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Hybrid Performance Among Six-Rowed × Two-Rowed Winter Barleys (*Hordeum vulgare* L. and *Hordeum distichum* L.)

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Summary. A two-rowed winter barley cultivar, Carstens, was crossed with 22 6-rowed barley cultivars and one 2-rowed cultivar. The parents and hybrids, which were 2-rowed, were grown at two locations in two seasons. An F_2 generation of each cross was included in the second season. The hybrids and parents were compared for winter survival, heading date, height, number spike bearing tillers, rachis nodes per spike, 1000-kernel weight, and grain weight. The hybrid significantly exceeded the higher parent in most crosses for height, number rachis nodes per spike, and in every cross for 1000-kernel weight. Significant midparent heterosis was observed in most crosses for winter survival. Heterosis for grain weight was obtained in the 2-rowed × 2-rowed cross. The 2-rowed parents were distinctly less hardy than the 6-rowed parents and expression of characters like number of tillers and grain weight was confounded with winter survival. In hybrids from 6-rowed × 2-rowed crosses the increased number of rachis nodes per spike and heavier kernels contribute to higher grain yields, but these influences are offset by the restricted row number and fewer kernels per spike.

Introduction

This study was initiated to obtain information concerning the performance of hybrids among 6-rowed × 2-rowed winter type barleys (*Hordeum vulgare* L. and *H. distichum* L.). Prior to 1961 barley breeding in Missouri had been concentrated on development of 6-rowed winter-type feed barleys. Our location in the northernmost fringe of the winter barley area necessitated that breeding for winter hardiness be emphasized since only genotypes with excellent winter hardiness perform satisfactorily at Columbia, Missouri.

In 1961 we began investigating the potential for growing winter malting barley. Preliminary studies suggested that the greatest opportunity for success would be with the 2-rowed types (Poehlman and Fleetwood, 1962) due to their more uniform seed characteristics and superior seed size. However, we found a dearth of 2-rowed cultivars with the required level of winter hardiness (Duclos, Poehlman and Hoskins, 1971). The most hardy 2-rowed strains tested were Carstens and Tschermak, both cultivars imported from Europe. Neither were sufficiently winter hardy to be grown in central Missouri, although small acreages of Carstens has since been grown commercially in the Southeast Delta Area of Missouri where winters are less severe.

Proposed procedures for commercial production of hybrid barley (Wiebe, 1960 and Ramage, 1965) prompted this investigation of the potential for the 6-rowed × 2-rowed crosses reported here. Most of the performance reports on barley hybrids have been concerned with crosses among 6-rowed × 6-rowed barley cultivars (Aastveit, 1964; Gebrekidan and Rasmusson, 1970; Grafius, 1959; Hagberg, 1953; Hayes, 1968; Immer, 1941; Sakai and Gotoh, 1955; Severson and Rasmusson, 1968; Suneson, 1962; Suneson and Riddle, 1944; Upadhyaya and Rasmusson, 1967; and Wienhues, 1968). In many of these reports results were based on spaced plantings which tends to favor a greater expression of heterosis than found in thickly spaced plantings. Crook and Poehlman (1971) and Pawlisch and Van Dijk (1965) reported on heterosis in 6-rowed × 6-rowed crosses among winter barley cultivars with near normal seeding rates. Hybrid performance of 2-rowed × 6-rowed crosses have been reported by Bray (1963), Carleton and Foote (1968), Hagberg (1953), and Lambert and Rasmusson (1959) and 2-rowed × 2-rowed crosses by Engledow and Pal (1934) and Hagberg (1953). All of the reports on crosses involving 2-rowed cultivars utilized spring types only. In the 2-rowed × 6-rowed crosses Hagberg (1953) reported midparent and, in some crosses, high parent heterosis for weight of plant, yield of grain, height of straw, length of ear, tillering, and 1000-grain weight. The largest expression of heterosis was for 1000-grain weight. Carleton and Foote (1968), as an average over 12 2-rowed × 6-rowed crosses, obtained an increase in the F_1 over the average of the parents for heads per plant, kernel weight, leaf length, and leaf width, and a decrease for kernels per head, total leaf blade area, and tillers per plant. Significant increases of the F_1 above the better parent (.05 level of significance) were obtained for heads per plant in two crosses, for kernel weight in 10 crosses, and for total leaf area in one cross.

In selecting parental materials for this study we were constrained by the limited number of cultivars that could be utilized. Although the 2-rowed winter cultivars were superior in seed size and quality they lacked the hardiness necessary for good winter survival. On the other hand the 6-rowed winter cultivars were superior in yield and in winter hardiness and constituted the best pool of hardiness genes available. The ability of the 6-rowed cultivars to outyield the 2-rowed cultivars in our climate is confounded with their superior hardiness, since stands of even the best adapted 2-rowed cultivars, Carstens and Tschermak, are usually reduced by winter injury to the point where yields are reduced also. Since the 2-rowed character is dominant to 6-rowed, it appeared desirable to evaluate a series of 2-rowed × 6-rowed crosses in order to determine whether the 2-rowed hybrids derived from these crosses would possess a level of hardiness, yield, and seed quality which would make it possible to utilize them for commercial hybrid production.

