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Intergenotypic Competition Studies in Corn (*Zea mays* L.)

I. Among Experimental Hybrids [1]

A. JURADO-TOVAR and W. A. COMPTON

University of Nebraska, Lincoln, Nebraska (USA)

Summary. Four experimental single-cross hybrids were evaluated for intergenotypic competition in a split-plot design with 7 replicates and a stand density of 51,700 plants/hectar in 1970, 1971 and 1972 at Lincoln, Nebraska. The arrangement of rows used in this study allowed the measurement of effects of different levels of competition on the traits grain yield, plant height and a selection index. There were some definite inter-genotypic competitive effects for all three traits among the pairs of hybrids studied. Variation in types of intergenotypic interaction was found.

A two-step process was suggested to take advantage of favorable competitive interactions for increasing grain yield. Failure of mixtures in corn to take advantage of favorable competitive situations was discussed.

Introduction and Literature Review

Plant research aimed at measuring competition effects is providing evidence that the performance of a genotype is often affected by other genotypes growing near-by. Thus we are faced with the fact that selective values of genotypes in pure stand are not always the same as the values that occur under intergenotypic competition. This situation is an important consideration in plant breeding, but to date, competition information has not been widely utilized in breeding programs.

The characterization of competitive responses by use of a hillplot arrangement of treatments, as originally suggested by Schutz and Brim (1967) in soybeans, has been made in other self-pollinated crops such as barley, wheat and oats (Allard 1969, Smith *et al.* 1970). Information on competitive effects among corn hybrids is very meager (Stringfield 1959, Eberhart *et al.* 1964 and Funk and Anderson 1964), and no results have been reported when more than 2 levels (dosages) of competition are operating. It also appears that critical competition information in broad-based mixtures or random-mating populations is virtually non-existent.

The major objective of this study was to evaluate and characterize responses under 3 levels of competition of experimental hybrids.

Materials and Methods

Pedigrees and reference codes of the corn hybrids used in this study are:

Pedigree	Reference Code
N128 (Nebr. B synthetic) × B67 (Iowa SSS)	A
N20 (Nebr. sel. of Stiff Stalk Synthetic) × A257 (Sel. from A73 × Os420)	B
N132 (Nebr. B synthetic) × N138 (Sel. from [B14 × Oh43] B14)	C
N20 × N2 (Nebr. B synthetic)	D

The experiment was planted in 1970, 1971 and 1972. It was analyzed as a split-plot arrangement of treatments with a hybrid pair as the 8-row main plot and combinations of the hybrids in sequence (as shown below) as subplots. Randomization was not done for the hybrid combinations. The total sequence (whether one starts with X or Y each time) was randomized. Seven replicates were used with 3 levels of competition that could be evaluated.

The arrangement of an 8-row main plot for comparing two hybrids, one represented by X and the other by Y can be demonstrated in the following way:

X	X	X	Y	X	Y	Y	Y	— discarded hills
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	
X	X	X	Y	X	Y	Y	Y	— discarded hills
Rows: 1	2	3	4	5	6	7	8	
X levels:	L_0	L_1		L_2				
Y levels:			L_2		L_1	L_0		
discarded row							discarded row	

X and Y designate one hill of an eight-hill row of a hybrid and its competitor hybrid, respectively. At harvest time the two rows on either end were discarded. Referring to the diagram above, rows 2, 3, and 5 provide information on level 0 (L_0), level 1 (L_1) and level 2 (L_2) of competition for hybrid X, and rows 7, 6, and 4 provide the same information on Y. Level 0 designates the variety in pure stand since the competitor rows on either side contain the same hybrid. Level 1 is used to designate that the hybrid was bordered by 1 competitor row and 1 row of the same hybrid, and level 2 means that the hybrid was bordered by two competitor rows. Level 2 also specified the maximum inter-row competition level. The assumption was made that, for instance AAB and

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BAA were equivalent with respect to the yield of the test genotype A in relation to the competitor or border genotype B.

