.057)	1.629(0.186)	53.98(0.68)	48.15(2.36)	40.00(0.35)	40.87(1.24)
PBP	1.937(0.057)	1.729(0.161)	49.47(0.68)	45.66(2.04)	40.67(0.35)	42.38(1.07)
LSD##	0.312		3.74		1.93	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76(P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 24. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for days to anthesis, days to maturity, and grain filling period.

Entry#	Days to anthesis		Days to maturity		Grain filling period	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	days					
ASA	43.20(0.31)	44.56(0.94)	71.60(0.41)	70.55(1.21)	28.40(0.42)	25.99(1.24)
ABA	44.53(0.31)	43.74(0.93)	73.04(0.41)	70.73(1.20)	28.51(0.42)	26.99(1.23)
APA	43.42(0.48)	45.92(0.87)	71.73(0.64)	74.35(1.13)	28.31(0.66)	28.42(1.16)
SAS	42.61(0.33)	44.27(0.94)	71.04(0.43)	70.03(1.22)	28.43(0.45)	25.76(1.25)
SBS	44.02(0.34)	45.62(1.04)	72.17(0.45)	73.39(1.34)	28.14(0.47)	27.76(1.37)
SPS	43.28(0.54)	45.37(1.19)	71.28(0.71)	72.19(1.53)	28.01(0.74)	26.82(1.57)
BAB	46.33(0.29)	45.90(0.93)	73.17(0.39)	70.88(1.21)	26.83(0.40)	24.93(1.23)
BSB	46.58(0.34)	48.08(1.04)	73.61(0.45)	74.06(1.34)	27.03(0.47)	25.97(1.37)
BPB	46.89(0.37)	48.75(1.03)	74.00(0.48)	72.34(1.33)	27.11(0.50)	23.59(1.36)
PAP	44.47(0.34)	46.30(0.88)	70.83(0.45)	73.09(1.13)	26.37(0.47)	26.80(1.16)
PSP	44.47(0.34)	46.04(1.19)	71.50(0.45)	71.46(1.53)	27.03(0.47)	25.42(1.57)
PBP	45.02(0.34)	46.96(1.03)	71.83(0.45)	70.95(1.33)	26.81(0.47)	23.99(1.36)
LSD##	1.68		2.45		2.55	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76(P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 25. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for percentage of powdery mildew, spike surface area, and plant height.

Entry#	Powdery mildew		Spike surface area		Plant height	
	Observed	Predicted	Observed	Predicted	Observed	Predicted
	%		sq. cm		cm	
ASA	22.23(2.67)	26.44(7.72)	19.98(0.49)	19.31(1.37)	86.69(1.20)	84.04(3.45)
ABA	32.95(2.67)	18.40(7.64)	22.66(0.49)	17.66(1.35)	92.68(1.20)	78.11(3.41)
APA	18.02(4.16)	36.63(7.20)	21.31(0.76)	23.56(1.27)	90.25(1.88)	92.79(3.21)
SAS	20.52(2.80)	25.15(7.76)	19.26(0.51)	18.88(1.37)	80.54(1.26)	82.97(3.46)
SBS	29.48(2.93)	22.94(8.53)	21.18(0.54)	21.79(1.51)	89.55(1.32)	87.33(3.81)
SPS	12.79(4.65)	48.26(9.76)	22.18(0.85)	19.48(1.73)	87.94(2.10)	87.02(4.36)
BAB	37.69(2.52)	28.34(7.68)	25.14(0.46)	20.91(1.36)	92.29(1.14)	78.36(3.43)
BSB	40.65(2.93)	34.16(8.53)	24.36(0.54)	25.49(1.51)	93.92(1.32)	88.65(3.81)
BPB	44.56(3.17)	34.15(8.46)	26.25(0.58)	23.58(1.50)	93.09(1.43)	82.00(3.78)
PAP	17.20(2.93)	30.57(7.21)	22.59(0.54)	25.60(1.28)	85.03(1.32)	88.99(3.22)
PSP	15.87(2.93)	43.49(9.75)	22.94(0.54)	21.93(1.72)	88.84(1.32)	84.29(4.36)
PBP	26.48(2.93)	18.15(8.45)	24.42(0.54)	22.34(1.49)	88.84(1.32)	77.95(3.77)
LSD##	16.01		2.92		7.22	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76(P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 26. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for top internode surface area, and seedling vigor.

Entry#	Top internode surface area		Seedling vigor	
	Observed	Predicted	Observed	Predicted
	-------- sq. cm --------		--------- rate ---------	
ASA	58.41(1.62)	55.19(4.61)	2.69(0.17)	2.38(0.51)
ABA	65.86(1.62)	44.64(4.56)	2.60(0.17)	1.60(0.51)
APA	57.83(2.52)	67.86(4.30)	2.95(0.27)	4.73(0.48)
SAS	52.18(1.70)	52.04(4.63)	2.79(0.18)	1.96(0.51)
SBS	56.32(1.77)	54.57(5.10)	3.01(0.19)	2.33(0.57)
SPS	62.16(2.82)	49.61(5.83)	2.34(0.30)	3.80(0.65)
BAB	64.91(1.53)	45.97(4.58)	3.33(0.16)	1.51(0.51)
BSB	62.80(1.77)	59.05(5.10)	3.34(0.19)	2.67(0.57)
BPB	65.67(1.92)	51.17(5.05)	3.23(0.21)	3.80(0.56)
PAP	56.79(1.77)	67.48(4.31)	2.01(0.19)	3.84(0.48)
PSP	57.60(1.77)	52.38(5.83)	2.12(0.19)	3.34(0.65)
PBP	61.59(1.77)	49.46(5.04)	1.90(0.19)	3.00(0.56)
LSD##	9.69		1.04	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76(P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 27. Least squares means and standard errors† of the observed backcross generation and predicted‡ (BCS_{∞}) values for spring vigor, and flag leaf area.

Entry#	Spring vigor		Flag leaf area	
	Observed	Predicted	Observed	Predicted
	rate		sq. cm	
ASA	5.00(0.39)	2.25(1.32)	19.40(1.24)	20.81(3.57)
ABA	5.00(0.39)	1.35(1.26)	23.61(1.24)	16.26(3.49)
APA	4.63(0.56)	4.53(0.46)	21.20(1.52)	27.74(3.80)
SAS	4.48(0.45)	2.03(1.32)	17.81(1.23)	20.65(3.58)
SBS	4.15(0.45)	4.93(1.41)	19.86(1.14)	22.20(3.76)
SPS	3.59(0.79)	5.38(1.68)	19.22(1.76)	23.08(3.84)
BAB	5.00(0.39)	1.63(1.27)	26.96(0.95)	20.59(3.49)
BSB	5.15(0.45)	5.43(1.41)	27.24(1.25)	26.70(3.74)
BPB	4.81(0.45)	4.62(1.37)	28.96(1.14)	24.90(3.40)
PAP	2.81(0.45)	3.91(0.46)	21.74(1.35)	29.35(3.79)
PSP	4.15(0.45)	4.98(1.68)	21.98(1.23)	24.86(3.84)
PBP	3.48(0.45)	3.72(1.37)	24.68(1.25)	22.18(3.43)
LSD##	2.56		6.97	

† Listed in parentheses.

‡ Predicted values are those of a population resulting from selfing the particular backcross to complete homozygosity.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76(P), female parent first. ASA indicates S x A or A x S backcrossed to A and so on.

Bonferroni multiple comparison LSD for significance at the 0.05 level.

Table 28. Percentage heterosis (Het.)† and inbreeding (Inb.)‡ for grain yield, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, and spikelets per spike.