Materials and Methods

A 2-rowed winter barley cultivar, Carstens (P_0) was crossed with 22 6-rowed winter barley cultivars or selections (P_1 through P_{22}) and one 2-rowed cultivar, Tschermak (P_{23}). The parent cultivars and their classification for spike row number are listed in Table 1. Crosses to obtain seed for planting the F_1 in the 1967–68 season were made in the greenhouse using Carstens as the pollen parent. The same crosses were repeated in the field in 1968, using a genetic male sterile Carstens as the female parent, to obtain the hybrid seeds planted in the 1968–69 season. Reciprocal crosses involving Carstens had been examined previously and no maternal effects had been observed.

The 24 parents and 23 F_1's were grown in each 1967–68 and 1968–69 seasons on the University of Missouri Bradford Farm, Columbia, and the Delta Research Center, Portageville, Missouri. As the Delta Research Center is located about 325 kilometers farther south than the Bradford Farm and mean daily temperatures average about 5 degrees C higher during the winter months, winter injury there is normally less severe than at Columbia. F_2 populations were included in the 1968–69 season. Cross $P_{10} \times P_0$ was dropped from the Portageville test in 1968–69 due to shortage of F_1 seeds. These experiments will be referred to hereafter as Columbia-68, Columbia-69, Portageville-68, and Portageville-69.

Table 1. *Parent barley cultivars or selections used in crosses*

Parent number	Spike row number	USDA C.I. no.	Cultivar or selection number	Origin
P_0	2-row		Carsten	Europe
P_1	6-row	9186	B-475	Missouri
P_2	6-row	9516	B893	Nebraska
P_3	6-row	11355	B1300	Missouri
P_4	6-row	11641	B1301	Missouri
P_5	6-row	15250	B1470	Missouri
P_6	6-row	15188	B1589	Missouri
P_7	6-row	6561	Reno	Kansas
P_8	6-row	8067	Hudson	New York
P_9	6-row	10667	Harrison	Indiana
P_{10}	6-row	13735	Cass	Michigan
P_{11}	6-row	11642	B 1318	Missouri
P_{12}	6-row	11356	B 1371	Missouri
P_{13}	6-row	13879	B 1597	Missouri
P_{14}	6-row	15249	B 1749	Missouri
P_{15}	6-row	13880	B 1751	Missouri
P_{16}	6-row	13877	B 1770	Missouri
P_{17}	6-row		B 1773	Missouri
P_{18}	6-row	13855	B 1780	Missouri
P_{19}	6-row	15251	B 1783	Missouri
P_{20}	6-row	15189	B 1790	Missouri
P_{21}	6-row		Ledeci Beta	Europe
P_{22}	6-row	6050	Kentucky 1	Kentucky
P_{23}	2-row		Tschermak	Europe

The parents and F_1's were grown in a randomized block design at each location with 6 replications in 1968 and 5 replications in 1969. A plot, except for the F_2 population, consisted of a single row 150 cm in length, with 30 cm between rows, and with spacing of 2.5 cm between plants within the row. The plots were planted in alternate rows with cultivar Harrison to reduce unequal competitive effects between hybrids and nonhybrids. F_2 plots consisted of two rows similar to the parents and F_1's in length, width, and plant spacing.

Poor stands were obtained in the Portageville-68 experiment and heavy rains prior to ripening resulted in heavy lodging in the Portageville-69 experiment. Consequently, the only data utilized from Portageville were the winter survival observations in 1969 and the 1000-kernel weight measurements in 1968 and 1969. At Columbia, except for winter survival which was recorded in 1969 only, all other observations were recorded both for the Columbia-68 and Columbia-69 experiments.

The observations recorded and how they were obtained follow:

Winter survival. Visual estimate in percent of top growth not killed and converted to angles by arcsin transformation. Winter survival observations were taken before spring regrowth began.

Heading date. Day in May when approximately 80% of stems had fully extruded spikes.

Plant height. From the ground surface to the tip of the spike excluding awns, in cm.

Number spike-bearing tillers. By count after plants had been dug and separated.

Number rachis nodes per spike. By count of 20 randomly selected spikes in each plot.

1000-kernel weight. Weight in grams was calculated from 200 randomly selected kernels.

Grain weight per stem and grain weight per plant. Obtained by calculation.

Grain weight per plot. Whole plot weight in grams after threshing.

Lateral spikelets with seed. By count of 20 randomly selected spikes in each F_1 plot of a 6-row × 2-row cross.

Comparisons between hybrids and parents were analyzed by repeated randomized block design. In addition the data were analyzed using the single array analysis of Aksel and Johnson (1964) for the characters winter survival (after angle transformation), heading date, plant height, number of spikes, 1000-kernel weight, and grain weight per stem.

Results and Discussion

Data for the 24 parents, P_0 through P_{23}, and for the 23 F_1 hybrids are given in Table 2. Each of the hybrids was then compared with its respective mid-parent and higher parent. The significance of the differences at .05 and .01 levels of probability are reported in Table 3. The single array analysis is reported in Table 4.

