Cultivar Heterosis between Sweet and Spanish Field Corn

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ADDITIONAL INDEX WORDS. *Zea mays*, heterotic patterns

ABSTRACT. Field corn (*Zea mays* L. var. *mays*) cultivar heterosis could improve sweet corn (*Zea mays* L. var. *rugosa* Bonaf) heterotic patterns. Two Spanish field corn (*Su*) and two sweet corn (*su*) heterotic patterns have been reported previously. The objective of this study was to determine which sweet x field corn crosses could be used to improve sweet corn heterotic groups. A diallel among three sweet corn cultivars ('Country Gentleman', 'Golden Bantam', and 'Stowell's Evergreen') that are representative of the variability among modern sweet corn cultivars, and three field corn synthetic cultivars ['EPS6(S)C3', 'EPS7(S)C3', and 'EPS10'] representing the heterotic patterns involving Spanish field corn, was evaluated for 2 years at two locations in northwestern Spain. Differences in heterosis effects (h_{ij}) and average heterosis (h) were significant for all traits except grain moisture. Differences for cultivar heterosis (h_i) and specific heterosis (s_{ij}) were significant for grain yield, plant height, and kernel row number. 'EPS6(S)C3' had lower s_{ij} for yield in crosses to 'Golden Bantam' than to 'Stowell's Evergreen', while 'EPS7(S)C3' had higher s_{ij} in crosses to 'Golden Bantam' than to 'Stowell's Evergreen'. The best crosses to establish enhanced sweet corn heterotic patterns involving Spanish maize would be 'Golden Bantam' x 'EPS6(S)C3' and 'Stowell's Evergreen' x 'EPS7(S)C3'. New *sugary 1* cultivars would require preliminary cycles of intrapopulational recurrent selection for agronomic performance and flavor prior initiating an interpopulational recurrent selection program to enhance heterosis.

Morphological and molecular variability in sweet corn (*Zea mays* var. *rugosa*) is small compared to field corn (*Zea mays* var. *mays*) (Revilla and Tracy, 1995a, 1995b). The genetic base of sweet corn used presently in breeding programs is relatively narrow, and genetically related inbreds are often crossed to meet strict requirements of market quality and appearance (Tracy, 1994). Heterotic patterns among sweet corn inbreds are not clearly defined. Most sweet corn inbreds are related to three open-pollinated cultivars, 'Golden Bantam', 'Stowell's Evergreen', and 'Country Gentleman' (Tracy, 1994). Heterotic patterns among sweet corn cultivars have been defined by Revilla and Tracy (1997), who found a significant heterotic pattern when 'Country Gentleman' was crossed to 'Golden Bantam', 'Pease Crosby', and 'Linsey Meyer Blue'. They found another heterotic pattern when the later three cultivars were crossed to 'Stowell's Evergreen'. The heterotic patterns among open-pollinated sweet corn populations are somewhat predictable from inbred breeding behavior (Tracy, 1990b, 1994). Sweet corn breeders have not relied on heterotic patterns in the development of commercial hybrids. Establishment and improvement of new heterotic patterns in sweet corn could be helpful for improving agronomic performance and adaptation of sweet corn in new regions of production. Furthermore, sweet corn breeders should theoretically be concerned with the risk of exhausting heterosis if the same inbreds are recombined repeatedly without introduction of new heterotic combinations.

Field corn has been used to improve agronomic performance of sweet corn in the United States (Tracy, 1994) and in Europe (Cartea et al., 1996a, b; Malvar et al., 1997a, b). Field corn heterotic patterns may be transferable into sweet corn. Davis et al. (1988) exploited knowledge of the 'Reid Yellow Dent' x 'Lancaster Sure Crop' field corn heterotic pattern and a similar, albeit weaker, pattern in sweet

corn to establish complementary sweet x field corn source cultivars for sweet corn inbred extraction.

Several heterotic patterns have been described in field corn, with 'Reid' x 'Lancaster' crosses being the most widely used in hybrid development (Hallauer et al., 1988). In addition two heterotic patterns involving Spanish field corn cultivars, Spanish maize x 'Corn Belt Dent' and northern x southern Spanish maize have been described (Ordás, 1991). The heterotic pattern Spanish maize x Corn Belt Dent is part of the generally known European flint x U.S. dent. The pattern of northern x southern Spanish maize reflects two genetically distant germplasms. Southern Spanish field corn is genetically more distant from U.S. dent than is northern Spanish.