The reference code for the hybrid pairs involved is as follows:

A and B = hybrid pair 1 (HP_1)
A and C = hybrid pair 2 (HP_2)
A and D = hybrid pair 3 (HP_3)
B and C = hybrid pair 4 (HP_4)
B and D = hybrid pair 5 (HP_5)
C and D = hybrid pair 6 (HP_6)

Four seeds per hill were planted and seedlings were thinned to three plants per hill for a final stand density of 51,700 plants/hectare. In 1970, hills with one or more plants missing were eliminated along with the surrounding hills. In 1971 and 1972, hills with 2 plants were utilized along with three plant hills and only those with two or three plants missing were removed along with the surrounding hills. The experiment was irrigated when needed. Nitrogen was applied at the rate of 168 kg/ha in 1970 and 1971 and 280 kg/ha in 1972.

Measured agronomic variables were the following: 1) Grain weight in quintals per hectare (q/ha) at 15.5% moisture content, 2) Percent moisture, 3) Average plant height of 10 competitive plants, 4) Percent broken stalks, and 5) Percent dropped ears. The selection index (S. I.) was calculated as $(S.\ I.) = X_1 \frac{(100 - X_2)}{100} \frac{(100 - X_3)}{100}$ where X_1, X_2 and X_3 are yield, percent lodging and percent dropped ears, respectively. This index has been used in the Nebraska Corn Project since 1969 and can be used as an estimate of machine-harvestable yield from hand-harvested data. It is very easy to apply and no parameter estimation is involved in its construction (Subandi, Compton and Empig, 1973).

Experimental Results

There were some definite intergenotypic competitive effects found in the hybrid pairs studied. On the whole, these effects were limited to a maximum of about 10 quintals/ha (about 10–13%) in this set of material.

Evidence of competitive effects is contained in the analyses of variance shown in Table 1. There is a consistent increase in the mean squares within each hybrid pair (HP_i) as one examines first the "within level 0" source, then the "within level 1", and finally the "within level 2" source. The only real variant from the pattern is in the comparison for HP_6.

Similar conclusions can be drawn from Fig. 1, where the means referred to in the above paragraph are presented graphically. Graphical displays are sometimes more easily understood than statistical jargon. Again note the general trend toward divergence of the means with increasing levels of competition.

Since the largest differences were found at competitive level 2, only those means are shown in Table 2 for comparison with pure stand values. Note that there were deviants that were highly significant.

Table 3 contains analyses of variance mean squares for the other two traits. The plant height mean squares for "within levels 0, 1, and 2" have a divergence trend opposite to that shown above for grain yield. In other words, increasing levels of compe-

Table 1. *Analyses of variance of mean grain weight in quintals/hectare of hybrid pairs 1 through 6 combined over years*

Analyses of variance							
	Mean squares						
Source of variation	Degrees of freedom	HP_1	HP_2	HP_3	HP_4	HP_5	HP_6
Entries/HP_i [1]	5	2125**	1435**	977**	294	284	89
Level 0 vs. levels 1 and 2/HP_i	1	56	4	128	83	107	28
Level 1 vs. level 2/HP_i	1	46	0	54	156	106	12
Within level 0/HP_i	1	2292**	133	55	29	2	320
Within level 1/HP_i	1	2297**	1533**	608*	639*	217	52
Within level 2/HP_i	1	5936**	5505**	4041**	562	987*	34
Pooled Error	60	147	147	147	147	147	147

[1] i subscript used to identify hybrid pairs 1, 2, –6.
* significant at the .05 level of probability.
** significant at the .01 level of probability.

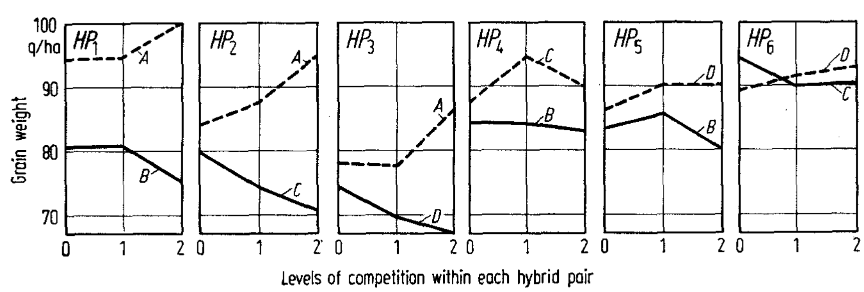

Fig. 1. Diagramatic illustrations of grain weight with increasing levels of competition for each hybrid within each hybrid pair

