Evaluation of Heterosis in Wheat

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Introduction

Currently there is much interest in developing commercial F_1 hybrid wheats. Hybrids have great potential for increasing the world's future food supply. The genetic mechanism for hybrid wheat is a cytoplasmic male sterile (CMS)—genetic fertility restorer system similar to the one widly used in sorghum. The cytoplasm of the A-line (female) currently used in commercial hybrid production is derived from the wheat relative *Triticum timopheevi*. The R-line (male) pollinator has the genetic nuclear restorer factors. The F_1 hybrid is fertile and is used for the commercial crop.

In breeding new A-lines and R-lines an early test for potential hybrid vigor in the F_1 generation is desirable. A-lines may be produced relatively easily by crossing an A-line (CMS) as female to a normal line (termed B-line) and backcrossing to the B-line several times to develop the new A-line with the agronomic type of the B-line. Developing R-lines has been much more complex and very few satisfactory ones have been produced. An early evaluation system for detection of exceptional levels of heterosis in wheat is needed so that efforts can be maximized in the development of A-lines and R-lines in germplasms which combine well in hybrids.

Early studies of hybrid vigor in wheat were conducted with handcrossed seeds and reduced seeding rates either by space-planting individual seeds or by planting in hill plots (2, 4, 7). The question of whether or not hybrid vigor under reduced seeding rates were greater than under seeding rates normal for the commerical crop still remains. Comparisons between hill plots and nursery yield plots have been made using the more plentiful F_2 generation seed (4). Unlike the case for corn, hybrid vigor in wheat in the F_2 generation is much less than 50% of that of the F_1 generation. Therefore, F_2 generation tests are not considered useful. Grain yield of hybrids has been subdivided and studied as individual components. Overdominance and heterosis is common for spike number and total yield. Additive gene action and partial dominance are more commonly observed for number of seeds per spike and weight per seed (2, 8). At reduced seeding rates and favorable environmental conditions one might expect greater heterosis for spike number and grain yield than under seeding rates normal for the commercial crop.

Chemical male gametocides hold excellent promise for the development of hybrids to evaluate hybrid vigor. Those chemicals now available commercially either are not completely effective as male gametocides or have a deleterious growth regulator effect carryover in the hybrid.

Lines termed "partial restorers" frequently occur in the development of R-lines (8). These have CMS cytoplasm and are fertile in the homozygous state.

The F_1 obtained from crosses of these partial restorers with A-lines are partially fertile. Crosses can be made in isolation using a partial restorer as the pollen parent and several A-lines as the female seed parents and utilizing wind-blown pollen (6, 8). Pollen of wheat is transported relatively short distances in a volume adequate for good seed set of A-lines (1).

Our experiment was designed to compare the expression of heterosis in F_1 wheat hybrids in hill plots at a reduced seeding rate with heterosis in nursery yield plots at a normal seeding rate. Heterosis, used in this contest, is that increase above the average of the two parents.

Materials and Methods

The amount of heterosis in wheat from hill plot measurements was compared to that from nursery yield plots for grain yield and kernel weight. F_1 hybrid seeds were obtained by crossing CMS A-lines with restored R-lines. The parents and crosses are show in Table I. The R-lines are of the Monon cultivar type with nuclear restorer factors from *T. timopheevi* and CMS cytoplasm from *T. timopheevi*, as described previously (7). The A-lines have CMS cytoplasm from *T. timopheevi*.

TABLE I *Parents and hybrid number designation.*

Female parent	Male parent 68846L1	68846L2	68846L3
CMS Monon	1	4	7
CMS 5724	2	5	8
CMS Knox 62	3	6	9

The hybrids and parents were planted in hills 30.5 cm apart at a seeding rate of 15 seeds per hill. One hill was considered as a plot. The hybrids and parents were planted also in nursery yield plots adjacent to the hill plot experiment. The nursery plot consisted of four rows, 2.44 m long and 30.5 cm apart, with the center two rows harvested for yield. Seeding rate was 25 seeds per 30.5 cm^2. A split-plot design was used in each type of planting with hybrid combinations as whole plots and parents and the F_1 generation as subplots. Eight to 40 replications were used in hill plots and one to four in nursery plots, as permitted by seed supplies. Within the subplot two-thirds of the plants (parents) were fertile and one third, F_1's, was partially fertile. Kernel weight was determined by weighing 200 randomly selected kernels. Pollen to fertilize the partial male-sterile F_1's was supplied by male fertile plants and fertile flowers in the experiment and from a wheat field adjacent on the west.

Analyses of covariance for the two experiments were used due to incomplete fertility restoration in the F_1 hybrid. Seed set (percent) was determined for each hybrid and for their corresponding parents, thus allowing adjustment of plot yields for incomplete seed set. For the hybrids, the means for seed set ranged from 60-70%, whereas means for parents ranged from 86-93%. The equation for an adjusted treatment is given by the following model:

$$\text{Adj } \hat{Y} = Y_{ijk} - b(X_{ijk} - \bar{\chi} ..)$$

The error regression coefficient is b with X and $\bar{\chi}$ as the covariate and mean of the covariates, respectively.

A fully least squares analysis generated a design matrix by computer programming using 0's and 1's. Simple linear regression analyses with all observations (Y) and all X's were calculated. The "extra sum of squares" principle (3) was used on the adjusted values (5). The sequential F-test (3) was used to obtain the error regression coefficient. A harmonic mean square was used to obtain the error mean square for the analysis of variance of the combined planting technique.