Entry#	Yield g/sq. m		Wt./seed mg		Seeds/spike no.		Spikes /sq. m no.		Seeds/sq. m no.		Spikelets /spike no.	
	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.
	%											
A x S	29**	10	7**	6*	2	-2	21**	7	23**	5	-1	-3*
S x A	25**	12	5*	6*	-4	-4	26**	10	20**	5	1	-1
A x B	36**	-3	29**	15**	-17**	-8	26**	-13	7	-22**	3**	3*
B x A	31**	9	27**	15**	-12**	-13*	19*	7	5	-5	4**	2
A x P	10	5	35**	21**	-31**	-35**	21**	14	-17**	-18*	0	-4**
P x A	15*	-1	31**	17**	-32**	-22**	28**	-4	-11	-23**	1	-2
S x B	40**	-6	30**	12**	-22**	-24**	38**	5	10	-20**	3*	0
B x S	42**	-6	31**	10**	-18**	-16**	32**	1	10	-17*	1	-1
S x P	12	-20*	36**	14**	-33**	-26**	29**	-8	-15*	-39**	0	-3
P x S	25**	-17*	41**	19**	-33**	-34**	35**	-8	-10	-45**	1	-0
B x P	69**	21**	8*	10**	11**	11**	42**	-2	56**	10	2	2
P x B	60**	17**	10**	7*	8**	10**	40**	2	48**	11*	2	3*

*,** Significantly different from zero at the 0.05 and 0.01 levels, respectively.

† Heterosis measured on the mid-parent basis [(F_1 - (midparent value)) * 100] / (midparent value).

‡ Inbreeding measured as the [(F_1 - F_2) * 100] / F_1.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P) female parent first.

Table 29. Percentage heterosis (Het.)† and inbreeding (Inb.)‡ for seeds per spikelet, test weight, days to heading, days to anthesis, days to maturity, and grain filling period.

Entry#	Seeds/ spikelet no.		Test wt. g/L		Days to heading no.		Days to anthesis no.		Days to maturity no.		Grain filling period days	
	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.
	%											
A x S	3	2	2	2	-2*	-2	-3**	-2	0	0	4*	3
S x A	-5	-3	2	2	-1	1	-2	0	0	1	4*	2
A x B	-19**	-11*	12**	1	-2	4**	-1	4**	2**	3**	9**	1
B x A	-16**	-16**	12**	10**	-1	0	-1	0	2**	0	8**	0
A x P	-31**	-30**	8**	8**	-2*	-6**	-2	-5**	3**	-2	11**	4*
P x A	-35**	-24**	4*	0	-1	0	-1	-1	3**	1	8**	3
S x B	-23**	-24**	10**	5**	-2	-1	-3**	-2	3**	0	13**	4
B x S	-18**	-15**	11**	4**	0	0	-1	0	3**	-2	9**	-3
S x P	-36**	-30**	6**	2	-2	-2	-2	-2*	4**	1	13**	5*
P x S	-33**	-30**	7**	3*	-1	-2	-1	-2*	3**	0	10**	4
B x P	9*	9*	1	2	-1	-1	-2	-2	4**	-1	16**	0
P x B	7	8*	4*	3	-3**	-2*	-3**	-2	3**	0	14**	4

*,** Significantly different from zero at the 0.05 and 0.01 levels, respectively.

† Heterosis measured on the mid-parent basis [(F_1 - (midparent value)) * 100] / (midparent value).

‡ Inbreeding measured as the [(F_1 - F_2) * 100] / F_1.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P) female parent first.

Table 30. Percentage heterosis (Het.)† and inbreeding (Inb.)‡ for percentage of powdery mildew, spike surface area, plant height, top internode surface area, seedling vigor, spring vigor, and flag leaf area.

Entry#	Powdery mildew %		Spike surface area sq. cm		Plant height cm		Top internode surface area sq. cm		Seedling vigor rate		Spring vigor rate		Flag leaf area sq. cm	
	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.	Het.	Inb.
	%													
A x S	-17	-35	4	1	6**	4	9*	0	7	-2	46**	11	-3	-11
S x A	17	10	2	4	8**	4*	6	2	10	9	38**	0	1	-7
A x B	18	25*	3	6	14**	7**	12**	7	18	13	37**	8	1	2
B x A	20*	10	6*	4	14**	2	12**	0	5	27**	37**	27*	11	-2
A x P	13	-59**	4	-1	13**	-2	8*	-3	36**	-32**	90**	9	15	-15
P x A	8	-11	9**	5	12**	-3	11**	3	15	-28**	21	-29	24**	8
S x B	23*	12	3	1	13**	-1	11**	1	28**	-16*	28*	-33	6	-6
B x S	23*	17	0	-2	14**	0	10**	-4	42**	20**	50**	14	3	0
S x P	37**	-24	10**	5	19**	4*	19**	8*	37**	-42**	58**	-15	7	-6
P x S	3	-35	11**	7**	18**	0	19**	2	49**	-14	62**	-6	20**	8
B x P	4	-27	7*	8**	14**	0	14**	4	53**	-19*	64**	7	18**	3
P x B	30*	2	8**	10**	11**	-4*	11**	5	20	-14	43**	5	24**	15**

*,** Significantly different from zero at the 0.05 and 0.01 levels, respectively.

† Heterosis measured on the mid-parent basis [(F_1 - (midparent value)) * 100] / (midparent value).

‡ Inbreeding measured as the [(F_1 - F_2) * 100] / F_1.

Arthur (A), Sullivan (S), Blueboy (B), Pioneer S76 (P) female parent first.

and it is positive and significant for the Blueboy x Pioneer S76 F_1 hybrid and reciprocal. A comparison of the percentage heterosis for spikelets per spike with seeds per spikelet indicates that heterosis for the number of seeds per spike in the F_1 was mainly due to heterosis for the number of seeds per spikelet rather than spikelets per spike.

The standardized values (mean=0, standard deviation=1.0) for grain yield, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet are plotted in Figures 1 through 6 for each F_1 hybrid combination including reciprocals and the parents making up the hybrid. These plots clearly indicate the nature by which the parents combined to produce the F_1 hybrid for these characteristics. All hybrid means were above the highest parent for grain yield and weight per seed. With the exception of the F_1 of Blueboy x Arthur, all hybrid means were above the highest parent for spikes per square meter. Only the Arthur x Sullivan and its reciprocal and the Blueboy x Pioneer S76 and its reciprocal had more seeds per square meter than the highest parent. The F_1 of Blueboy x Pioneer S76 and reciprocal, the highest yielding hybrid combinations, were the only hybrids to be above the highest parent for all six traits.

The phenotypic correlations among grain yield and the primary yield components; weight per seed, seeds per spike, and spikes per square meter; are listed in Table 31. All three of the primary yield components had highly significant positive correlations with grain yield. Weight per seed had a highly significant positive correlation

