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Genetic similarity of sweet corn inbred lines in correlation with heterosis

Jelena Srdić*, Ana Nikolić, Zorica Pajić, Snežana Mladenović Drinić, Milomir Filipović

Maize Research Institute Zemun Polje, Slobodana Bajića 1, 11080 Zemun – Belgrade, Serbia
*Corresponding author: E-mail: jsrdic@mrizp.rs

Abstract

The narrowness of sweet corn genetic base limited to the great extent its genetic improvement. This is associated to the fact that sweet corn does not have well defined heterotic groups such as those important in field corn breeding, and therefore application of marker assisted selection becomes a necessity. The objective of this study was to determine genetic similarity (GS) of six sweet corn inbred lines selected at Maize Research Institute Zemun Polje, based on SSR markers and to compare it with data of specific combining ability (SCA) and heterosis for fresh ear yield, obtained in a diallel study. SSR markers showed that all genotypes had specific genetic pattern. Estimates of GS varied from 0.422 (L4 - L2) up to 0.756 (L6 - L5). Cluster analysis and PCA showed clear groupings of inbreds into two subclusters, with inbred L3 less related to the others. Results of diallel analysis showed that data of heterosis and SCA were in concurrence with the data of GS based on SSR markers. Hybrid combinations with higher estimates of SCA and heterosis expressed less genetic similarity with each other (such in hybrids L2 x L1; L6 x L2; L3 x L2 and L5 x L2), while inbreds that were genetically most similar L5 and L6 expressed low heterosis and SCA in their hybrid combination. That was confirmed by rank correlation coefficients, whose estimates were negative and in most cases significant, indicating that more similar inbreds produced less expressed effects of heterosis and SCA.

Keywords: sweet corn, SSR markers, heterosis, specific combining ability

Introduction

Sweet corn has been grown on a relatively small acreage, e.g. 5,000 ha in Serbia, but there is an increasing trend in its production mainly due to its high economic return (Pajić and Srdić, 2007). Breeding of sweet corn in Maize Research Institute Zemun Polje, Serbia was initiated in 1970's and up to now 28 sweet corn hybrids of different maturity groups were released. All ZP sweet corn hybrids are based on the recessive su gene which alters normal starch synthesis that results in accumulation of phytoglycogen rather than starch. This provides sweet corn with characteristic smooth texture and creaminess (Marshall and Tracy, 2003). Although the *su1* gene is one of the earliest genes genetically well characterized (Marshall and Tracy, 2003; Tracy et al, 2006), and various research identified genetic variation among germplasm containing the *su1* gene, that could not be reliably related to heterotic patterns (Gerdes and Tracy, 1994; Tracy et al, 2000; Revilla et al, 2005; Bered et al, 2005), such as those important in field corn breeding (Hallauer et al, 1988; Reif et al, 2003). Only few authors have reported significant genetic diversity in sweet corn germplasm that could suggest formation of heterotic groups (Revilla et al, 2006; Rupp et al, 2009). The narrowness of present genetic variability of su sweet corn is the result of the fact that most of today's sweet corn germplasm originates from only few open-pollinated varieties Golden Bantam, Country Gentleman, and Stowell's Evergreen (Gerdes and Tracy, 1994).

The development of molecular markers provides a powerful tool for assessing genetic diversity at DNA level in plant species (Melchinger and Gumber, 1988). Molecular markers can also be used to dissect polygenic traits into quantitative trait loci (QTLs), thus increasing our understanding of the inheritance and gene action for such traits and allowing us to use marker-assisted selection (MAS) as a complement to conventional selection procedures. Yousef and Juvik (2001) concluded that MAS in sweet corn can economically compete with phenotypic selection, because of the reduction in population size and duration of breeding programs. MAS also provided simultaneous improvement for multiple traits, while many of them require laboratory evaluation and are difficult and expensive to characterize. SSR markers are applied in sweet corn breeding in order to obtain information on its genetic diversity and genetic structure (Amorim et al, 2003; Rupp et al, 2009), or to identify QTL's for quality traits (Qi et al, 2009). In sweet corn Amorim et al (2003) detected significantly larger variability among genotypes by the method of SSR markers, but clusters obtained by RAPD markers were more correlated to the pedigree data.