Table 2. *Agronomic data for parents (P_0 through P_{23}) and hybrids ($P_1 \times P_0$ through $P_{23} \times P_0$)*

Parent or hybrid[a]	Spike row no.	Winter[b] survival	Heading[c] date	Ht[d] cm	No.[d] spike bearing tillers	Rachis[d] nodes per spike	1000-[e] kernel weight g	Grain[d] weight per stem g	Grain[d] weight per plant g	Grain[d] weight per plot g	Lateral[d] spikelets with seeds %
P_0	2	37.9	15.3	93	8.0	18.6	35.8	.55	4.67	124.3	
P_1	6	48.0	11.8	102	6.2	16.8	29.1	.90	5.60	177.2	
P_2	6	61.1	13.3	95	6.0	17.9	26.7	.86	5.02	126.9	
P_3	6	48.9	9.4	100	5.3	15.8	31.8	1.05	5.42	192.7	
P_4	6	47.6	7.8	100	5.8	15.4	33.1	1.02	5.93	187.4	
P_5	6	39.2	10.5	97	5.6	15.1	29.0	.77	4.37	176.4	
P_6	6	56.5	11.0	93	6.5	15.6	30.0	.91	5.97	218.6	
P_7	6	58.3	9.7	96	6.8	15.9	28.2	.86	5.89	194.1	
P_8	6	44.7	13.2	97	6.7	18.2	27.8	.97	6.54	150.5	
P_9	6	55.2	13.4	94	4.9	16.6	33.6	1.14	5.65	180.5	
P_{10}	6		10.8	98	5.7	15.7		1.00	5.66	186.6	
P_{11}	6	60.8	10.3	108	6.2	17.3	31.1	.91	5.63	220.0	
P_{12}	6	50.2	9.1	106	7.2	17.2	27.6	.92	6.54	225.5	
P_{13}	6	56.1	15.4	101	6.1	16.9	29.7	.85	5.37	156.8	
P_{14}	6	52.2	13.0	99	6.9	17.5	27.5	.92	6.53	215.5	
P_{15}	6	58.2	13.0	96	5.6	17.0	26.8	.95	5.35	186.4	
P_{16}	6	56.9	11.0	95	5.8	17.0	30.5	1.03	5.98	217.8	
P_{17}	6	61.5	13.1	99	5.8	16.9	29.1	.90	5.16	158.5	
P_{18}	6	61.0	10.1	109	6.2	16.4	29.9	.83	5.12	174.2	
P_{19}	6	58.7	12.4	100	6.8	17.0	26.7	.88	6.04	178.9	
P_{20}	6	62.0	11.4	97	6.9	17.5	27.7	.92	6.27	199.8	
P_{21}	6	47.7	16.5	107	5.8	19.3	34.1	1.19	7.08	156.5	
P_{22}	6	55.8	15.6	114	5.7	20.7	30.8	1.14	6.49	175.9	
P_{23}	2	27.3	16.5	95	5.2	25.6	36.2	.77	4.29	77.1	
Mean, P_1 through P_{23}		53.1	12.1	100	6.1	17.4	29.8	.94	5.74	179.7	
$P_1 \times P_0$	(6 × 2)	50.5	12.7	109	7.6	19.9	44.2	.75	5.82	131.7	0.026
$P_2 \times P_0$	(6 × 2)	53.0	14.4	102	7.3	19.6	41.1	.66	4.75	106.9	0.029
$P_3 \times P_0$	(6 × 2)	55.2	12.8	108	7.3	19.7	44.3	.71	5.12	131.5	0.067
$P_4 \times P_0$	(6 × 2)	51.1	9.8	105	6.9	18.6	45.7	.73	5.12	132.7	0.070
$P_5 \times P_0$	(6 × 2)	56.3	12.5	109	7.3	19.7	42.9	.77	5.53	133.5	0.067
$P_6 \times P_0$	(6 × 2)	52.6	13.7	97	6.1	18.6	44.3	.75	4.63	104.6	0.066
$P_7 \times P_0$	(6 × 2)	55.8	12.7	103	7.3	18.1	44.6	.71	5.24	137.3	0.007
$P_8 \times P_0$	(6 × 2)	44.2	15.5	104	6.4	20.5	43.4	.73	4.70	81.5	0.009
$P_9 \times P_0$	(6 × 2)	50.5	12.6	109	7.0	20.4	47.3	.83	5.72	160.5	0.026
$P_{10} \times P_0$	(6 × 2)		12.2	107	6.6	18.2		.72	4.78	154.8	0.130
$P_{11} \times P_0$	(6 × 2)	51.3	12.0	106	7.3	20.3	45.0	.79	5.84	145.0	0.033
$P_{12} \times P_0$	(6 × 2)	56.2	10.5	108	7.6	19.8	42.4	.73	5.44	165.7	0.057
$P_{13} \times P_0$	(6 × 2)	51.2	14.5	108	7.3	20.5	42.9	.78	5.73	167.5	0.014
$P_{14} \times P_0$	(6 × 2)	51.1	13.4	107	6.9	20.5	45.4	.77	5.36	127.5	0.036
$P_{15} \times P_0$	(6 × 2)	51.1	13.2	97	6.4	19.8	40.4	.70	4.42	89.1	0.033
$P_{16} \times P_0$	(6 × 2)	63.8	11.9	105	7.8	19.9	45.2	.80	6.25	166.0	0.020
$P_{17} \times P_0$	(6 × 2)	59.5	12.6	105	6.6	19.5	45.0	.82	5.49	148.0	0.060
$P_{18} \times P_0$	(6 × 2)	55.9	13.6	104	7.3	19.8	42.9	.69	5.06	114.2	0.018
$P_{19} \times P_0$	(6 × 2)	61.1	13.6	103	7.7	19.3	44.8	.49	3.59	93.0	0.017
$P_{20} \times P_0$	(6 × 2)	65.0	11.4	103	7.5	18.5	43.7	.72	5.35	150.5	0.025
$P_{21} \times P_0$	(6 × 2)	52.8	16.2	115	7.4	21.7	46.4	.84	6.27	175.1	0.005
$P_{22} \times P_0$	(6 × 2)	50.6	13.5	110	7.2	21.4	43.8	.83	6.08	158.5	0.026
$P_{23} \times P_0$	(2 × 2)	36.3	14.0	101	6.9	25.5	37.9	.80	5.60	130.3	
Mean		53.5	13.0	105	7.1	20.0	43.6	.74	5.30	135.0	0.037