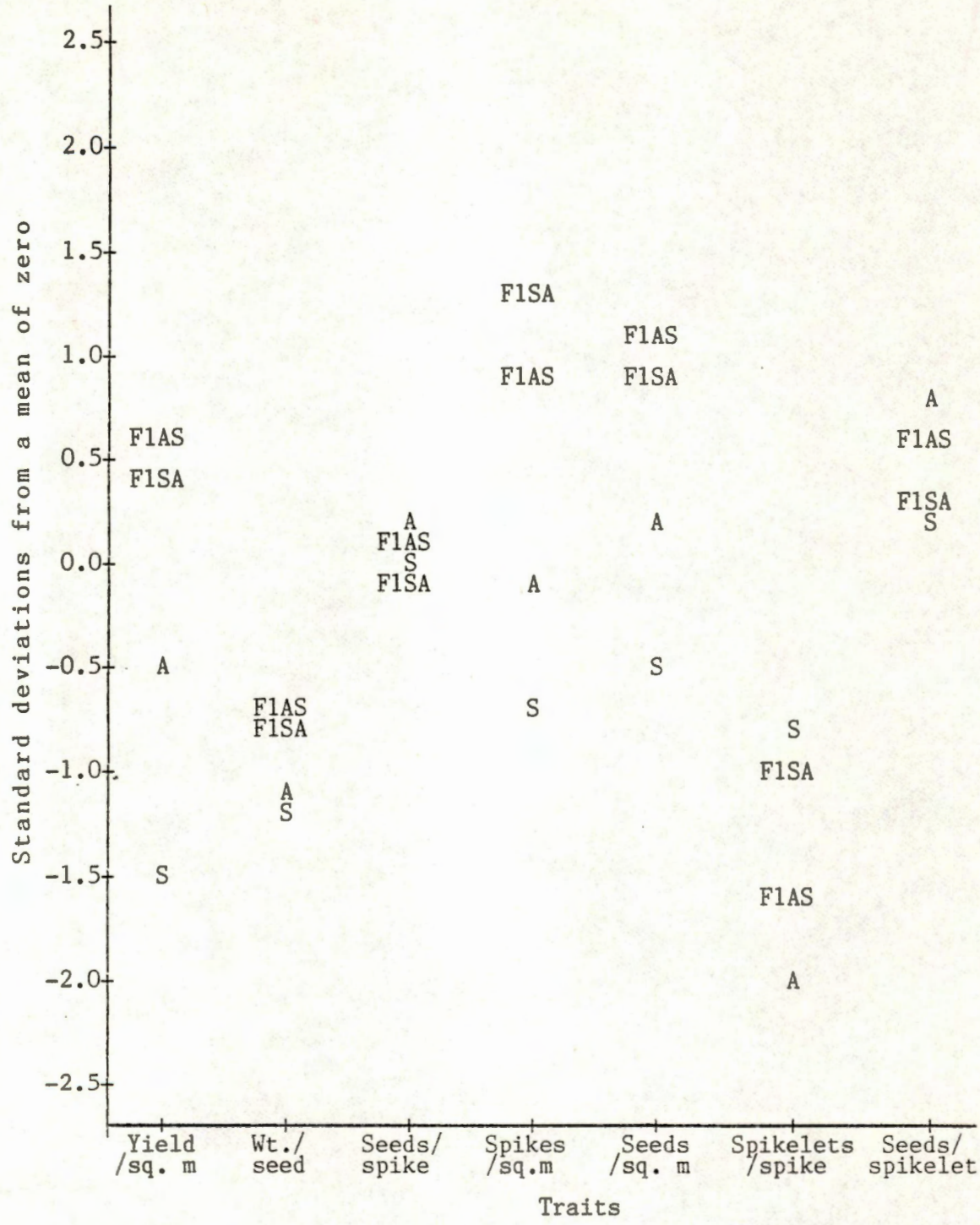


Figure 1. Graph of the standardized least squares means for grain yield per square meter, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet for Arthur (A), Sullivan (S), F_1 Arthur x Sullivan (F1AS) and reciprocal (F1SA).

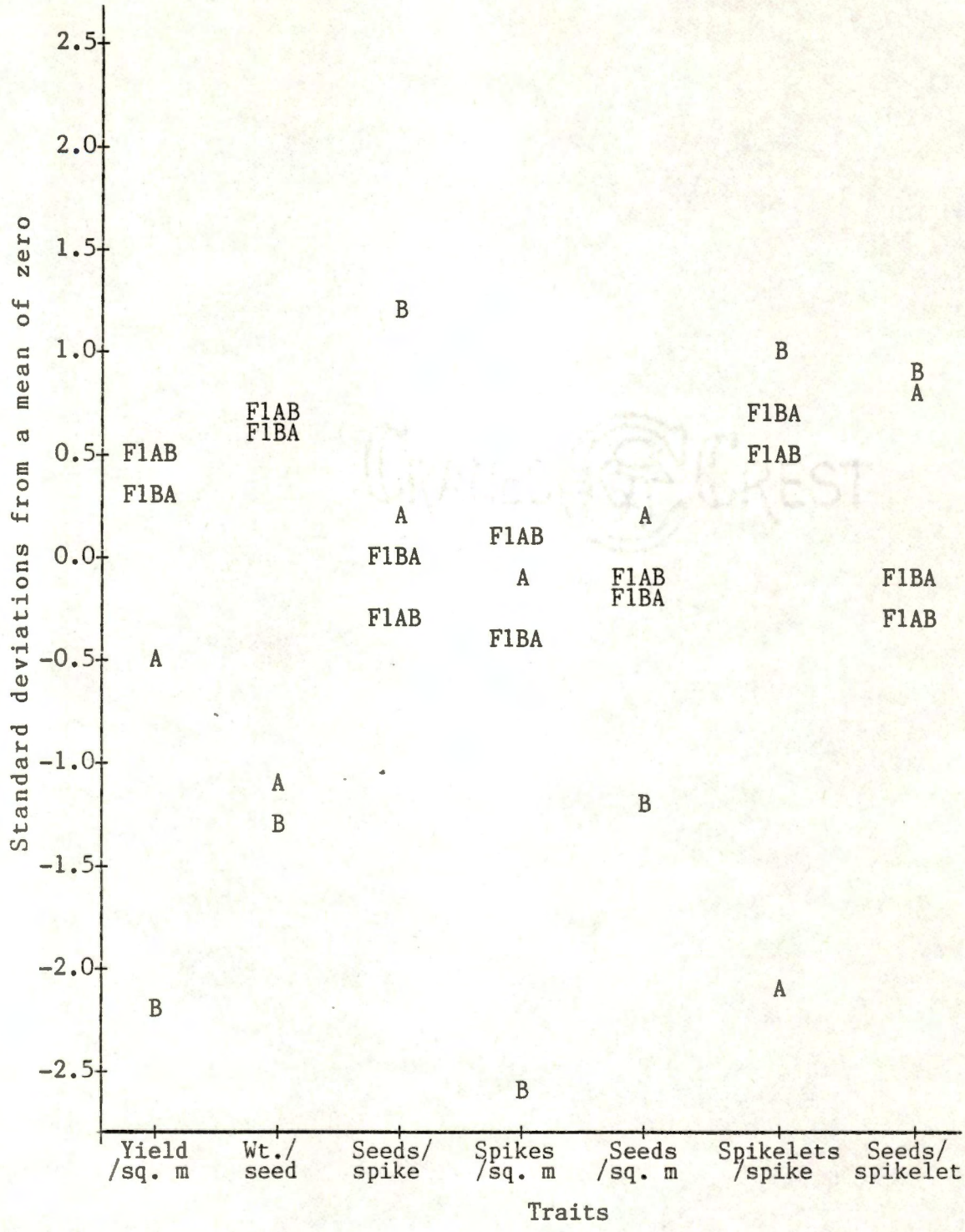


Figure 2. Graph of the standardized least squares means for grain yield per square meter, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet for Arthur (A), Blueboy (B), F_1 Arthur x Blueboy (F1AB) and reciprocal (F1BA).