Since throughout the world there is a lack of information about the genetic diversity and heterotic models in sweet corn germplasm our research is also

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Table 1 - Polymorphic SSR primers

Locus	Sequence	Bin	Locus	Sequence	Bin
umc1282	5'- TACACTACACGACTCCCAACAGGA-3' 5'-ACAACCGGACAAGTCAGCAGATTG-3'	1.01	phi087	5'-GAGAGGAGGTGTTGTTTGACACAC-3' 5'- GCGAGGGTTCTTTCCATAGAGAAT-3'	5.06
umc1070	5'-GGTCTCTCTATCGTCCGGTGAGTA-3' 5'-AACTGCTGTGGATGAAAGAGGAAG-3'	1.02	umc1883	5'-GAATAATCAATCCATCGATCTCGC-3' 5'-CCGGAGATGGGAAAGAAGATAAC-3'	6.00
bnlg1643	5'-ACCACCGTCCACCTCCAC-3' 5'ATTGACCCCGTGACCCTC-3'	1.08	umc1857	5'- TTCCTTGCCAACAAATACAAGGAT-3' 5'- GTTCATTGCTTCATCTTGGAACCT-3'	6.04
umc2047	5'-GACAGACATTCCTCGCTACCTGAT-3' 5'-CTGCTAGCTACCAAACATTCCGAT-3'	1.09	bnlg1443	5'- TACCGGAATCCTCTTTGGTG-3' 5'- TTTGACAACCTCTTCCAGGG-3'	6.05
umc1184	5'- CTTCCTTACGTGTCACCGCTCT-3' 5'- GTGGAGTGATGTGATCGATGATG-3'	1.09	umc1695	5'- CAGGTAATAACGACGCAGCAGAA-3' 5'- GTCCTAGGTTACATGCGTTGCTCT-3'	7.00
umc1331	5'- TTATGAACGTGGTCGTGACTATGG-3' 5'- ATATCTGTCCCTCTCCCACCATC-3'	1.11	umc1841	5'- CTGCATGATTCTCCTGAACACG-3' 5'- ATGATGCACCCGCAGCTACTAC-3'	7.03
umc1605	5'-CCAGGAGAGAAATCAACAAAGCAT-3' 5'- CGTTTCTATCTATGGAGGAGTGCG-3'	1.12	umc1295	5'- GTCGATCTTCCTCCCCATCA-3' 5'-GGAGAAGCACGCCTTCGTATAG-3'	7.04
umc1265	5'-GCCTAGTCGCCTACCCTACCAAT-3' 5'- CGCACACTAAAGCATCCTTAACCT-3'	2.02	umc1708	5'- GATATGTCGAGCTTCGCTGGAG-3' 5'-TGTCTTGATTGGGTGAGACAT-3'	7.04
umc2129	5'-ACGTGGTCATCACTCACCGC-3' 5'-AAGGAGGAGCGTTCTCGTGG-3'	2.07	umc1782	5'-CGTCAACCTGGCGAAGAA-3' 5'TCGCATACCATGATCACTAGCTTC-3'	7.04
bnlg1520	5'- TCCTCTTGCTCTCCATGTCC-3' 5'- ACAGCTGCGTAGCTTCTTCC-3'	2.09	bnlg2235	5'-ATCCGGAGACACATTCTTGG-3' 5'CTGCAAGCAACTCTCATCGA-3'	8.02
phi036	5'-CCGTGGAGAGACGTTTGACGT-3' 5'- TCCATCACCACTCAGAATGTCAGTGA-3'	3.04	umc1040	5'-CATTCACTCTCTTGCCAACTTGA-3' 5'-AGTAAGAGTGGGATATTCTGGGAGTT-3'	9.01
bnlg197	5'-GCAAGAAGAAAGCGAGCAGA-3' 5'-CGCCAAGAAGAAACACATCACA-3'	3.06	phi033	5'-TCGCTCCTCGGCCTATAGTA-3' 5'-GGTGGCAGACCCAAGATTTA-3'	9.01
bnlg1350	5'-TGCTTCAGCGCATTAAACTG-3' 5'-TGCTCGTGTGAGTTCCTACG-3'	3.08	umc1492	5'-GAGACCCAACCAAAACTAATAATCTCTT-3' 5'-CTGCTGCAGACCATTTGAAATAAC-3'	9.04
umc1594	5'-GCCAGGGGAGAAATAAAATAAAGC-3' 5'-CACTGCAGGCCACACATACATA-3'	3.09	umc1310	5'-AACTCCGAGATCTACGACAACAGC-3' 5'-GAGGAAGAGTTGGCCAGGATG-3'	9.06
umc2039	5'-CATCTCCTACCAGCTCACCCC-3' 5'-GCTCGGGGTAGTAGTGTTCTCCTT-3'	4.03	umc1104	5'-CAACAATTCCAATCATGGCACTAA-3' 5'- GTAACTCTGGTGAACTCAGAGGGC-3'	9.07
umc1418	5'- TCACACACACACTACACTCGCAAT-3' 5'- GAGCCAAGAGCCAGAGCAAAG-3'	4.08	umc1432	5'-GGCCATGATACAGCAAGAAATGAT-3' 5'-TACTAGATGATGACTGACCCAGCG-3'	10.02
umc1109	5'-GCAACACAGGACCAAATCATCTCT-3' 5'-GTTCGGTCCGTAGAAGAACTCTCA-3'	4.10	umc1506	5'-AAAAGAAACATGTTCAGTCGAGCG-3' 5'-ATAAAGGTTGGCAAAACGTAGCCT-3'	10.05
bnlg589	5'-GGGTCGTTTAGGGAGGCACCTTTGGT-3' 5'- GCGACAGACAGACAGACAAGCGCATTGT-3'	4.10	umc1507	5'-GATTCAAACCAAACACTTTTCCCA-3' 5'-CGAACCTTGCTGTGTGTTTATCAG-3'	10.05
bnlg557	5'-TCACGGGCGTAGAGAGAGA-3' 5'- CGAAGAAACAGCAGGAGATGAC-3'	5.03	umc1993	5'-CTTTTCTGCTACTCCTGCCTGC-3' 5'-CTAGCTGATGGAGGCTGTAGCG-3'	10.06
umc126	5'-CAACAGGGTGAACCCTCTGTACTT-3' 5'-AATATGGTGTTGTGATTTGCATCG-3'	5.06	bnlg153	5'- TCCACTGCTCCTCCACTGC-3' 5'- CACTTCAAACTGTCAAATCTCCA-3'	10.07