According to Edwards and Leng (1965), most Spanish maize originated from Central American or West Indian germplasm. Isozyme data indicate southern Spanish field corn is related to Central American field corn, but field corn from northern Spain has significant contributions from North America (Revilla et al., 1998b). This germplasm has been used for human consumption both in Central America and northern Spain, and selection against off-flavors can be assumed. However, field x sweet corn crosses could unmask new off-flavors not heretofore seen due to gene interactions, dosage effects, disruption of linkage groups, etc., that should be taken into account in any subsequent breeding program.

Old Spanish open-pollinated cultivars originated from tropical germplasm and have been adapted to temperate regions by ≈ 4 centuries of selection, and could confer adaptation to colder regions with short growing seasons (Revilla et al., 1998a). Combining heterotic patterns involving Spanish maize (Ordás, 1991) with sweet corn heterotic patterns (Revilla and Tracy, 1997) could increase genetic variation, expand the adaptation range, and enhance sweet corn heterotic patterns. Therefore, the objective of this study was to determine which sweet x field corn crosses could be used to improve sweet corn heterotic patterns.

Materials and Methods

Three sweet corn cultivars, 'Golden Bantam' (PI 255976) from the North Central Regional Plant Introduction Station, Ames, Iowa,

Received for publication 1 Nov. 1999. Accepted for publication 30 June 2000. Research supported by the Committee for Science and Technology of Spain (Project Cod. AGF95-0891) and Excm. Diputación Provincial de Pontevedra, Spain. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked advertisement solely to indicate this fact.

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Table 1. Mean squares from the analysis of variance of five traits for a diallel of three sweet and three field corn cultivars grown in three environments in northwestern Spain.

Source	df	Grain yield (Mg·ha ⁻¹)	Grain moisture (g·kg ⁻¹)	Plant ht (cm)	Ear length (cm)	Kernel row no.
Genotypes	20	18.46**	87.68*	3209.10**	12.88**	39.59**
Cultivar (v_j)	5	36.08**	311.02 ^{NS}	5359.57**	17.74**	148.59**
Heterosis (h_{ij})	15	12.58**	13.23 ^{NS}	2492.27**	11.26**	3.26**
Average (h)	1	143.40**	24.71 ^{NS}	26482.21**	124.37**	10.64**
Cultivar (h_j)	5	4.49**	24.27 ^{NS}	1089.99**	2.72 ^{NS}	3.11**
Specific (s_{ij})	9	2.54**	5.83 ^{NS}	605.77*	3.44 ^{NS}	2.52**
Environment × genotype	40	1.75**	46.48**	385.29*	2.01**	0.68 ^{NS}
Environment × v_j	10	2.13*	111.33**	611.17 ^{NS}	3.00**	
Environment × h_{ij}	30	1.62*	24.86**	310.00 ^{NS}	1.68**	
Environment × h	2	5.41**	129.11**	150.27 ^{NS}	0.78 ^{NS}	
Environment × h_j	10	1.35 ^{NS}	33.15**	334.76 ^{NS}	1.67*	
Environment × s_{ij}	18	1.35 ^{NS}	8.67 ^{NS}	314.00 ^{NS}	1.79**	
Error ^z	120	0.96	10.44	255.56	0.75	0.75

^zThe number of degrees of freedom for the error term of kernel row number was 119.

^{NS},*,** Nonsignificant, or significant at $P = 0.05$ or 0.01 , respectively.

and ‘Country Gentleman’ and ‘Stowell’s Evergreen’ from Cornell University, plus three field corn synthetics cultivars [‘EPS6(S)C3’, ‘EPS7(S)C3’, and ‘EPS10’], were used as parents. The sweet corn cultivars are representative of much of the variability among modern sweet corn cultivars, and the three field corn synthetics represent the heterotic patterns involving Spanish field corn. ‘EPS6(S)C3’ and ‘EPS7(S)C3’ have been selected for three cycles using S_1 intrapopulational recurrent selection for yield from the synthetics cultivars ‘EPS6’ and ‘EPS7’, respectively. The synthetic ‘EPS6’ was developed from the local northern Spanish cultivars ‘Tuy’,