Table 2. *Mean competitive and pure stand grain yields (q/ha) for each individual hybrid and level 2 of competition, averaged over 3 years*

Test hybrid	Competitor hybrid	Grain yield (q/ha) With competition	Pure stand	Difference+
A	B	98.62	96.26	2.36
B	A	74.84	81.49	−6.65
A	C	93.82	83.72	10.10**
C	A	70.92	80.17	−9.25*
A	D	85.73	78.41	7.32
D	A	66.12	76.12	−10.00**
B	C	83.27	85.75	−2.48
C	A	90.59	87.41	3.18
B	D	80.55	84.34	−3.79
D	B	90.24	84.78	5.46
C	D	81.19	85.47	−4.28
D	C	82.98	79.94	3.04

\+ Differences (column 3 — column 4).
* Significant at the 0.05 level of probability.
** Significant at the 0.01 level of probability.

No significant differences were found among levels for any of the traits. In other words, when one hybrid increased in value, the other tended to decrease proportionately. This implies that the effects are largely of a complementary nature.

Discussion

The results of this experiment indicate clearly that intergenotypic competition as observed between thirty-inch rows can have an effect upon yield. It is also shown that the responses of a maize genotype to the sharing of the environment with a different genotype cannot be described entirely in terms of complementary effects.

Table 4 presents a summary of the inter-genotypic relationships for grain yield at the diffeient levels of competition. Values greater or less that 5% of the pure stand values were used to characterize overcompensatory and undercompensatory effects, respectively. Complementary effects accounted for 50% of the competitive interactions. Neutral, undercompensatory and overcompensatory effects accounted for the other 50% of the competitive interactions in proportional amounts (16.6%). These percentages reflect consideration of both levels of competition. However, when the test genotype is surrounded on both sides by the competitor genotype (level 2), then only complementary effects (67%), neutral effects

Table 3. *Means squares for plant height and the selection index from the analyses of variance combined over years*

Mean squares — Plant height (cms.)

Source of variation	d.f.	HP_1	HP_2	HP_3	HP_4	HP_5	HP_6
Entries/HP_i[1]	5	3661**	333	2346**	1905**	32	1586
Level 0 vs level 1 & 2/HP_i	1	75	65	420	149	5	19
Level 1 vs level 2/HP_i	1	15	22	43	118	62	19
Within level 0/HP_i	1	7809**	653*	3696**	4248**	74	3060**
Within level 1/HP_i	1	5964**	617*	5522**	3741**	3	3020**
Within level 2/HP_i	1	4441**	307	2053**	1268**	16	1810**
Pooled error	60	149	149	149	149	149	149

Mean squares — Selection index (q/ha)

Source of variation	HP_1	HP_2	HP_3	HP_4	HP_5	HP_6
Entries/HP_i[1]	2119**	374	566*	595	603*	339
Level 0 vs level 1 & 2/HP_i	267	1	1	0	33	19
Level 1 vs level 2/HP_i	60	57	295	174	121	38
Within level 0/HP_i	1160*	338	550	271	130	1089*
Within level 1/HP_i	2010**	141	33	1077*	397	435
Within level 2/HP_i	7046**	1330*	1950**	1455**	2332**	113
Pooled error	117	117	117	117	117	117

[1] i subscript used to identify hybrid pairs 1, 2, —6.
* significant at .05 level of probability.
** significant at .01 level of probability.

tition *reduce* differences in plant height between two competing hybrids.

The selection index values, as one might expect, are much less consistent than are those for grain yield. There is a slight trend for an increasing difference with increasing levels of competition, but probably not enough to warrant further pursuit.

Table 4. *Characterization of intergenotypic relationships for grain yield of 4 hybrids grown under 2 levels of competition. 3 years data*+

			Hybrids		
			B	C	D
Hybrids	A	L1	N	C	UC
		L2	UC	C	C
	B	L1		OC	OC
		L2		N	C
	C	L2			C
		L1			C

L1 = Level 1 of competition
L2 = Level 2 of competition
N = Neutral
C = Complementary
OC = Overcompensatory
UC = Undercompensatory
+ Based on Schutz et al., 1968.

(17%) and undercompensatory effects (17%) were observed. We should be reminded that these specific characterizations of competitive interactions apply only to the restricted sets of hybrids studied. The experimental hybrids were selected without any morphological or physiological considerations.