Results and Discussion

Yield and kernel weight comparison for hybrids, R-lines, and fertile female parent counterparts of A-lines are presented for three hybrids (Table II). The yields in nursery plots were considerably higher than those in hill plots where seeding rates were reduced. The precision of measurement of differences in yields was higher also in the nursery plots as shown by LSD estimates. Differences between nursery plots and hill plots for kernel weights were small. Kernel weight was measured with somewhat greater precision in nursery plots.

TABLE II *Means of three hybrids and their parents for yield (adjusted for fertility) and for kernel weight.*

	Yield (bu/A)		Kernel weight (g)	
Genotype	Hill plot	Nursery plot	Hill plot	Nursery plot
Hybrid 1	32.7	45.0	6.16	6.32
Monon	31.5	47.9	6.47	6.31
68846L1	33.4	44.5	6.37	6.26
LSD*	5.6	2.1	0.21	0.11
Hybrid 2	35.3	42.8	6.68	6.79
Purdue 5724	25.5	49.5	6.74	6.70
68846L1	34.7	49.1	6.31	6.27
LSD*	5.9	2.2	0.21	0.11
Hybrid 3	33.2	40.1	6.53	7.06
Knox 62	31.8	49.0	7.20	6.82
68846L1	33.0	49.3	6.36	6.38
LSD*	10.5	3.8	0.38	0.20

*LSD at .05 level of significance.

For the nursery experiment highly significant differences among hybrids were found for grain yield and for kernel weight. Three of 9 hybrids were significantly different from their parents for yield and 7 of 9 for kernel weight (Table III). Yields of the parents ranges from 40.4 to 50.0 bu/A. Heterosis above the mid-parent value was not significant for adjusted yields or kernel weight for any hybrid. Most hybrids exceeded the lower yielding parent but not the higher yielding parent.

The absence of heterosis was unexpected although the parents were somewhat related. Patterson and Bitzer (9) observed significant heterosis expressed in hybrids tested with the greatest amounts produced in hybrids of

TABLE III *F values from analysis of variance for yield and kernel weight in the nursery row experiment.*

Source	df	F. values	
		Yield	Kernel weight
Hybrids (X)	9	23.24**	22.47**
S.E.	18	5.06	0.13
Parents/hybrid 1	2	2.04	0.06
2	2	1.73	5.95**
3	2	1.20	3.91*
4	2	7.11**	1.24
5	2	4.21*	4.29*
6	2	0.52	10.83**
7	2	1.45	4.52*
8	2	3.58**	11.78**
9	2	1.38	3.33*
S.E.	35	3.25	0.17

*,**Significant at the .05 and .01 levels, respectively.

unrelated parents. Heterosis for yields may be expressed better in more favorably environments. Heterosis was not expressed for kernel weights where hybrids had fewer kernels per spike due to sterile flowers. Kernels formed from wind-blown pollen tend to be shriveled, perhaps from delayed fertilization of the flowers (our observation and hypothesis). Kernel weight has not been shown generally to exhibit heterosis (2, 8).

In the hill plot experiment, yields ranged from 22.8 to 40.1 bu/A for the parents. Differences among hybrids were significant for kernel weight but not for yield. Differences between parents and hybrids were significant for yield in 7 of 9 comparisons and in all 9 comparisons for kernel weight (Table IV). However, heterosis was not significant for grain yield or kernel weight.

TABLE IV *F values from analysis of variance for yield and kernel weight in the hill plot experiment.*

Source	df	F. values	
		Yield	Kernel weight
Hybrids (X)	8	1.73	6.94**
S.E.	182	7.53	.41
Parents/hybrid 1	2	0.29	5.81**
2	2	8.33**	11.24**
3	2	0.05	13.16**
4	2	3.39*	3.27*
5	2	8.18**	14.36**
6	2	4.92**	28.49**
7	2	7.36**	6.82**
8	2	10.18**	15.52**
9	2	20.23**	27.67**
S.E.	340	8.87	0.32

*,**Significant at the .05 and .01 levels, respectively.

The analysis of variance for the two plot techniques revealed significant interactions in grain yeilds for plot type x hybrids; parents x hybrids; and plot type x parents x hybrids (Table V). No significant interaction occurred for

TABLE V *F values from the analysis of variance for yield and kernel weight with combined plot techniques.*

Source	df	F values	
		Yield	Kernel weight
Plot types (K)	1		
Hybrids (H)	8	1.77	1.37
K x H	8	2.11*	0.08
Parents P x H	18	7.08**	1.30
K x P x H	18	6.48**	0.30
S.E.		2.16	0.32

*,**Significant at the .05 to .01 levels, respectively.

kernel weights. In general the hybrids expressed a lower magnitude of different from their parents in the nursery plots. The precision of measure of differences was better in the nursery row plots. The individual LSD's for comparing hybrids with parents for yields ranged from 2.0 to 3.8 and averaged 2.4 whereas LSD's for the hill plots ranged from 5.5 to 10.5 and averaged 6.4.

Our experiment failed to detect the hybrid vigor expected. Three probable reasons for this failure are somewhat related parents, a below average environment, and incomplete seed set. The experiment could be improved by providing a high pollen load using a mixture of cultivars in alternate strips of pollen source to yield test areas in about 1:1 ratio of areas (eg. 2.44 m strips) (1). We belive that partially restored R-lines can be utilized in a systematic search for germplasm combinations which express exceptional levels of hybrid vigor.

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