‘Moeche’, ‘Gallego’, and ‘Norteño’, while ‘EPS7’ was developed from local southern Spanish cultivars ‘Enano Levantino/Hembrilla’, ‘Rastrojero’, ‘Tremesino’, and ‘Amarillo temprano de Aragón’. ‘EPS10’ was developed from the U.S. Corn Belt cultivar ‘Minnesota No. 13’ and the synthetic cultivars ‘AS-A’, ‘AS-B’, and ‘AS-3(HT)C3’ (Ordás, 1991).

A diallel among the three field corn synthetics was produced by Vales et al. (2000) in 1993, using paired rows with 15 plants per row. Five sets of paired rows were used for each cross, using each plant once, as only female or male but never as both. The remaining

Table 2. Means for the six parents and 15 hybrids of a diallel among three sweet and three field corn cultivars grown in three environments in northwestern Spain.

Genotype	Grain yield (Mg·ha ⁻¹)	Grain moisture (g·kg ⁻¹)	Plant ht (cm)	Ear length (cm)
EPS6(S)C3	7.0 bcd ^z	27.3 ghi	215.9 efg	16.7 def
EPS7(S)C3	6.0 efg	27.7 gh	224.2 defg	16.3 fg
EPS10	6.3 def	25.8 hi	220.3 efg	15.9 fgh
Golden Bantam	4.4 hi	32.4 bcd	186.6 h	14.3 i
Stowell’s Evergreen	3.7 ij	31.5 bcde	215.9 efg	14.6 i
Country Gentleman	2.8 j	38.1 a	185.9 h	15.2 hi
EPS6(S)C3 × EPS7(S)C3	7.6 abc	28.2 fgh	228.3 defg	17.6 abc
EPS6(S)C3 × EPS10	8.1 a	24.5 i	231.9 bcdef	17.2 bcd
EPS6(S)C3 × Golden Bantam	6.8 cde	30.1 cdefg	210.9 g	17.1 cde
EPS6(S)C3 × Stowell’s Evergreen	7.9 ab	28.0 gh	248.4 ab	18.4 a
EPS6(S)C3 × Country Gentleman	7.6 abc	29.1 efg	229.5 cdefg	18.0 ab
EPS7(S)C3 × EPS10	7.2 abcd	28.0 gh	233.4 bcde	17.3 bcd
EPS7(S)C3 × Golden Bantam	6.7 cde	31.1 bcdef	224.9 defg	16.3 ef
EPS7(S)C3 × Stowell’s Evergreen	7.0 bcd	30.2 cdefg	258.0 a	17.8 abc
EPS7(S)C3 × Country Gentleman	7.3 abc	32.8 bc	247.6 abc	18.4 a
EPS10 × Golden Bantam	6.7 cde	27.3 ghi	227.8 defg	16.6 def
EPS10 × Stowell’s Evergreen	7.5 abc	27.7 gh	256.8 a	17.9 abc
EPS10 × Country Gentleman	7.8 ab	29.6 defg	241.9 abcd	17.6 abc
Golden Bantam × Stowell’s Evergreen	5.2 gh	32.7 bc	230.5 bcdef	15.5 gh
Golden Bantam × Country Gentleman	5.4 g	32.7 bc	213.3 fg	16.2 fg
Stowell’s Evergreen × Country Gentleman	5.5 fg	33.3 b	231.6 bcdef	16.6 def
LSD _(0.05)	0.9	3.0	18.7	0.8

^zMean separation within columns by LSD, $P = 0.05$.

crosses to complete the six-parent diallel (a diallel among the sweet corn cultivars and the sweet x field corn crosses) was made in 1995 using blocks of six rows. For the sweet x field corn crosses, the field corn synthetic was used as female. Reciprocal crosses were bulked for field x field and sweet x sweet crosses. About 50 ears were obtained for each cross.