It appears that the grain yield response of different corn hybrids under different levels of competition has not been reported previously. However, for purposes of comparison, we can relate our findings to other experiments in corn where intergenotypic competition effects of some sort were measured. Stringfield (1959), using mixtures involving equal numbers of seed from two contributing members, reported no advantages in grain yield of the mixtures over the average of the contributing hybrids grown separately. Since the arrangement of 4 seeds per hill of the component hybrids was at random, it appears that intra- and intergenotypic competition within a row was involved. Neither distance between rows nor plant density was reported. Funk and Anderson (1964) reported that the blending of two corn hybrids in alternate rows did not appear to increase grain yield over the mean of the component hybrids grown separately. Inter-row competitive effects were considered with only one border row as a competitor genotype, which in our study was designated as level 1 of competition. The distance between rows was 36 inches. The results of their experiment are in agreement with our study when only one level of competition is considered. Eberhart *et al.* (1964) measured intra-plot competition among two sets of maize single crosses. The blending of two hybrids was done either in the hill or in alternate hills every 13 inches. Only intergenotypic competition within a row was involved since only one plant represented a particular hybrid. The competition effects were of a comparative type (complementary) similar to the results of Stringfield. Caution should be exercised in making comparisons of within-row competition and between-row competition. We will elaborate on this point later in the discussion.

That certain hybrids show a constancy of intergenotypic competitive effects in response to different genotypes is shown by the behavior of hybrid D under level 2 of competition. The complementary effects of hybrid D are displayed regardless of the competitor present and the increases or decreases in grain yield of hybrid D are specific to the competitor involved. Also, it appears that for some hybrid pair combinations, the similarity in response to intergenotypic competition may not be affected by the levels of competition involved. The competitive situation of most interest is the one where cooperation is involved (overcompensation). These favorable interactions have been reported mainly in self-pollinated crops (Schutz and Brim 1967, Jensen and Federer 1964).

In the search for increased productivity, new imaginative approaches will have to be taken by breeders and ecologists. If the environments and the genotypes can be specified whereby favorable interactive relationships are established, then potential yield levels can be raised over the yield levels of the pure stands of the genotypes themselves. In this connection, the following statement by Haldane is suggestive.

"While the most obvious symbiosis to look for and to exploit, if discovered, to increase agricultural production, is between different species, particularly cereals and legumes; nevertheless, if such symbiotic relations are common, they should be looked for between different genotypes of the same species".

Use of favorable competitive interactions has been suggested by Jensen and Federer (1964) in wheat and by Schutz and Brim (1967) in soybeans. In inter-row competitive situations only two levels of competition are well defined. They are determined by the number of adjacent rows used as competing genotypes. When the genotype is in pure stand, then intergenotypic competition is not operating. If we want to take advantage of favorable interactions for increasing grain yield a two-step process is required:

1. Determination of the appropriate competition level for a pair of hybrids such that a net increase over the sum of both genotypes in pure stand is shown.

2. Duplication of the experimental combinations on large scale using the favorable interacting genotypes and the defined competitive environment.

If we proceed to step 2 with the hybrids B and C, from our study, using level 1 of competition for hybrid C and level 2 for hybrid B, we could expect to have a net increase of 4.1% over the pure stand value of the component genotypes, or 3.1% over C in pure stand (for values see Appendix Table A1). The highest yielding genotype (C) constitutes 2/3 of the component genotypes, but some increase from having B as a competitor gives the combination an advantage. For obtaining level 1 for C and level 2 for B, using a six-row planter, we would proceed in the following way:

```
C B C C B C C B C C B C
| | | | | | | | | | | |
1 2 3 4 5 6 6 5 4 3 2 1
    ↑             ↓
```

In the first pass the C B C C B and C are planted and in the following pass the inverted sequence.

The question that arises is then "Why can we not take advantage of the favorable competitive situtions in mixtures in corn?" The results of experiments utilizing mixtures in corn are very meager. The experiments reported by Stringfield (1959), Funk and Anderson (1964) and Kannenberg and Hunter (1972) show that no consideration was given to the intergenotypic relationships for the establishment of mixtures. The evidence available in other crops that within-row competition is different from between-row competition (Jensen and Federer 1964, Schutz and Brim 1967 and Smith et al. 1970) could also be true in corn. If optimization of proportions in mixtures is required, additional characterization of intergenotypic competition effects as observed in hill-plot arrangement may be helpful. Also, competition effects between drilled rows might also be observed and utilized.