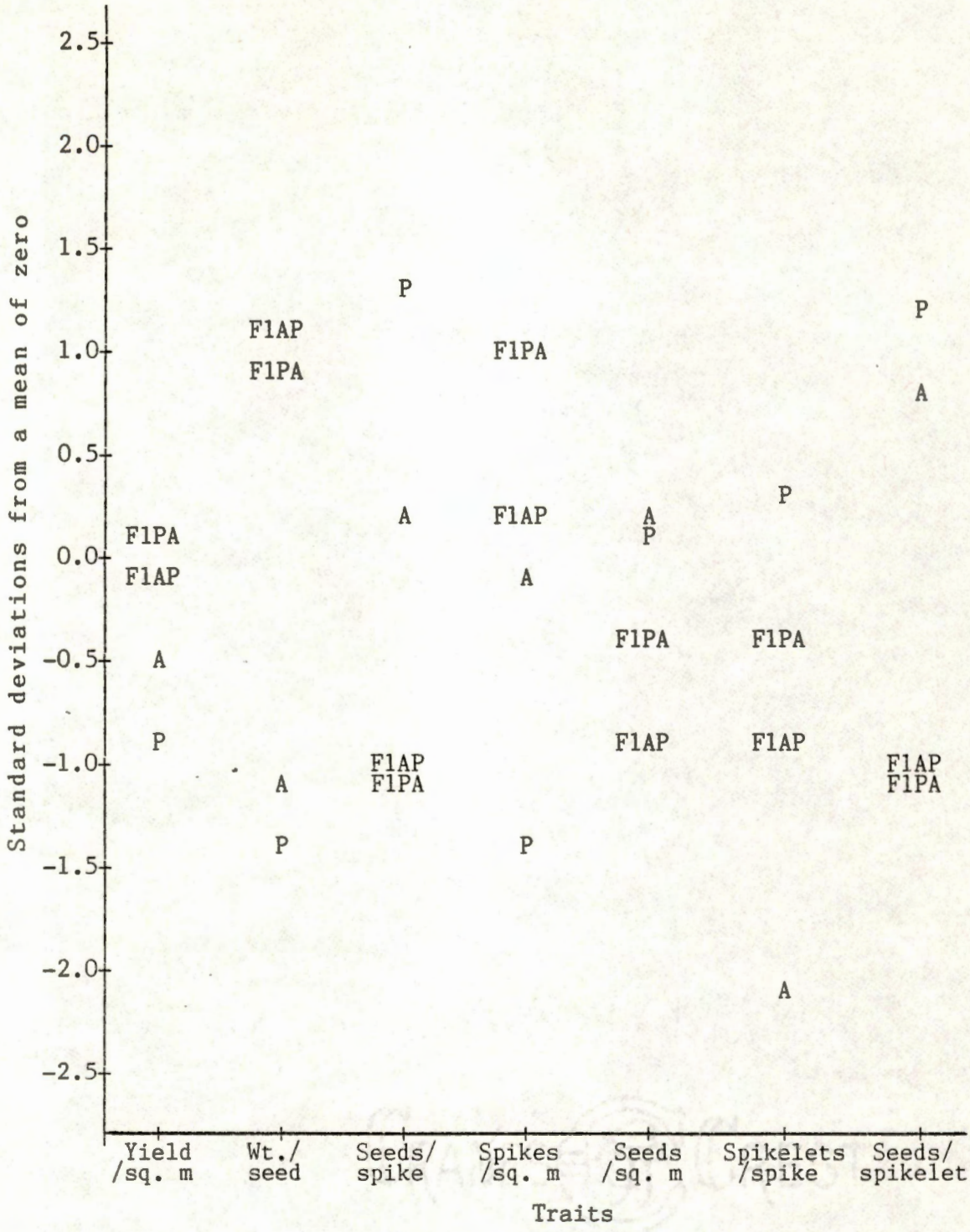


Figure 3. Graph of the standardized least squares means for grain yield per square meter, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet for Arthur (A), Pioneer S76 (P), F_1 Arthur x Pioneer S76 (F1AP) and reciprocal (F1PA).

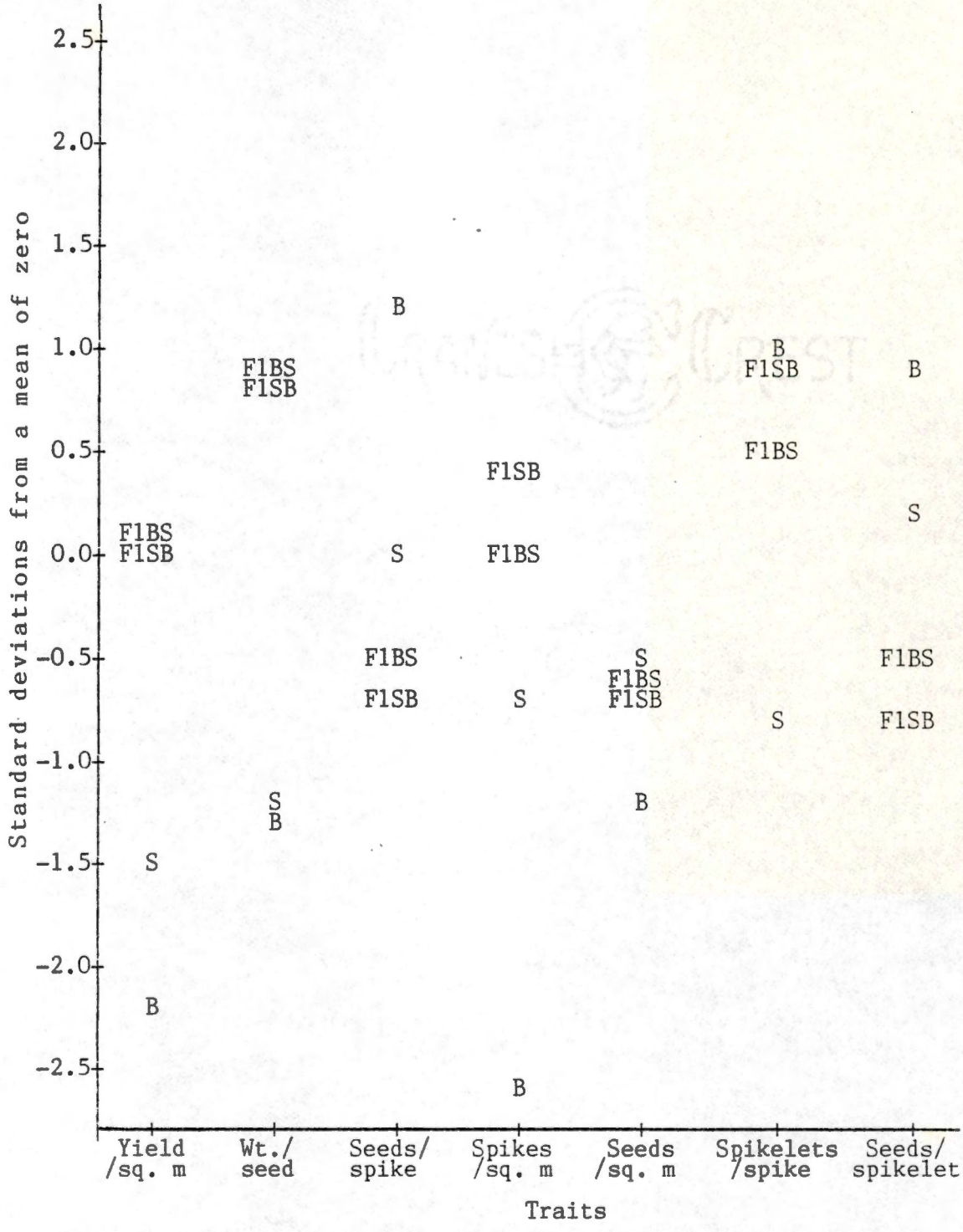


Figure 4. Graph of the standardized least squares means for grain yield per square meter, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet for Sullivan (S), Blueboy (B), F1 Sullivan x Blueboy (F1SB) and reciprocal (F1BS).