[a] Reciprocal crosses grown in 1968.
[b] Winter survival is mean 'arcsin $\sqrt{\text{percent}}$' for Columbia-69 and Portageville-69 experiments.
[c] Heading date is mean 'days in May' for Columbia-68 and Columbia-69 experiments.
[d] Height, number tillers, number rachis nodes, grain weights, and lateral spikelets with seeds are means for Columbia-68 and Columbia-69 experiments.
[e] 1000-kernel weight is mean for Columbia-68, Columbia-69, Portageville-68 and Portageville-69 experiments.

Winter survival

Parents with highest survival were P_{20}, P_{17}, P_2, P_{18}, and P_{11} (Table 2). These results substantiate previous observations on these cultivars obtained over a period of several seasons in the field at Columbia. The lowest survival was for the 2-rowed parents, P_0 and P_{23}. The hybrids with the highest survival were $P_{20} \times P_0$, $P_{16} \times P_0$, $P_{19} \times P_0$ and $P_{17} \times P_0$ (Table 2). Every hybrid exceeded the mean of its respective parents in winter survival, the differ-

Table 3. *Significance of difference when hybrid is compared with midparent and with higher parent*

Cross	Spike row no.	Winter survival	Heading date[a]	Height	No. spike bearing tillers	Rachis nodes per spike	1000-kernel weight	Grain weight per stem	Grain weight per plant	Grain weight per plot
Comparison of hybrid with midparent:										
$P_1 \times P_0$	(6 × 2)	*		**	None significant	**	**			
$P_2 \times P_0$	(6 × 2)			**		**	**			
$P_3 \times P_0$	(6 × 2)	**		**		**	**			
$P_4 \times P_0$	(6 × 2)	*		**		**	**			
$P_5 \times P_0$	(6 × 2)	**		**		**	**	*	*	
$P_6 \times P_0$	(6 × 2)					**	**			
$P_7 \times P_0$	(6 × 2)	*		**		*	**			
$P_8 \times P_0$	(6 × 2)			**		**	**			
$P_9 \times P_0$	(6 × 2)		(−)*	**		**	**			
$P_{10} \times P_0$	(6 × 2)	b		**		*	b			
$P_{11} \times P_0$	(6 × 2)			*		**	**			
$P_{12} \times P_0$	(6 × 2)	**	(−)*	**		**	**			
$P_{13} \times P_0$	(6 × 2)			**		**	**			
$P_{14} \times P_0$	(6 × 2)			**		**	**			
$P_{15} \times P_0$	(6 × 2)					**	**			
$P_{16} \times P_0$	(6 × 2)	**		**		**	**		*	
$P_{17} \times P_0$	(6 × 2)	**		**		**	**			
$P_{18} \times P_0$	(6 × 2)					**	**			
$P_{19} \times P_0$	(6 × 2)	**		**		**	**			
$P_{20} \times P_0$	(6 × 2)	**	(−)*	**			**			
$P_{21} \times P_0$	(6 × 2)	**		**		**	**			
$P_{22} \times P_0$	(6 × 2)			**		**	**			
$P_{23} \times P_0$	(2 × 2)			**		**	*	**	**	**
Mean percent hybrids as percent of their respective midparent mean:		118	−0.6[c]	110	101	111	134	100	102	90
Comparison of hybrid with higher parent:										
$P_1 \times P_0$	(6 × 2)		None significant	*	None significant	**	**	None significant	None significant	None significant
$P_2 \times P_0$	(6 × 2)			**		*	**			
$P_3 \times P_0$	(6 × 2)			**		*	**			
$P_4 \times P_0$	(6 × 2)						**			
$P_5 \times P_0$	(6 × 2)	**		**		*	**			
$P_6 \times P_0$	(6 × 2)						**			
$P_7 \times P_0$	(6 × 2)			*			**			
$P_8 \times P_0$	(6 × 2)			*		**	**			
$P_9 \times P_0$	(6 × 2)			**		**	**			
$P_{10} \times P_0$	(6 × 2)	b		**			b			
$P_{11} \times P_0$	(6 × 2)					**	**			
$P_{12} \times P_0$	(6 × 2)					*	**			
$P_{13} \times P_0$	(6 × 2)			*		**	**			
$P_{14} \times P_0$	(6 × 2)			**		**	**			
$P_{15} \times P_0$	(6 × 2)					*	**			
$P_{16} \times P_0$	(6 × 2)			**		**	**			
$P_{17} \times P_0$	(6 × 2)			*			**			
$P_{18} \times P_0$	(6 × 2)					*	**			
$P_{19} \times P_0$	(6 × 2)						**			
$P_{20} \times P_0$	(6 × 2)			*			**			
$P_{21} \times P_0$	(6 × 2)			**		**	**			
$P_{22} \times P_0$	(6 × 2)					*	**			
$P_{23} \times P_0$	(2 × 2)			*			*			
Mean percent hybrids as percent of their respective higher parent mean:		101	1.1[c]	106	89	105	122	80	93	76

*, ** Hybrid superior to midparent or higher parent at .05 and .01 level of probability, respectively.

[a] Negative value for heading date indicates earlier than midparent.

[b] No data.

[c] Mean days earlier or later than midparent or earlier parent.