The 21 genotypes (15 crosses plus six parents) were planted in 1996 and 1997 at two locations in northwestern Spain: Pontevedra (lat. 42°24'N, long. 8°38'W, 20 m above sea level) and Pontecaldelas (lat. 42°23'N, long. 8°32'W, 300 m above sea level). Both locations have a humid climate with annual rainfall of ≈ 1600 mm. Each four-row experimental plot consisting of 15 hills per row with two kernels per hill. Rows were spaced 0.80 m apart and hills 0.21 m. Hills were thinned to one plant to achieve a final plant density of $\approx 60,000$ plants/ha. The experimental design was a randomized complete block with three replications. All traits were recorded on the two central rows of the four row plots to avoid competition and to minimize the xenia effect on the sugary genotype. Traits recorded on all plants of the two central rows were dry grain yield ($\text{Mg}\cdot\text{ha}^{-1}$) and grain moisture ($\text{g}\cdot\text{kg}^{-1}$). Data were also recorded for plant height (cm) from the soil surface to the top of the tassel, ear length (cm), and kernel row number from random samples of 10 mature plants or ears of the two central rows. Dry grain yield was measured instead of yield based on fresh ears at the normal eating stage following Revilla and Tracy (1997) to estimate more closely physiological efficiency and to reduce the cv. Quality was not measured, not only because field corn eating quality cannot be determined accurately, but flavor of open pollinated sweet corn cultivars cannot be compared to modern sweet corn cultivars.

Individual analyses of variance were performed for all traits for each environment. The trial at Pontecaldelas in 1996 performed poorly due to unfavorable weather conditions from planting to silking. The proportion of missing data in Pontecaldelas in 1996 was high and some data were thus not reliable. That environment was not included in the final analysis. Sources of variation, cultivars, and crosses were considered fixed, and all other effects were considered random. Sums of squares were partitioned according to the Analysis II of Gardner and Eberhart (1966). When the genotype $\times$ environment interaction was significant, its sum of squares was also partitioned according to Analysis II. GLM procedures of SAS were used for all analyses (SAS Institute Inc., 1989a), and calculations with matrices were made using the module IML (SAS Institute Inc., 1989b).

Results and Discussion

Genotypes were significantly different and genotype $\times$ environment interactions were significant for all traits, except for kernel row

number (Table 1). Results of the individual analyses for environments are discussed below whenever the genotype $\times$ environment interaction altered the conclusions based on the combined analyses.

Comparison of yield among genotypes segregating at the *sug-ary1* locus must be made with caution due to the different endosperm types involved. Field x sweet corn crosses should have 25% sweet corn kernels, but ears were open-pollinated and affected randomly by the pollen from bordering rows. However, yield was measured in the two central rows of the four-row plots. Therefore, comparisons among field x sweet corn crosses should not have been affected by different endosperm types (Cartea et al., 1996a; Tracy, 1990a).

Average grain yield was $6.4 \text{ Mg}\cdot\text{ha}^{-1}$, ranging from 2.8 for 'Country Gentleman' to 8.1 for 'EPS6(S)C3' $\times$ 'EPS10'. The lowest yields were produced by the sweet corn cultivars, followed by the crosses among them (Table 2). The highest yields were for the crosses among field corn synthetic cultivars, along with the crosses between 'Country Gentleman' or 'Stowell's Evergreen' and each field corn synthetic. Also the field corn synthetics had high yields. The six genotypes with the highest moisture included crosses to 'Country Gentleman' or 'Golden Bantam', while all field corn synthetic cultivars and the crosses between them were among the genotypes with lowest moisture (Table 2). The crosses involving sweet corn cultivars generally had a higher harvest moisture than the field corn synthetics and its crosses, except for 'Golden Bantam' $\times$ 'EPS10' and for the crosses of 'Stowell's Evergreen' with 'EPS6(S)C3' or 'EPS10'. This was expected as *su1* blocks normal starch synthesis, and thus *su1* material may dry more slowly. The tallest genotypes were five sweet x field corn crosses involving 'Stowell's Evergreen' or 'Country Gentleman', and the shortest genotypes were 'Country Gentleman' and 'Golden Bantam' (Table 2). Similarly, the sweet x field corn crosses involving 'Stowell's Evergreen' or 'Country Gentleman' had the longest ears, with the shortest ears observed for the sweet corn cultivars. Kernel row number usually behaves as an additive trait, but all the crosses involving 'Country Gentleman' were similar to the other parent for kernel row number (data not presented). This behavior of ear row number was expected because of the unique genetic control of kernel row number in 'Country Gentleman' (Tracy, 1994).