faced with that problem. Determining performances of inbred lines as potential hybrid parents in field experiments and diallel crosses, are still widely used in sweet corn breeding programs (Kashiani et al, 2010; Assunacao et al, 2010), since they provide information on the type of the predominant gene action, asses heterotic potential and general and specific combining ability of genotypes (Hallauer and Miranda, 1988), but they are also time and material consuming. Therefore the aim of our study was to assess genetic diversity of six ZP sweet corn inbred lines by SSR markers and to compare that information with data obtained through conventional diallel study, heterosis and specific combining ability – SCA. The concurrence between those data could contribute to efficiency of the sweet corn breeding programs.

Materials and Methods

For this study six sweet corn inbred lines carrying the *su* gene were chosen. All of them were selected at Maize Research Institute "Zemun Polje", but they originated from different varieties. Inbred L1 was derived from a Mexican sweet corn variety and L2 from

Table 2 - Estimates of heterosis for fresh ear yield of hybrid combinations obtained from six sweet corn inbred lines

Hybrid comb	2008 T1	T2	T3	average	2009 T1	T2	T3	average	Total Average
L2 x L1	208.52**	184.68*	138.10**	177.1	201.26**	146.03**	234.60**	193.96	185.53
L3 x L1	102.24**	108.95*	51.65**	87.61	70.39	102.41**	130.78*	101.19	94.40
L4 x L1	49.45*	103.38*	53.95	68.92	113.95*	77.89	99.61*	97.15	83.04
L5 x L1	119.25*	100.84*	69.58**	96.56	45.06	38.67	92.54**	58.76	77.66
L6 x L1	39.28	68.45**	44.20	50.98	132.02**	38.95*	192.73**	121.23	86.10
L3 x L2	151.67**	84.28**	133.87**	123.27	134.22*	152.03**	227.96**	171.40	147.34
L4 x L2	45.03*	104.65	90.75**	80.14	75.96*	51.86*	121.48*	83.10	81.62
L5 x L2	203.76**	109.83**	114.08*	142.56	107.73**	68.10*	126.14	100.66	121.61
L6 x L2	65.77	95.71*	78.04*	79.84	257.02**	111.64*	260.09*	209.58	144.71
L4 x L3	53.41*	99.77*	51.02**	68.07	33.84**	30.55	99.69*	54.69	61.38
L5 x L3	149.81**	100.93*	106.71**	119.15	104.38**	77.52	117.78**	99.90	109.52
L6 x L3	55.56*	101.63**	51.09*	69.42	65.73	35.05	222.58**	107.78	88.60
L5 x L4	-5.88	43.02	14.93	17.36	22.46	12.27	32.78	22.50	19.93
L6 x L4	33.71*	41.46*	48.69*	41.17	38.68	25.71	77.22**	47.20	44.24
L6 x L5	43.89	40.58	39.05		75.60	26.91	66.67*	56.39	48.78