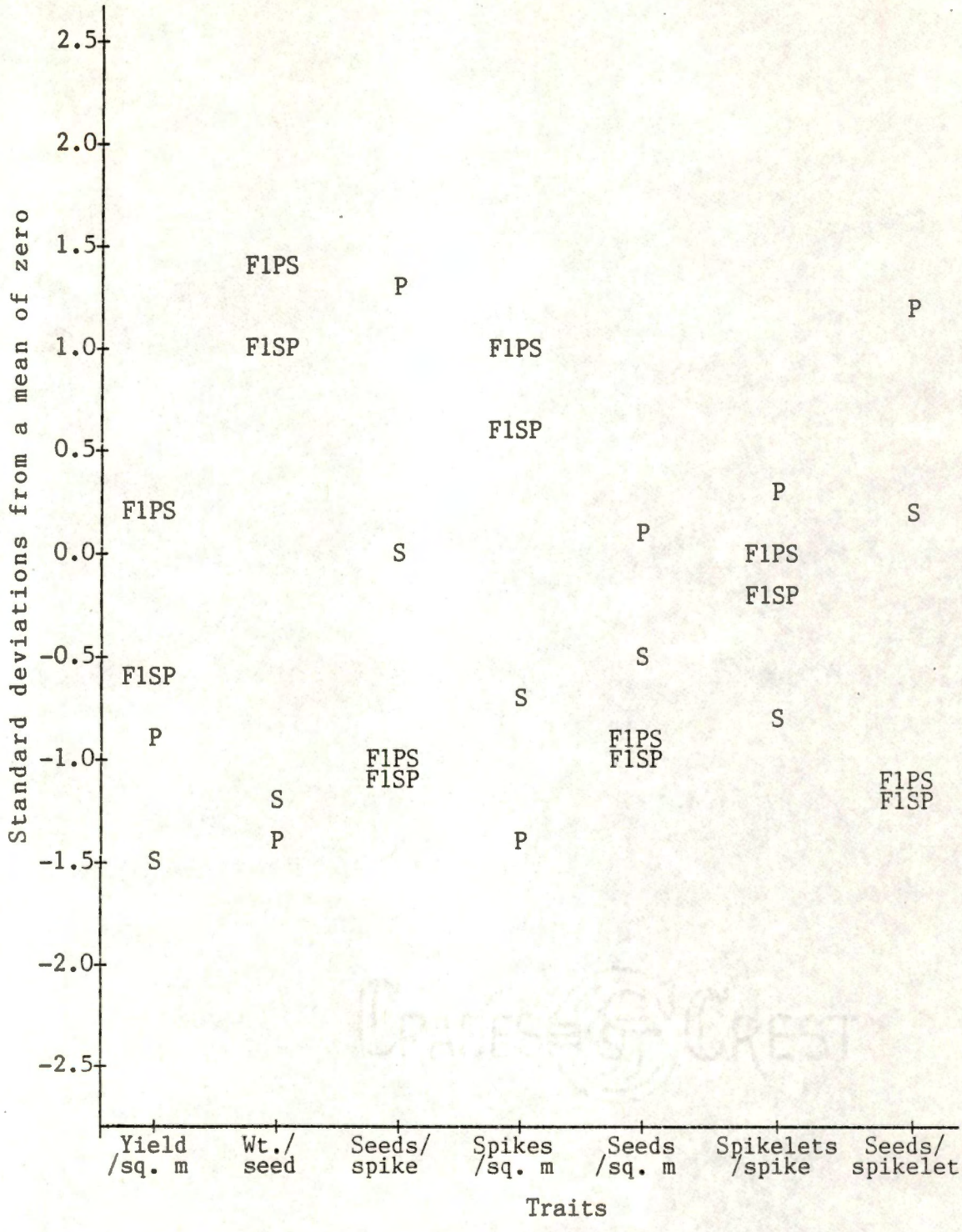


Figure 5. Graph of the standardized least squares means for grain yield per square meter, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet for Sullivan (S), Pioneer S76 (P), F_1 Sullivan x Pioneer S76 (F1SP) and reciprocal (F1PS).

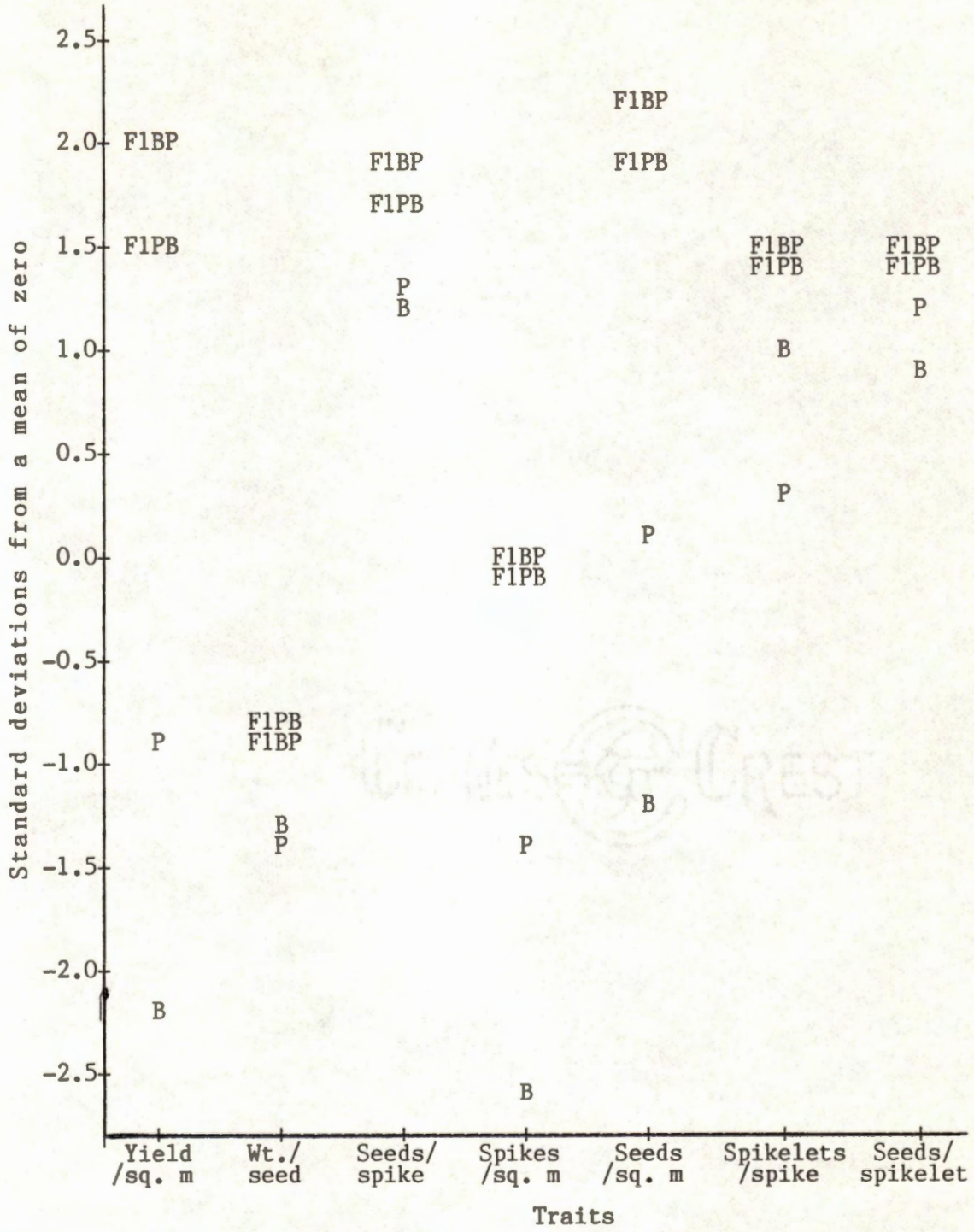


Figure 6. Graph of the standardized least squares means for grain yield per square meter, weight per seed, seeds per spike, spikes per square meter, seeds per square meter, spikelets per spike, and seeds per spikelet for Blueboy (B), Pioneer S76 (P), F_1 Blueboy x Pioneer (F1BP) and reciprocal (F1PB).

Table 31. Phenotypic correlations among yield and the primary yield components weight per seed, seeds per spike, and spikes per square meter.

	Wt./seed	Seeds/spike	Spikes/sq. m
Yield/sq. m	0.65**	0.21**	0.78**
Wt./seed		-0.24**	0.45**
Seeds/spike			-0.28**

** Significant at the 0.01 level.

with spikes per square meter, but it had a highly significant negative correlation with seeds per spike. There was a highly significant negative corelation between seeds per spike and spikes per square meter.

The compensation occurring among the developmentally flexible yield components is exemplified by the path-coefficient diagram in Figure 7 and the path analysis in Table 32 for the natural logarithm of grain yield and the primary yield components. The direct effect of each primary yield component on yield is positive; however, the direct effect of seeds per spike on weight per seed and spikes per square meter on seeds per spike is negative. This indicates that entries with a higher number of spikes per square meter will compensate by producing fewer seeds per spike and that the entries with more seeds per spike will compensate by producing seeds of a lower weight. Such negative relationships among yield components are evidence of stress.

The standardized (mean=0, standard deviation=1.0) values for the primary yield components; spikes per square meter, seeds per spike, and weight per seed; along with grain yield per square meter for each F_1 hybrid and reciprocal are plotted in Figure 8. Figure 8 reveals that compensation is occurring among the yield components and in terms of high grain yield some compensation patterns are more favorable than others. On the basis of the compensation patterns, the F_1 hybrids may be separated into three groups. Arthur x Sullivan and reciprocal with their high number of spikes per square meter but lower weight per seed would be one group. Blueboy x Pioneer S76 and reciprocal with their