Estimation of genetic parameters relies on certain assumptions inherent in the model (Hallauer and Miranda, 1988). If the assumptions are not met, estimations would be biased, however there are no reasons to think that any particular assumption fails in this experiment.

Midparent heterosis for grain yield ranged from 16.6% for 'EPS7(S)C3' $\times$ 'EPS10' to 70.9% for 'Country Gentleman' $\times$ 'EPS10'. These values were larger than those reported by Ordás (1991) for crosses among these field corn cultivars, and among

Table 3. Cultivar effects (v_i) and cultivar heterosis (h_j) from the analysis of variance of three traits for a diallel of three sweet and three field corn cultivars grown in three environments in northwestern Spain.

Cultivar	Cultivar effects			Cultivar heterosis	
	Grain yield ($\text{Mg}\cdot\text{ha}^{-1}$)	Plant ht (cm)	Ear length (cm)	Grain yield ($\text{Mg}\cdot\text{ha}^{-1}$)	Plant ht (cm)
EPS6(S)C3	1.93	7.73	1.24	-0.18	-9.53
EPS7(S)C3	0.95	16.04	0.86	-0.24	-2.86
EPS10	1.31	12.15	0.47	-0.01	-1.03
Golden Bantam	-0.65	-21.52	-1.09	-0.65	-5.28
Stowell's Evergreen	-1.36	7.82	-0.84	0.28	9.51
Country Gentleman	-2.18	-22.22	-0.65	0.80	9.18
LSD _(0.05)	1.38	15.86	1.63	0.71	9.84

Table 4. Heterosis effects (h_{ij}) from the analysis of variance of grain yield (above the diagonal) and plant height (below the diagonal) for a diallel of three sweet and three field corn cultivars grown in three environments in northwestern Spain.

Cultivar	Cultivar					
	EPS6(S)C3	EPS7(S)C3	EPS10	Golden Bantam	Stowell's Evergreen	Country Gentleman
EPS6(S)C3		1.11	1.42	1.16	2.56	2.68
EPS7(S)C3	8.32		1.02	1.49	2.18	2.88
EPS10	13.82	11.17		1.38	2.53	3.26
Golden Bantam	9.66	19.56	24.39		1.22	1.77
Stowell's Evergreen	32.49	37.94	38.72	29.22		2.28
Country Gentleman	28.62	42.57	38.74	27.07	30.69	

$LSD_{(0.05)} = 1.74$ for grain yield for hybrids sharing a parent

$LSD_{(0.05)} = 1.67$ for grain yield for unrelated hybrids

$LSD_{(0.05)} = 13.25$ for plant height for hybrids sharing a parent

$LSD_{(0.05)} = 10.82$ for plant height for unrelated hybrids

sweet corn cultivars in an early planting by Revilla and Tracy (1997), but lower than the estimates for a late planting. Revilla and Tracy (1997) reported that the large midparent heterosis for the late planting was a consequence of stressful conditions depressing the parental cultivars per se more than the hybrids. In the present study stress probably resulted from lack of adaptation. All traits differed significantly for heterosis effects (h_{ij}) and for average heterosis (h) except grain moisture (Table 1). Differences for cultivar heterosis (h_i) and specific heterosis (s_{ij}), were significant for yield, plant height, and kernel row number.

Comparison of yield and grain moisture for sweet x field corn crosses is confounded by biochemical and physiological differences between sugary and starchy endosperms. On the other hand, plant height should not be affected significantly since all sowed grains had starchy phenotype. Therefore, discussion will focus on yield and plant height.

Cultivar effects (v_i) estimates were positive for yield, plant height, and ear length for the three field corn synthetics, and negative for the sweet corn cultivars, except for plant height of 'Stowell's Evergreen' (Table 3). These results agree with previous studies reporting that sweet corn has poorer agronomic performance (Tracy, 1990b, 1994) and adaptation to the Atlantic Coast of Europe (Cartea et al., 1996a, 1996b; Malvar et al., 1997a, 1997b; Ordás et al., 1994) than field corn. 'Golden Bantam' and 'Country Gentleman' had the lowest v_i estimate for plant height (Table 3).