*,** - significant at the 0.05 and 0.01 probability level, respectively

the crossing of (Talqueno x R588) x sweet corn variety from USA, where Talqueno is a Mexican dent variety and R588 is a line obtained from domestic dent population "Rumski zuban". Inbred L3 is selected from sweet corn synthetic populations developed at Maize Research Institute, with the origin from USA. Two inbreds originated from the crossings of sweet corn variety from USA and Iranian dent verities (L4), and sweet corn variety and inbred line K8 (dent line from the Iranian variety) (L5). Dent varieties obtained from Iran, were used in sweet corn breeding as they are characterized as tolerant to drought stress and with deep kernel. Inbred L6 was derived from F2 population of hybrid Jubilee. Inbred lines were crossed in a diallel fashion without reciprocal combinations [n(n-1)/2] (n-number of parental lines), which produced 15 F1 combinations. Field experiments were conducted in 2008 and 2009 at Maize Research Institute, Zemun Polje, in the vicinity of Belgrade (44°52'N 20°20'E) in Serbia. The soil was slightly calcareous chernozem with 47% clay and silt and 53% sand. The 15 hybrid combinations and six parental lines were included in a randomized complete block design with three replications in three treatments, arranged in a factorial design. The treatments were: T1 - no irrigation; T2 - with irrigation; T3 - late sowing. Hybrids and inbreds were sown at the same time in separate plots with two border rows for each plot. The experimental unity was 14m^2 and encompassed two rows for each entry with inter-row distance of 0.7m while the within-row plant distance was 25cm, with 80 plants and the final density of 57.143 plants/ha. Harvest of fresh ears was performed 24 days after silking, since from the long term experience with our material (Pajić et al, 1994; Videnović et al, 2003) and literature data (Rosenbrook and Andrew, 1970) this was found to be optimal harvest date.

Processing of data obtained from diallel analysis was done by PC program Genetic Analysis (Dick, 1987). General (GCA) and specific (SCA) combining ability were analyzed according to the Griffing (1956) mathematical model I, method 2.

Genomic DNA was isolated from leaves by Mini CTAB method (Williams et al, 1993). SSR analysis was done by the method of Senior and Heun (1993). A total of 47 SSR primers were used for polymorphism evaluation, and 40 of them presented clear bands (Table 1) while in seven no amplification was recorded or it was very weak.

The amplified bands were scored based on 1/0 (presence/absence) system. Genetic similarities (GS) among all possible pairs of inbred lines were estimated from SSR data according to Simple matching coefficient - SM (Sokal and Michener, 1958):

$$GSij = a+d/a+b+c+d,$$

where: a - band present in both genotypes i and j (1.1); b - band present in genotype i and absent in genotype j (1.0); c - band present in genotype j and absent in genotype i (0.1); d - band absent in both genoptypes i and j (0.0).

Cluster analysis was carried out on the matrix of genetic similarities by the UPGMA method, and the dendrogram was constructed with NTSYS-pc, 2.11a software (Rohlf, 2000). PCA was constructed by the GGE biplot program, and the results are given in 2D diagram form. Correlations between GS and SCA and GS and heterosis, based on SSR markers were calculated by Spearman's rank correlation coefficient (Zar, 1999).