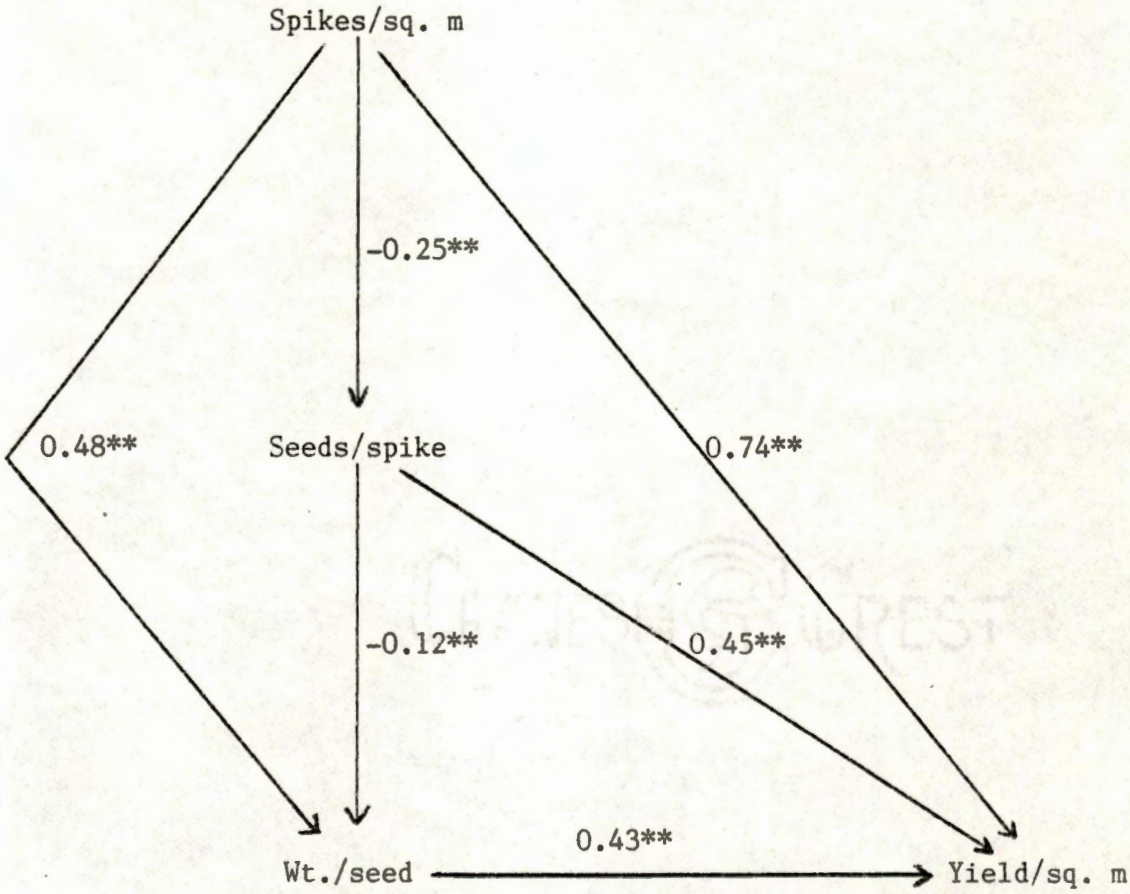


Figure 7. Path-coefficient diagram for the natural logarithm of yield per square meter, weight per seed, seeds per spike, and spikes per square meter. Numerical values are the path coefficients. ** Indicates significance at the 0.01 level.

Table 32. Path-coefficient analysis of the natural logarithm of yield per square meter, weight per seed, seeds per spike, and spikes per square meter.

Bivariate relationship[#]	Coefficient of total correlation	Causal effects			Noncausal correlation
		Direct	Indirect	Total	
Yield/sq. m and Wt./seed	0.70**	0.43**	0.00	0.43	0.26
Yield/sq. m and Seeds/spike	0.16**	0.45**	-0.05	0.40	-0.24
Yield/sq. m and Spikes/sq. m	0.85**	0.74**	0.22	0.96	-0.11
Wt./seed and Seeds/spike	-0.24**	-0.12**	0.00	-0.12	-0.12
Wt./seed and Spikes/sq. m	0.51**	0.48**	0.03	0.51	0.00
Seeds/spike and Spikes/sq. m	-0.25**	-0.25**	0.00	-0.25	0.00

The first variable listed in each line is the dependent variable.

** Indicates significance at the 0.01 level.

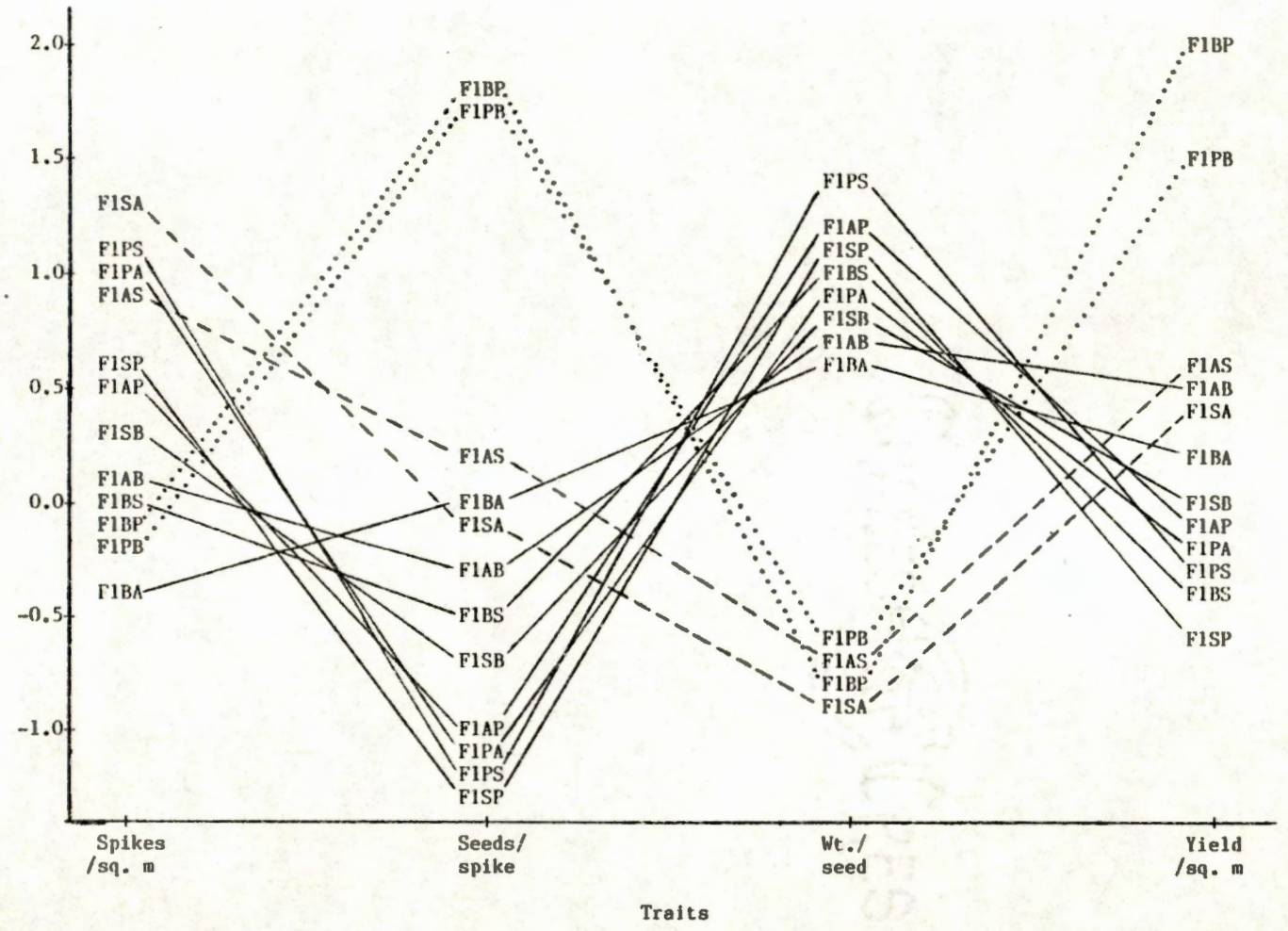


Figure 8. Graph of the standardized least squares means for spikes per square meter, seeds per spike, weight per seed, and grain yield per square meter. F1AS indicates Arthur x Sullivan, F1SA indicates Sullivan x Arthur, and so on.

high number of seeds per spike and low weight per seed would be in a second group. The remaining hybrids and reciprocals would be in a third group with lower seeds per spike and higher weight per seed. The combination of primary yield components exhibited by Blueboy x Pioneer S76 and reciprocal was the most ideal since it resulted in the highest grain yield.