Table 4. *Estimates of genetic parameters for several agronomic characters at Columbia-69 in a single array analysis*

Parameter[a]	Winter survival	Heading date	Plant height	Number of spikes	1000 kernel weight unadjusted	1000 kernel weight adjusted	Grain *wt*/stem
$\hat{V}ar(d)_i$	28.62 ± 2.78**	−1.37 ± 0.19**	7.06 ± 0.82*	0.116 ± 0.002**	1.64 ± 0.23*	3.30 ± 0.20*	0.002 ± 0.001*
$\hat{C}ov\ (d)_i(h_0)_i$	−8.64 ± 6.01	0.06 ± 0.40	−1.19 ± 1.77	−0.053 ± 0.003**	0.07 ± 0.60	−0.72 ± 0.40	−0.002 ± 0.001
$\hat{V}ar\ (h_0)_i$	40.96 ± 15.53	0.72 ± 1.04	6.71 ± 4.56	0.054 ± 0.009*	1.24 ± 1.28	1.27 ± 1.11	−0.005 ± 0.003
$\hat{V}ar\ (\Delta)_i$	−0.36 ± 11.92	−0.63 ± 0.80	−2.55 ± 3.50	−0.079 ± 0.007**	−1.01 ± 0.94	−0.61 ± 0.80	−0.001 ± 0.002
MDD	1.20	0.72	0.98	0.68	0.87	0.61	1.37
$r(h_0)_i/(d)_i$	−0.25	0.07	−0.17	−0.67*	0.05	−0.35	−0.61**
$\overline{h_0}$	11.78 ± 2.78**	−2.00 ± 0.57**	13.40 ± 2.10**	0.890 ± 0.271**	12.10 ± 0.22*	5.48 ± 0.24**	0.005 ± 0.079
$\overline{\Delta}$	−1.16 ± 1.66	0,32 ± 0.34	2.50 ± 1.39	−0.448 ± 0.192*	−3.06 ± 0.24*	0.06 ± 0.22	0.030 ± 0.040

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

[a] $(d)_i = \frac{P_0 - P_i}{2}$ $(i = 1, 2, \ldots, 23)$

$(h_0)_i = F_1 - \frac{P_0 + P_i}{2}$

$(\Delta)_i = F_2 - 1/2\,F_1 - 1/4\,(P_0 + P_i)$

$\text{MDD} = [\hat{V}ar\ (h_0)_i/\hat{V}ar\ (d)_i]^{1/2}$ = mean degree of dominance.

$r(h_0)_i/(d)_i$ = Correlation between $(h_0)_i$ and $(d)_i$.

ence being significant at the .01 level of probability in 8 crosses and significant at the .05 level of probability in 3 additional crosses (Table 3). Overall, the hybrids exceeded the midparents by 18% in survival. Nine hybrids were superior to the higher parent in winter survival, but in only one cross was the difference significant (Table 3). When the hybrid exceeded the higher parent, usually both parents had low survival. These results are similar to those reported by Crook and Poehlman (1971). In seven 6-rowed × 6-rowed crosses they obtained a mean survival percentage which exceeded the mean of the respective midparents by 32% and the mean of the respective higher parent by 21%. The higher survival of the hybrid in relation to the parent may result from its increased vigor which enables it to (a) establish itself better in the fall and (b) recover from winter injury to a greater extent than the parent lines.

The single array analyses (Table 4) showed that a large proportion of the variation was due to additive effects, especially when the degree of winter injury was moderate. Existence of dominant effect for winter-hardiness with variable potence ratios are shown by the significant $\bar{h}_0$ and $\hat{V}ar(d)_i$ values and nonsignificant $\hat{V}ar\ (h_0)_i$. Rohde and Pulham (1960) suggested winter hardiness in barley to be controlled by different combinations of additive and nonadditive genes in different varieties. In a reanalysis of Rohde and Pulham's data, Eunus, Johnson, and Aksel (1962) suggested winterhardiness to be controlled by both dominant and recessive genes with the former being greater and with a highly significant positive correlation between mean winter survival and degree of dominance.

Since lack of winter hardiness is a notable weakness in the 2-rowed barley varieties available to us, these results and those of Crook and Poehlman (1971) are of considerable practical interest. It appears that hybrids may be obtained frequently that would exceed the midparent in hardiness, but only rarely would a hybrid be found that would significantly exceed the hardy parent. Since relatively few 6-rowed barley varieties and no 2-rowed varieties known to us have the desired hardiness level for our climatic area, we would be greatly restricted in parent materials available for developing two-rowed hybrids in a winter malting barley breeding program.

Heading date

The mean heading dates in May of the parents ranged from 7.8 to 16.5 (Table 2), with four varieties heading later than the common parent (P_0). Considering that the varieties were planted the previous September and had been in the ground for over 225 days, this represents a relatively narrow range in heading. Over the 23 crosses the hybrids headed 0.6 days earlier than the midparent and 1.1 days later than the average of the early parents. Looking at individual crosses, 15 hybrids headed earlier than their midparent with the difference being significant at the .05 level of probability in three crosses (Table 3). Five hybrids headed earlier than their earlier parent but none of the differences were significant (.05 level). These results conform to previous studies in which the F_1 was reported to be intermediate or earlier than the mean of the parents by Aksel and Johnson (1961); Crook and Poehlman (1971); Hagberg (1953); and Harlan and Martini (1929). Severson and Rasmusson (1968) reported the F_1 to be intermediate or slightly later than the average of parents. Except for the report of Crook and Poehlman (1971), all of the studies were with spring type barleys.