Results

Analysis of variance of diallel crosses showed highly significant estimates ($p<0.01$) of SCA for fresh ear yield in all three treatments in both years. Estimates of the GCA were in some treatments significant, but in all treatments lower than estimates of SCA. That points to the fact that non additive gene effect is predominant in the expression of this trait. This was confirmed by the results of the analysis of the components of variance, where it was also found that non additive components (H1 and H2) were significant in all cases, while dominant component (D) was lower and significant only in T2 in both years. Predominant non additive gene effect concerning

Table 3 - Estimates of specific combining ability for fresh ear yield of hybrid combinations obtained from six sweet corn inbred lines

Hybrid comb	2008 T1	T2	T3	average	2009 T1	T2	T3	average	Total Average
L2 x L1	2.26*	3.30**	2.05*	2.54	3.95**	2.11*	2.66**	2.91	2.72
L3 x L1	1.10	2.67*	0.04	1.27	-0.48	0.75	-0.16	0.03	0.65
L4 x L1	2.08*	3.02**	1.37	2.16	3.47**	1.20	2.21**	2.29	2.22
L5 x L1	1.84	2.65*	1.59*	2.03	-0.53	0.88	2.00**	0.78	1.40
L6 x L1	1.48	0.67	0.43	0.86	1.76	1.22	2.50**	1.82	1.34
L3 x L2	2.79*	1.93	1.91*	2.21	1.23	2.47**	1.99**	1.90	2.05
L4 x L2	1.77	2.22*	3.24**	2.41	3.52**	1.21	3.25**	2.66	2.54
L5 x L2	4.51**	2.58*	1.60*	2.90	2.03*	2.11*	2.74**	2.29	2.60
L6 x L2	1.84	2.79*	1.58*	2.07	4.11**	2.01*	1.73*	2.62	2.34
L4 x L3	2.18*	1.88	1.40*	1.82	1.21	2.31**	3.04**	2.19	2.00
L5 x L3	3.13**	2.80*	2.91**	2.95	3.19**	1.43*	2.78**	2.47	2.71
L6 x L3	0.86	2.61*	1.05	1.51	1.23	1.12	1.36*	1.23	1.37
L5 x L4	-1.93	-1.04	-0.51	-1.16	-0.15	-0.58	-1.46*	-0.36	-0.84
L6 x L4	0.73	-0.78	1.01	0.32	1.51	0.88	1.36*	1.25	0.78
L6 x L5	0.76	-1.04	0.75	0.16	1.15	0.08	0.39	0.54	0.35

*,** - significant at the 0.05 and 0.01 probability level, respectively

fresh ear yield both with husk and without it was also found in research of Dutta et al (2004).

Estimates of heterosis for fresh ear yield were in most cases high and significant. Hybrid combination L2 x L1 and L3 x L2 expressed highly significant estimates of heterosis in all treatments in both years. Those two hybrid combination had highest estimates of heterosis on average in two years and also highest average heterosis. High estimates of heterosis was found in hybrid combination L5 x L2 in 2008, while it expressed lower heterosis in 2009, which is similar to the hybrid combination L6 x L2 which in 2008 expressed low heterosis, while in 2009 had the highest heterosis on average (Table 2). The lowest estimates of heterosis were noticed in hybrid combinations L5 x L4 (-5.88), L6 x L4 and L6 x L5.

Among 15 F1 combinations, three had highly significant estimates of SCA in all cases (L2 x L1, L5 x L2 and L5 x L3). The lowest expression of SCA was found in same hybrid combinations like in heterosis (L5 x L4), which was ranked 15th in all treatments in both years except T1 in 2009 (Table 3).

SSR markers showed that each of the studied genotype had specific genetic profile. Thirty two primers were polymorphic, while 8 showed monomorphic picture. The total of 84 alleles was scored and it ranged from 1 to 4 per primer. Genetic similarity between 6 sweet corn inbred lines ranged from 0.422 (L4 - L2) up to 0.756 (L6 - L5), with the average value 0.559 (Table 4). Low similarity (0.444) was also found between L5 - L2 and L2 - L1.

Estimates of genetic similarity between six sweet corn lines were used to form dendogram performing cluster analysis (CA) (Figure 1). This cluster encompassed two main groups of inbreds. First subcluster was formed by inbreds L5 and L6 with the highest level of similarity, and inbred L1. Inbred L3 was loosely attached to this subcluster. The other subcluster consisted of L4 and L2. Results of the PCA analysis were in correspondence with CA. The first two axes included 74.9% of the total variability (PC1 – 52.4% and PC2- 22.5%). Inbreds L5 and L6 were like in CA very closely grouped, which was also the case with L4 and L2. The inbred line L3 was by the PC2 axis most distant from others and also expressed negative interactions with them.