The primary yield components, spikes per square meter and seeds per spike, were combined to produce the variable seeds per square meter; and the standardized values for seeds per square meter, weight per seed, and grain yield per square meter were plotted in Figure 9. Such a plot can be interpreted in terms of a source-sink relationship. Hybrids producing a high number of seeds per square meter would be considered to have a large sink. The higher seed weight exhibited by some F_1 hybrids suggests that sink size is more of a limiting factor than the source in regard to grain yield. Hybrids with a low seed weight suggest that the source is limiting grain yield more than the sink. At the same time, this plot gives evidence of a compensation type of relationship between seeds per square meter and weight per seed.

The phenotypic correlations of the secondary yield components; days to heading, grain filling period, spike surface area, top internode surface area, seedling vigor, spring vigor; and flag leaf area with grain yield, weight per seed, seeds per spike, spikes per square meter, and seeds per square meter; are listed in Table 33. Such associations indicate that it may be desirable in terms of increasing

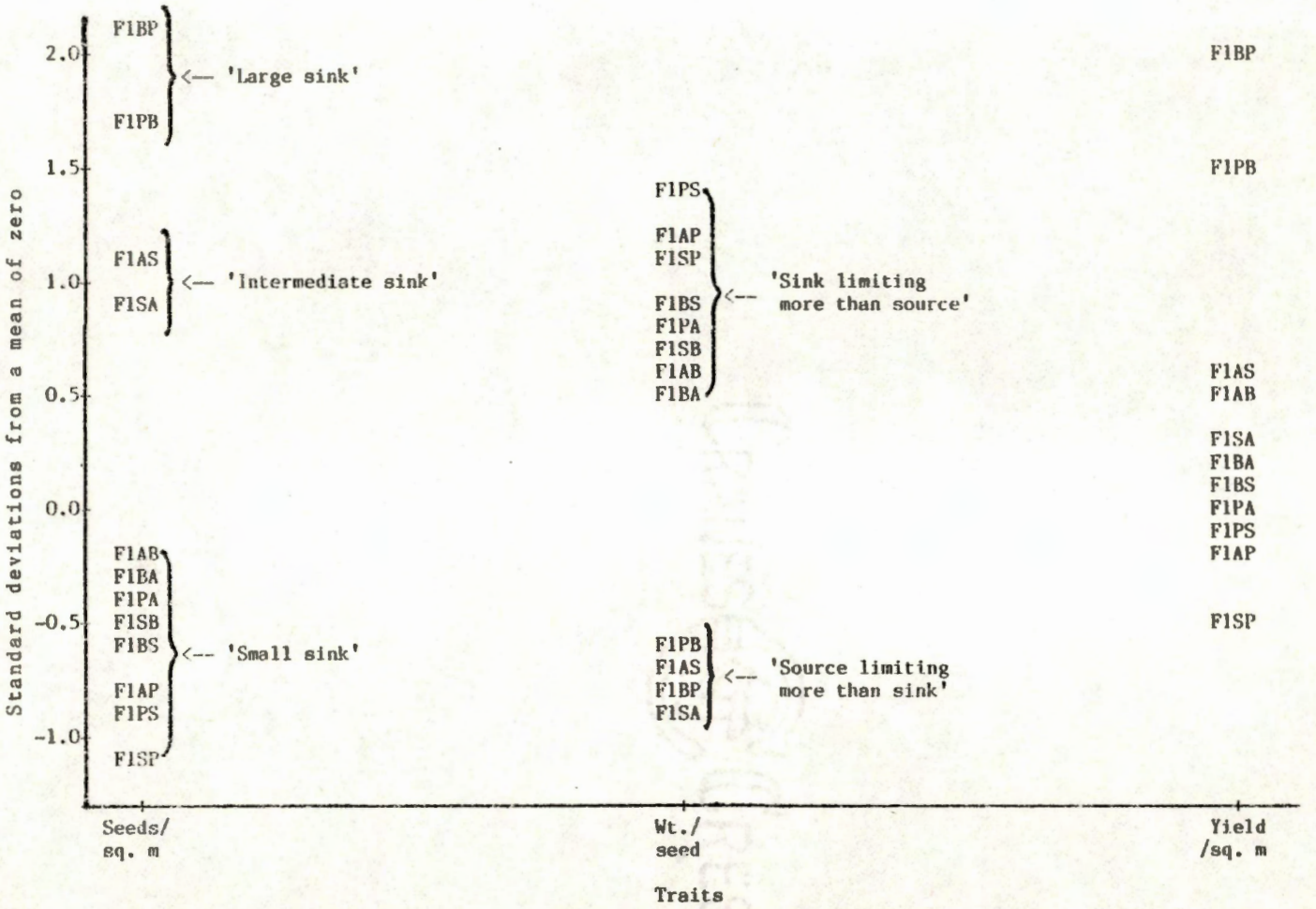


Figure 9. Graph of the standardized least squares means for seeds per square meter, weight per seed, and grain yield per square meter for the F_1 generation. F1AS indicates Arthur x Sullivan, F1SA indicates Sullivan x Arthur, and so on.

Table 33. Phenotypic correlations of the secondary yield components days to heading, grain filling period, percentage of powdery mildew, spike surface area, top internode surface area, seedling vigor, spring vigor, and flag leaf area with yield and the primary yield components weight per seed, seeds per spike, spikes per square meter, and seeds per square meter.

	Days to heading	Grain filling period	Powdery mildew	Spike surface area	Top internode surface area	Seedling vigor	Spring vigor	Flag leaf area
Yield/sq. m	-0.56**	0.43**	-0.68**	0.22**	0.31**	0.16**	0.50**	-0.09
Wt./seed	-0.36**	0.27**	-0.59**	0.22**	0.23**	0.18**	0.29**	-0.15*
Seeds/spike	-0.15**	0.10*	-0.07	0.56**	0.41**	-0.10	-0.11	0.40**
Spikes/sq. m	-0.43**	0.33**	-0.53**	-0.22**	-0.02	0.18**	0.44**	-0.34**
Seeds/sq. m	-0.53**	0.41**	-0.55**	0.13**	0.26**	0.10*	0.42**	-0.05

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

grain yield to develop cultivars that have an earlier heading date, a longer grain filling period, an increased resistance to powdery mildew, a larger spike and top internode surface area, and increased seedling and spring vigor. The significant negative correlation between spike surface area and spikes per square meter may again be an indication of compensation with entries producing fewer spikes per square meter compensating by producing more spikelets per spike and/or seeds per spikelet thereby resulting in a larger spike surface area.

CHAPTER V

DISCUSSION

When quantitative genetic traits are studied at the phenotypic level, the individual influence of different genes cannot be measured; therefore, their effects must be considered collectively. This intrinsic characteristic of quantitative genetics makes it difficult to make definite conclusions as to the type of gene action occurring. Another difficulty in making an interpretation in terms of gene action is that the genetic parameters used in this analysis are not orthogonal (Eberhart and Gardner, 1966; Moreno-Gonzales and Dudley, 1981). When only additive effects are significant, an interpretation of all additive gene action is possible. Due to the nonorthogonality of the parameters when other genetic effects such as dominance or epistatic effects are significant, the only conclusion that can be made is that the gene action was not all additive and that dominance and/or epistasis is important. Such was the case for all traits studied here.

Even though the genetic parameters are not orthogonal, the model has shown itself to be useful in terms of predicting the performance of the F_1 generation with better accuracy and the parents with near equal accuracy compared to the least squares means. Use of the model in terms of prediction is analogous to using several variables in a multiple regression equation to develop a model for the prediction of a future outcome. The accuracy of such a model will depend on the range of observations included in developing the model, and extensions to

prediction outside such a range would be expected to be less accurate.

The genetic parameters developed here were used to predict the future performance of generations not observed in the study. Such information is very valuable to the plant breeder in terms of making decisions concerning future breeding plans. The inclusion of more advanced generations such as the F_3 or BCS_1 should give a more accurate measurement of the effect of inbreeding resulting in predicted values with smaller standard errors and, hence, better estimates of the performance of advanced generations resulting from selfing.

Significant residual effects were present for the following characteristics: test weight, days to heading, anthesis, and maturity, and seedling and spring vigor. The significant residual effects indicate that a model containing more parameters would be necessary to explain all of the significant variation present. Therefore, a better model could be obtained for these variables with the addition of more populations and more parameters. However the predictive power of the existing model is still of value, and the improvement by the inclusion of more parameters may be small as shown by the largest change of only 0.063 in the coefficients of determination listed in Table 6.