The diversity of genotypes and environments involved make a difficult task of ascertaining the factor or factors involved in competitive situations. Plant height undoubtedly plays a role in plant competition. The best competitor in our study turned out to be the tallest genotype in relation to the other genotypes. Also, it was observed that genotypes virtually identical in plant height showed a yield response due to competition. The basic function of the corn canopy is the interception of light. One can speculate that tall genotypes adjacent to shorter genotypes in border rows should intercept more light while the short ones may be expected to be at a disadvantage for available light. Is it possible to make a general statement about the plant height and grain yield relationship under competitive conditions? The answer is yes, but with some reservations. Earlier we mentioned the consistent increase and decrease in the size of the mean squares for grain yield and plant height, respectively. In fact the tallest genotype (hybrid A), which also was the stronger competitor with respect to grain yield, decreased in plant height in all the combinations analyzed under competitive conditions. The opposite effect was found for the shortest genotype (with two exceptions). From the above considerations, it appears that the shorter plants (shaded) tend to elongate more rapidly than the taller plants (unshaded). Hozumi *et al.* (1955) also using corn, noted that under closely spaced conditions, the shorter plants had a higher elongation rate than the taller ones that were shading them. We have to keep in mind that in that group of species which has a low compensating point, of which corn is one, light saturation is not reached even at full sunlight intensities (Hesketh and Moss 1963). The resistance to carbon dioxide diffusion in the leaf is low, and the photosynthetic rate correspondingly high (El-Sharkawy and Hesketh 1965). On the other hand, in the high compensating group, such as soybeans, there is little response to light under a fixed level of carbon dioxide (Brun and Cooper 1967). In response to the question of relating plant height to grain yield under competitive conditions, perhaps one should expect a significant response for grain

Appendix

Table A1. *Over-all mean of grain yield (q/ha), plant height (cms), and selection index (q/ha) for 6 entries within each hybrid pair, averaged over 1970, 1971 and 1972*

Hybrid pair	Entries	Level	Grain yield (q/ha)	Plant height (cms)	Selection index (q/ha)
1	A	L_0	96	302	83
	A	L_1	96	299	82
	A	L_2	99	296	87
	B	L_0	81	270	72
	B	L_1	81	270	69
	B	L_2	75	271	61
2	C	L_0	80	285	73
	C	L_1	76	285	67
	C	L_2	71	285	65
	A	L_0	84	295	67
	A	L_1	88	293	71
	A	L_2	94	292	76
3	A	L_0	78	294	58
	A	L_1	78	293	59
	A	L_2	86	287	71
	D	L_0	76	271	65
	D	L_1	71	266	61
	D	L_2	66	270	57
4	B	L_0	86	266	77
	B	L_1	86	265	76
	B	L_2	83	266	72
	C	L_0	87	289	82
	C	L_1	94	287	86
	C	L_2	91	279	84
5	B	L_0	84	265	74
	B	L_1	85	267	71
	B	L_2	81	266	64
	D	L_0	85	268	70
	D	L_1	90	267	77
	D	L_2	90	264	79
6	C	L_0	85	287	79
	C	L_1	80	289	75
	C	L_2	81	286	75
	D	L_0	80	268	68
	D	L_1	82	269	75
	D	L_2	83	271	72

yield under competitive conditions when height differences are involved in the low compensating group. Light interception measurements were not included in this study but they should be tried in future studies. Likewise, measurements of root systems might help to further understand below-ground factors in explaining competitive interactions among different genotypes.

The influence of tillering ability on competitive interactions was not evaluated since visual observations detected no tillering among the different genotypes. Also, maturity differences as determined by moisture content of the grain were not detected. Data on number of ears per plant (not included in this paper) suggested the absence of prolificacy.

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A. Jurado-Tovar
Assistant Professor
Universidad Nacional Tecnia de Piura
Piura (Peru)

W. A. Compton
Associate Professor
University of Nebraska
Lincoln, Nebraska 68508 (USA)