Inheritance of heading date is complex involving both genetic and environmental interactions. Of the latter, not the least is winter survival since varieties severely injured may take longer to recover and renew growth in the spring than those less injured. This does not appear to have influenced our results, however, since the hybrids earlier than the midparent were uniformly distributed over the entire array of hybrid survival percentages. A single array analysis of the Columbia-69 data (Table 4) suggests partial dominance for early heading. The dominant effect for early heading was uniform ($\hat{\text{V}}\text{ar}\ (h_0)_i$ not significant) with variable potence ratio ($r_{h_0/d} = 0.07$, nonsignificant) in the array of crosses tested.

Height

The 23 hybrids averaged 105 cm in height compared to 100 cm for the 23 paternal parent cultivars (Table 2). This was an average of 10% over the midparent means and 6% over the respective taller parent means. Every hybrid exceeded the midparent in height with the difference being significant at the .01 level in 19 crosses and the .05 level in one additional cross (Table 3). The hybrid exceeded the taller parent in 20 crosses with differences significant at the .01 level of probability in 8 crosses and the .05 level in 7 additional crosses. A single array analysis of the Columbia-69 data (Table 4) suggests a variable degree of dominance for tallness among the crosses ($\bar{h}_0$ and $\hat{\text{V}}\text{ar}\ (d)_i$ significant but not $\hat{\text{V}}\text{ar}\ (h_0)_i$).

Heterosis for height in 2-rowed × 6-rowed crosses was reported by Bray (1963) and Hagberg (1953) and in 6-rowed × 6-rowed crosses by Crook and Poehlman (1971), Hagberg (1953), Hayes (1968) and Severson and Rasmusson (1968). In general, larger heterosis for height has been reported for 2-rowed × 6-rowed crosses than for 6-rowed × 6-rowed crosses. Also, more heterosis is expressed with wide spacing of plants than with close spacing. Previous studies as well as the data reported here emphasize the need for short parent varieties if short hybrids are to be obtained, and for evaluating hybrids under normal field planting rates rather than in spaced plantings.

Number spike-bearing tillers

The number of spike-bearing tillers of the 6-rowed parents averaged 6.1 compared to 8 for the common two-rowed (P_0) (Table 2). The overall mean was 7.1 for hybrids. Although 15 of the hybrids exceeded the midparent in number of tillers, none of the differences were significant (Table 3), and none of the hybrids exceeded the high parent (P_0). A single array analysis of the Columbia-69 data (Table 4) indicated partial dominance of high spike number. The potence ratio was rather constant within the array since $r(h_0)_i/(d)_i$ was significant. The dominant genes are in excess in P_0 since $\hat{\text{C}}\text{ov}\ (d)_i(h_0)_i < 0$ and significant. A wide variation in winter injury among parents and hybrids was probably responsible for the significant epistatic effect shown in the analysis as well as the negative value of the variance which is theoretically impossible.

Comparisons of number of spikes of parents and hybrids have been reported by several workers. Crook and Poehlman (1971), Hayes (1968), Immer (1941), Pawlisch and Van Dijk (1965), Severson and Rasmusson (1968), and Upadhyaya and Rasmusson (1967) found the F_1 to be intermediate and generally exceeding the midparent in 6-rowed × 6-rowed crosses. Similar results were reported by Carleton and Foote (1968), Hagberg (1953), and Lambert and Rasmusson (1959) with 2-rowed × 6-rowed crosses. The F_1 has been reported to exceed the higher parent in tiller number by Grafius (1959), Hayes (1968), Immer (1941), and Sakai and Gotoh (1955). Except for the experiments of Grafius the higher tiller number occurred only in an occasional cross. Bray (1963) reported partial dominance for low tiller number in a 2-rowed × 6-rowed cross.

Number of tillers per unit area is one of the components of yield. In our experiment and in the experiments reported by Bray (1963) and Lambert and Rasmusson (1959), the 2-rowed parents exceeded the mean tiller number for the 6-rowed parents. Recovery of high tiller number is desirable to offset the effects of the lower grain number in two-rowed spikes. Tiller number is influenced by environmental factors, such as moisture, nutrient supply, spacing of plants, and winter injury. Good winter survival is of major importance in our area and tiller number could be enhanced if winter hardiness of the hybrids could be further improved. Otherwise, tiller number becomes confounded with winter survival.

Number rachis nodes per spike

Number of kernels per spike is a second component of yield. In crosses between 6-rowed × 6-rowed varieties, number of kernels in the hybrid has been reported to exceed the midparent in most crosses but may exceed the high parent in specific crosses

(Crook and Poehlman, 1971; Grafius, 1959; Hagberg, 1953; Immer, 1941; Pawlisch and Van Dijk, 1965; and Upadhyaya and Rasmusson, 1967). In 6-rowed × 2-rowed crosses the hybrid, which is 2-rowed, has a physical restriction to number of kernels which negates the utility of comparisons made to the mid-parent or to the 6-rowed parent. Since number of kernels is a function of the number of rachis nodes per spike, we have examined this characteristic rather than number of kernels.