On the basis of grain yield, the cross between Blueboy and Pioneer S76 or reciprocal would be the best choice among the F_1 entries for hybrid wheat production. An examination of the yield components and the compensation patterns in Figure 8 reveals that this hybrid achieved its higher level of grain yield primarily by producing more seeds per spike. When working with oats, Grafius and Thomas (1971) found a

similar compensation pattern with the higher yielding cultivars producing more seeds per inflorescence.

Since genotypes with more seeds per spike tend be the result of compensation due a reduced number of spikes per unit area, the variables spikes per square meter and seeds per spike were combined to form seeds per square meter, and the standardized values were plotted in Figure 9. In Figure 9 the F_1 crosses of Blueboy x Pioneer S76 and reciprocal had the highest, and Arthur x Sullivan and reciprocal the next highest number of seeds per square meter. In contrast to the Blueboy x Pioneer S76 and reciprocal crosses, the Arthur x Sullivan and reciprocal crosses achieved their higher number of seeds per square meter by producing more spikes per square meter rather than seeds per spike. Hence, the actual sink size may be difficult to determine on the basis of either spikes per square meter or seeds per spike alone and can probably best be determined on the basis of seeds per square meter rather than either of its two components.

Examination of Figure 9 reveals that hybrids with a larger sink compensate by producing seed of a lower weight. An opposite type of compensation pattern was exhibited by hybrids with smaller sinks which compensated for their smaller sink size by producing seed of a higher weight. The Arthur x Sullivan and Blueboy x Pioneer S76 F_1 crosses and their reciprocals both had nearly identical seed weights. Given the same source size, we would have expected Blueboy x Pioneer S76 with its greater sink size to have compensated more than Arthur x Sullivan or reciprocal by producing seed of a lower weight, but such was not the

case. The closeness of seed weight for these two hybrids indicates that Blueboy x Pioneer S76 and reciprocal probably had the greater source capacity. For both of these higher seeds per square meter crosses it appears that source capacity is limiting grain yield more than sink size, but an even larger sink may further increase grain yields. For the hybrids in Figure 9 producing fewer seeds per square meter, it appears that sink capacity is limiting grain yields more than source capacity. Since sink size appears to be limiting for these hybrids, their full source capacity has probably not been utilized and cannot be determined from this data.

It appears that grain yield can be improved in wheat by increasing the size of the sink to ensure full utilization of the source and by increasing the source capacity especially during grain filling. The significant positive associations of grain filling period, spike surface area, and top internode surface area with grain yield indicate that increases of these characters may result in additional source capacity. Increased resistance to powdery mildew and other leaf diseases would also be expected to increase source capacity by preserving leaf area. Such associations do not prove that one variable is necessarily a cause of another but may simply be a result of the entries included in the experiment. The variable flag leaf area in this research is a good example. This variable has been shown in many controlled experiments (Quinlan and Sagar, 1962; Voldeng and Simpson, 1967; Rawson and Evans, 1971; Patrick, 1972) to be an important source of photosynthates during the grain filling period, while the

correlation of flag leaf area with weight per seed in Table 33 is negative and highly significant. It appears that of the entries included in this research, those with a larger flag leaf also had a large number of seeds per spike; examples of this are the cultivar Blueboy and the F_1 hybrid Blueboy x Pioneer S76 or its reciprocal.

On the basis of sink size and source capacity, the F_∞ populations Arthur x Pioneer S76 or reciprocal were chosen as sources for the development of new high yielding cultivars. The F_∞ generation of these populations should have a large sink capacity as predicted by their high number of seeds per square meter. These populations with their predicted large spike, top internode, and flag leaf surface areas also have many of the features necessary in achieving a high source capacity.

An examination of the predicted BCS_∞ population means indicated that one backcross to either of the parents for the Arthur x Pioneer S76 or reciprocal hybrid should also result in favorable source populations for cultivar development. Both of the BCS_∞ generations of these hybrid combinations are expected to have a large sink capacity or seeds per square meter. They are also expected to have a large source capacity from their predicted longer grain filling period, large spike surface, top internode surface, and flag leaf surface areas.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The soft red winter wheat cultivars 'Arthur', 'Sullivan', 'Blueboy', and 'Pioneer S76'; their 12 F_1 and reciprocal F_1 crosses; the 12 F_2 families derived from the F_1 crosses; and the 12 backcrosses of the F_1's to the cultivars were grown in a randomized complete block design with four replications at three East Tennessee locations during the 1981-82 winter wheat season. The significance of additive, dominance, and first-order epistatic effects and their interactions with locations for grain yield, the primary yield components, and secondary yield components were tested using an analysis of variance.

Additive effects were significant for all characteristics except grain yield. Dominance and/or one or more epistatic effects were significant for all characteristics. The significance of these effects indicates that for all characteristics investigated, the gene action is not all additive and that dominance and/or epistatic types of gene action are also present. Genetic parameter estimates of additive, dominance, and first-order epistatic effects were used to determine the predicted values for the parental, F_1, F_∞, and BCS_∞ generations.

Compared to the midparent values, the F_1 hybrids showed trends towards having a higher grain yield, weight per seed, spikes per square meter, test weight, plant height, seedling and spring vigor, reaching maturity later and having a longer grain filling period.

Path-coefficient analysis of the logarithm of grain yield and the

primary yield components indicates that compensation was taking place among the primary yield components. Entries with a higher number of spikes per square meter compensated by producing fewer seeds per spike, and entries with more seeds per spike produced seed of a lower weight.

Using seeds per square meter as an estimate of sink capacity, a plot of the standardized (mean=0, standard deviation=1.0) F_1 least squares means for seeds per square meter, weight per seed, and grain yield per square meter identified the highest yielding F_1 hybrids, Blueboy x Pioneer S76 and reciprocal, as hybrids with a large sink. The same graph indicated that compensation was occurring between seeds per square meter and weight per seed.

Sink capacity, source capacity during grain filling, or both may be limiting grain yield. On the basis of a large sink and a high source capacity, the predicted F_{∞} of Arthur x Pioneer S76 or reciprocal and the predicted BCS_{∞} of Arthur x (Arthur x Pioneer S76 or reciprocal) or Pioneer S76 x (Arthur x Pioneer S76 or reciprocal) were selected as favorable future populations for cultivar development.

Grain yield was positively associated with a longer grain filling period, an increased resistance to powdery mildew, a larger spike and top internode surface area, and increased seedling and spring vigor.

Both primary and secondary yield components may be useful as selection criteria for increasing grain yield in wheat. Failure to select simultaneously for all the primary components of grain yield can be expected to cause the components excluded from selection to compensate for any increase in the levels of the selected components. Given this

situation, it is recommended that selection be based primarily on grain yield or its two major components, seeds per unit area and weight per seed, in addition to selection for secondary yield components. A sufficient sink size appears to be necessary to ensure full utilization of the available sources of photosynthate. Selection for increased sink capacity alone would be expected to increase grain yield until the point where the source capacity is fully utilized. Photosynthetic capacity may be increased by altering the level of certain secondary yield components via selection. The association of the secondary yield components investigated in this research indicates that selection for early heading, longer grain filling period, and a larger spike and top internode surface area may result in increased source capacity.

Improving grain yield by selecting for secondary yield components deserves more attention. Actual selection experiments designed to measure the response in grain yield resulting from selection for the secondary yield components should be initiated. By studying the changes in the primary and secondary yield components across cycles of selection, the complex interrelationships between these components could be further clarified, and the potential usefulness and ramification of using these components as selection criteria evaluated further.

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Crane's Crest

VITA

Paul Linnen was born September 14, 1954, in Oak Park, Illinois. After attending public schools in Illinois, he received the following degrees: B.S. in Agriculture from Western Illinois University at Macomb (1977); M.S. in Agronomy from the University of Missouri at Columbia (1980); and Ph. D. in Plant and Soil Science from the University of Tennessee at Knoxville (1984). Married to the former Catherine Snell of Downers Grove, Illinois, he is presently a plant breeder with Interstate Seed and Grain Company, Fargo, North Dakota.