Concurrence between GS and heterosis and GS and SCA was established by Spearman's rank correlation coefficient. Correlations were negative and in most cases significant, ranging from -0.436 up to -0.614 (GS/heterosis) and -0.161 up to -0.575 (GS/SCA), for treatments (Table 5). When estimates of average heterosis in 2008 and 2009 were compared with GS, correlations were not significant, while estimate of the total average heterosis and GS were in significant negative correlation (-0.604). All average estimates of SCA and GS were in significant negative correlations.

Table 4 - Genetic similarity of six sweet corn inbred lines based on SSR markers

Genotype	L1	L2	L3	L4	L5
L2	0,444				
L3	0,556	0,489			
L4	0,422	0,667	0,556		
L5	0,689	0,444	0,511	0,556	
L6	0,667	0,422	0,578	0,622	0,756

Discussion

Analyzing genetic similarity among investigated inbred lines it is found that it is mostly based on the long term selection made in Maize Research Institute. Although inbreds L4 and L5 in their genetic background contained in some proportion similar genetic origin, and L1 and L2 are partly from the same geographic regions, but of different genetic background, values of GS showed that they are not closely related. Literature data show that there are no evidence on the correlations between geographic origin and genetic similarities between maize populations (Reif et

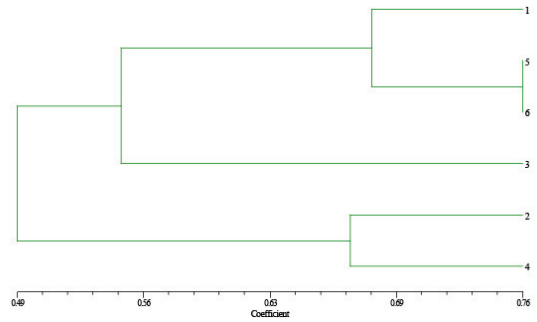

Figure 1 - Cluster analysis of genetic similarity for six sweet corn inbred lines

al, 2003), due to the different routes of its introduction, but also due to the active exchange between countries and scientists (Revilla et al, 2003).

Evidence of the efficiency of genotype grouping by CA and PCA in prediction of heterotic patterns is found in researches that have compared results of the quantitative genetics analysis and genetic distances based on molecular markers (Pinto et al, 2003; Fan et al, 2003). Figures of CA and PCA in our research also correspond with the results of heterosis and SCA for fresh ear yield from the diallel study. The best performance of heterosis and SCA was noticed in hybrid combinations L2 x L1, L6 x L2, L3 x L2 and L5 xL2, accordingly inbreds that formed those F1 combinations were grouped in different CA sublusters. Also it is found that L2 which was the component of hybrids with best performances is potentially most valuable sweet corn inbred among the studied genotypes. Hybrid combinations that showed lowest performances both concerning SCA and heterosis were L5 x L4 and L6 x L5. Characteristically L5 and L4 had in their genetic background to some extent same genetic origin, i.e. both are selected from the crossings of sweet corn varieties and dent variety obtained from Iran (L4), or dent line from variety introduced from Iran (L5). On the other hand SSR markers revealed greatest genetic similarity among L6 and L5 inbreds. This is probably associated to the original narrowness of the sweet corn gene pool and the fact that most of our germplasm originates from US sweet corn varieties and populations.

Significance of estimates of correlations between GS and heterosis or SCA, point to the agreement of results of SSR markers with the results of the diallel study, for one of the most important sweet corn traits fresh ear yield. Estimates of correlations were negative, i.e. if the higher GS between inbred lines was the lower estimates of heterosis and SCA were.

Molecular techniques provide accurate assessment of relationship between sweet corn inbred lines (Gerdes and Tracy, 1994), like it is in inbreds of the standard grain quality (Drinić Mladenović et al, 2002; Reif et al, 2003). Although our date showed relatively low to medium correlation between GS and heterosis/SCA, concerning the narrow genetic base and the lack of information about heterotic patterns in sweet corn, SSR markers could be very valuable in sweet corn breeding programs.

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Table 5 - Spearman's rank correlation coefficient between GS obtained by SSR markers, and fresh ear yield heterosis and SCA of sweet corn

	2008				2009				Total
	T1	T2	T3	average	T1	T2	T3	average	Average
Heterosis	-0.470	-0.575*	-0.543*	-0.417	-0.518*	-0.614*	-0.436	-0.443	-0.604*
SCA	-0.554*	-0.575*	-0.303	-0.546*	-0.571*	-0.543*	-0.161	-0.532*	-0.578*

* - significant at the 0.05 probability level

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