The mean number of rachis nodes per spike for the 22 6-rowed parents was 17.0 compared to 18.6 (Table 2) for the common 2-rowed parent (P_0). P_0 was exceeded in rachis node number by only two 6-rowed parents, P_{21} and P_{22}, and by the 2-rowed parent, P_{23}. Seventeen of the 22 hybrids involving a 6-rowed parent exceeded the high parent in number of rachis nodes, eight significantly at the .01 level of probability and an additional seven at the .05 level (Table 3). These data support the proposition that 6-rowed parents may contribute genes for increased number of rachis nodes hence increased kernel number over the 2-rowed parent to a 2-rowed hybrid. In the 2-rowed × 2-rowed cross significant midparent, but not high parent heterosis, for number of rachis nodes was obtained.

1000-kernel weight

Of the yield components studied, the largest and most consistent expression of heterosis in the 6-rowed × 2-rowed crosses was recorded for kernel weight. The mean of the hybrids was 43.6 g compared to 29.8 g for the parents (Table 2). Each of the 21 6-rowed × 2-rowed hybrids exceeded both mid- and highparent at the .01 level of probability (Table 3). The 2-rowed × 2-rowed cross ($P_{23} \times P_0$) exceeded the mid- and highparent at the .05 level of probability (Table 3). These data support results of Carleton and Foote (1968), Hagberg (1953), and Suneson and Riddle (1944) with 6-rowed × 2-rowed crosses. Heterosis for kernel weight in 6-rowed × 6-rowed crosses have been reported by Crook and Poehlman (1971), Grafius (1959), Hagberg (1953), Hayes (1968), and Upadhyaya and Rasmusson (1967), but relatively few of the hybrids reported on showed kernel weight outside the range of the parents. A single array analysis of the Columbia-69 data (Table 4) showed significant values for dominant and epistatic effects.

Wells (1962) substituted vv for the VV gene in Compana (2-rowed) and VV for vv in Vantage (6-rowed) barley. A calculation made from his data showed that for 1000-kernel weight the ratios for 2-rowed vs 6-rowed spikes were 1.3 for Compana and 1.4 for Vantage background. In the present study, the 1000-kernel weight ratios for 2-rowed vs 6-rowed segregants from the 22 F_2 populations of 6-rowed × 2-rowed crosses ranged from 1.32 to 1.55 with a mean of 1.47 (Table 5). Thus the ratio of kernel weight for vv vs V- genotype in a common genetic background is probably around 1.4. Single array analysis on data from Columbia-69 was made again after adjustment of the 1000-kernel weight for the 6-rowed parents by the factor 1.4 and only 2-rowed segregants were used to represent the F_2-populations. By this adjustment the dominant effects were reduced and the epistatic effect disappeared. Thus the phenotypic over-dominance of 1000-kernel weight in the F_1 hybrid of the 6-rowed × 2-rowed crosses were likely due to the physical restriction imposed by the phenotypic difference of vv and V- genotypes.

Table 5. *1,000-kernel weight and grain weight per stem of parents and F_2 segregants in 22 6-rowed × 2-rowed barley crosses*

Population	1,000-kernel weight gm	Grain weight per stem mg
P_0 (2-rowed parent)	39.2	497
Mean of 22 6-rowed parents	33.1	733
Mean of 2-rowed segregants in F_2 of 22 6-rowed × 2-rowed crosses	45.8	539
Mean of 6-rowed segregants in F_2 of 22 6-rowed × 2-rowed crosses	31.2	703
Ratio $\frac{\text{2-rowed } F_2 \text{ segregants}}{\text{6-rowed } F_2 \text{ segregants}}$	1.47	.77

These data suggest that the 1000-kernel weight of a 6-rowed barley would not likely be improved by crossing to a 2-rowed variety with 1000-kernel weight of less than approximately 140% of the 6-rowed variety. This view is supported by a significant negative correlation ($r = -0.92$) between the increase of 1000-kernel weight of the 6-rowed segregants in the F_2 populations over the respective 6-rowed parent and the 6-rowed parent itself. Also, by the fact that the positive increase was shown only in the crosses where the 6-rowed parent had 1000-kernel weight of about 30 grams or less. This corresponds to about 42 grams for the 2-rowed counterpart (if the factor 1.4 is applied) which is close to the 2-rowed parent in the present study. Most of the 6-rowed parents used in the present study would be assumed then to have larger kernels than Carstens (P_0) if they possessed the 2-row genes. Thus it appears possible to improve upon the kernel weight and winter hardiness of Carstens through these crosses since a large proportion of the variance is additive (Table 4). On the other hand, these results suggest that there would be little possibility of improving the kernel weight of the 6-rowed varieties used in this study through these crosses.

Grain weight per stem

Grain weight of barley plants may be broken down into two components, number of spike bearing stems and grain weight of each stem. Yield will be the multiplicative product of these two components. In this experiment the grain weight per stem of the 6-rowed parents ranged from 0.77 to 1.19 g compared to 0.55 g and 0.77 g for the two 2-rowed parents, P_0 and P_{23}, respectively (Table 2). The 23 2-rowed hybrids averaged 0.74 g grain weight per stem (Table 2). Of the 22 6-rowed crosses only one cross ($P_5 \times P_0$) was significantly higher than the midparent (Table 3), although every hybrid except one exceeded the P_0 (two-rowed) parent in grain weight per stem. Thus it appears that grain weight per stem of 2-rowed barley could be enhanced by crossing with 6-rowed varieties, but with little prospect of approaching the heavier 6-rowed parent. This would require that the increased number of rachis nodes per spike and the heavier kernel weight in the hybrids would offset the loss in number of kernels at each rachis node. In the cross between the two-rowed varieties, $P_{23} \times P_0$, the hybrid exceeded the midparent by 21% (significant at .01 level) and the high parent by 4% (nonsignificant).