Neither the h_{ij} differences among field corn crosses nor among

sweet corn crosses were significant in our study (Table 4). The lowest h_{ij} for yield among sweet x field corn crosses were for the three crosses involving 'Golden Bantam', and the highest were for those involving 'Country Gentleman' (Table 4). 'Golden Bantam' had the largest heterosis effect in crosses to 'EPS7(S)C3', 'Stowell's Evergreen' in crosses to 'EPS6(S)C3', and 'Country Gentleman' in crosses to 'EPS10' (Table 4). For plant height, the largest h_{ij} among crosses involving 'Golden Bantam' or 'Stowell's Evergreen' was with 'EPS10'. Among crosses involving 'Country Gentleman' the largest h_{ij} for plant height was with 'EPS7(S)C3' (Table 4). With few exceptions, these comparisons are consistent with results from the analysis of individual environments (data not presented).

The h_{ij} estimates discussed above may have been biased by the poor adaptation of the sweet corn cultivars, particularly the late season 'Country Gentleman'. Therefore, the genetic potential may be underestimated. Indeed, 'Country Gentleman' had the most favorable estimates of h_{ij} and h_i , with v_i estimates less favorable for yield, ear length, and plant height (Table 3). 'Golden Bantam' had the lowest h_i estimates, in addition to low v_i estimates for yield, plant height, and ear length (Table 3).

The smallest s_{ij} estimate for yield among the sweet x field corn crosses was for 'Golden Bantam' x 'EPS6(S)C3', followed by 'Golden Bantam' x 'EPS10' and 'Country Gentleman' x 'EPS6(S)C3' (Table 5). For the crosses of 'Stowell's Evergreen', the smallest s_{ij} was for 'EPS7(S)C3'. For the individual environments, s_{ij} was only significant for Pontevedra in 1997, for which the

Table 5. Specific heterosis effects (s_{ij}) from the analysis of variance of grain yield (above the diagonal) and plant height (below the diagonal) for a diallel of three sweet and three field corn cultivars grown in three environments in northwestern Spain.

Cultivar	Cultivar					
	EPS6(S)C3	EPS7(S)C3	EPS10	Golden Bantam	Stowell's Evergreen	Country Gentleman
EPS6(S)C3		-0.40	-0.32	0.06	0.53	0.13
EPS7(S)C3	-5.49		-0.66	0.46	0.21	0.39
EPS10	-1.82	-11.14		0.11	0.33	0.53
Golden Bantam	-1.74	1.50	4.50		-0.33	-0.31
Stowell's Evergreen	6.30	5.09	4.03	-1.22		-0.74
Country Gentleman	2.76	10.05	4.44	-3.04	-14.21	

$LSD_{(0.05)} = 0.98$ for grain yield for hybrids sharing a parent

$LSD_{(0.05)} = 0.67$ for grain yield for unrelated hybrids

$LSD_{(0.05)} = 16.03$ for plant height for hybrids sharing a parent

$LSD_{(0.05)} = 13.09$ for plant height for unrelated hybrids

previous comparisons partially hold. The s_{ij} and h_{ij} arrays for yield in the sweet x field corn crosses were similar. The ranking of the sweet x field corn crosses for s_{ij} and for h_{ij} for plant height were also similar, but both parameters differed from those based on yield.

The combination of sweet and field corn heterotic patterns should take into account those that are best for both as well as the genetic proximity of the groups. Based on s_{ij} estimates for yield and plant height, the best heterotic pattern involving Spanish maize would be among 'Golden Bantam' x 'EPS6(S)C3' and 'Stowell's Evergreen' x 'EPS7(S)C3' because 'EPS6(S)C3' had a lower s_{ij} for yield in crosses to 'Golden Bantam' than to 'Stowell's Evergreen', the opposite being true for 'EPS7(S)C3'. These crosses would have to be recombined at least twice to approach equilibrium followed by selection for sugary kernels. The new sugary cultivars would probably require a few cycles of intrapopulation recurrent selection for agronomic performance and flavor before starting an interpopulation recurrent selection program to enhance the heterotic pattern.

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