The lower grain weight per stem in 2-rowed as compared to 6-rowed barley is apparently due to the lower row number. Realistic comparisons of ratios of grain weight per stem in the two types can not be made in the parent varieties used here due to the lower winter hardiness of the two-rowed Carstens parent as compared to the 6-rowed parent. However, comparisons were made over all F_2 populations (Table 5) and the 2-rowed segregants had grain weight per stem of approximately 77% of that of the 6-rowed segregants. If the 6-rowed parents were adjusted by this amount the grain weight per stem in the F_1's would appear essentially equal to that in the 6-rowed parent and thus show complete dominance as in the case of the 2-rowed × 2-rowed crosses.

The barley spikes are active photosynthetic organs (Thorne, 1963; Hozyo and Kobayashi, 1969). Photosynthesis in the spike has been estimated to contribute about 30 to 40% of the total grain weight (Thorne, 1963). The photosynthetic area of the 2-rowed spike would be approximately 1/3 of the 6-rowed counterpart assuming equal surface area for the central and lateral spikelets in 6-rowed spikes. Then, one would expect a loss of about 20 to 26% in total grain weight of 2-rowed spikes due to the loss of 2/3 of the photosynthetic area. This figure is comparable to that found in F_2 progenies in the present study.

A single array analysis showed that potence ratio was rather constant within the array since the correlation between (h_0) and (d) was significant. Equal proportions of dominant and recessive genes were distributed to the P_0 to P_{23} parents as indicated by the nonsignificant $\hat{\mathrm{C}}\mathrm{ov}\,(d)(h_0)$.

Grain yield per plant

The grain yield per plant is the product of the number of tillers and grain yield per stem. In this experiment the grain weight per plant of the 6-rowed parents ranged from 4.37 to 7.08 g (Table 2). The two 2-rowed parents, P_0 and P_{23}, had grain weights of 4.67 and 4.29 g, respectively. Of the 22 6-rowed × 2-rowed hybrids, all but three exceeded the grain weight of the common 2-rowed parent (P_0) indicating that the yield per plant of the 2-rowed hybrids had been enhanced by crossing to a 6-rowed variety. However, only two hybrids significantly exceeded their midparent at the .05 level (Table 3). It is difficult to access how much of this improvement was due to the enhanced winter hardiness in the hybrids as compared to the hardiness of the 2-rowed parent. In the cross between the two-rowed varieties, $P_{23} \times P_0$, the hybrid exceeded the midparent by 25% (significant at .01 level) (Table 3) and the high parent (P_0) by 20% (nonsignificant).

Grain yield per plot

Grain yields per plot varied from 126.9 to 225.5 g for the 6-rowed parents (Table 2). The common 2-rowed parent (P_0) yielded 124.3 g but the other 2-rowed parent (P_{23}) yielded only 77.1 g. The mean yield of the hybrids exceeded that of the P_0 parent, but was less than the mean yield of the 22 6-rowed varieties. Six of the hybrids from the 6-rowed × 2-rowed cross exceeded the yield of the midparent and two exceeded the yield of the high parent but none of the differences were significant. The cross between the 2-rowed varieties ($P_{23} \times P_0$) exceeded its midparent by 29% (significant at .01 level) (Table 3) and the high parent by 5% (nonsignificant). Hagberg (1953) reported the hybrid exceeded the yield of the higher parent in 2 of 4 crosses of 2-rowed × 6-rowed parents. Carleton and Foote (1968) reported that 12 2-rowed × 6-rowed hybrids averaged 0.1% over the midparent, none exceeded the high parent.

In 1968 winter injury was more severe than in 1969 and the hybrids were lower in yield than the midparents. In 1969 the average of the hybrids was significantly higher than the midparent and identical to the high parent. This emphasizes the importance of improving winter hardiness in order to measure the full potential for grain yield.

The additivity or partial dominance for larger number of spike bearing tillers combined with complete dominance in grain weight per stem might contribute to an increase in yield in the F_1 hybrid over the higher yielding parent. However, the dominant effect in the productivity of each stem is greatly offset by the loss in kernel row number in the F_1 of the 2-rowed × 6-rowed crosses. Unless there is a significant contribution from the dominant effect for a large number of spike bearing tillers, the hybrid from the 2-rowed × 6-rowed combination may not be expected to outyield the high yielding parent. This would be essential for the commercial production of hybrid barley. However, the hybrids may be expected to outyield currently available 2-rowed parents in our environment if the 6-rowed parent has winter hardiness and yield potential comparable to the 6-rowed parents used in this experiment.

Lateral kernels in hybrids

Kernels may develop in the lateral florets of hybrids from 6-rowed × 2-rowed crosses with certain parents and under certain environmental conditions (Woodward, 1949). Since the seeds developed in the lateral florets are usually much smaller than seeds developed in central florets they would normally be screened out and discarded before malting thereby reducing the value of the barley grain. To check on this point the kernels developed in lateral florets of the hybrids were measured in the Columbia-68 and Columbia-69 experiments. The number of lateral florets with seeds varied from 0.005% in cross $P_{21} \times P_0$ to 0.13% in cross $P_{10} \times P_0$ (Table 2). Differences among hybrids were significant at the .01 level of probability, but no significant differences between years, or hybrid × year interaction, were obtained. The weight of the lateral kernels constituted only 0.003 to 0.065% of the total kernels harvested. In most hybrids this represented such a small percent of the total weight that it may be ignored.

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