Diallel analysis of local sweet corn varieties for grain chemical quality

Análise dialélica de variedades locais de milho doce para qualidade química dos grãos

Análisis dialélico de variedades locales de maíz dulce para la calidad química de los granos

Abstract
Local varieties of sweet corn from the far west of Santa Catarina, southern Brazil, show outstanding potential for several important agronomic traits aimed at sweet corn genetic breeding. However, there is no data in the literature on the general and specific combining ability of these varieties for the chemical quality of the grains and the interactions of the general and specific combining ability with the environment. The percentage of total soluble sugars, starch content, and the relationship between sugars and starch of the grains were evaluated in experiments designed in complete randomized blocks, with two replications, in two environments of this region. The splitting of the diallel analysis into general and specific combining ability indicated a predominance of non-additive effects for all evaluated traits and showed non-significant effects (p ≤ 0.05) of the interactions of the general and specific combining ability x environment. Varieties 2255A and 2276A presented a higher concentration of favorable alleles for increasing the chemical quality of grains. The intervarietal hybrids F1’s 2255A x 319A, 2255A x 2029A, 2255A x 2276A, Cubano x 2276A, 2276A x 2029A and 2255A x 741B stood out for interpopulation improvement. The biparental compounds derived from the combinations 2255A x 319A and 2255 x 2276A, the triple compound 2255A x 2276A x 2029A, and the quadruple compounds 2255A x 741B x 2276A x 319A and 2255A x 2276A x 2029A x 319A are the most suitable for the formation of composite populations followed by a cyclic process of recurrent selection, aiming to increase the chemical quality of the grains.

Keywords: Zea mays L.; Starch; Total soluble sugars; Combining ability.

Resumo
Variedades locais de milho doce cultivadas no extremo Oeste de Santa Catarina, no sul de Brasil, apresentam notável potencial para diversos caracteres agronômicos importantes no melhoramento genético de milho doce. Entretanto, não existem dados na literatura sobre a capacidade geral e específica de combinação destas variedades para a qualidade química dos grãos, bem como os efeitos de suas interações com o ambiente. A porcentagem de açúcares solúveis totais, porcentagem de amido e relação entre açúcares e amido dos grãos foram avaliadas a partir de experimentos delineados em blocos completos casualizados, com duas repetições, em dois ambientes desta região. O desdobramento da análise dialélica em capacidade geral e capacidade específica de combinação indicou predominância de efeitos não aditivos para todos os caracteres avaliados e evidenciou efeitos não significativos (p ≤ 0,05) das interações das capacidades geral e específica de combinação x ambiente. As variedades 2255A e 2276A apresentaram maior concentração de alelos favoráveis para o aumento da qualidade química dos grãos. Os híbridos intervarietais F1’s 2255A x 319A, 2255A x 2029A, 2255A x 2276A, Cubano x 2276A, 2276A x 2029A e 2255A x 741B destacaram-se para o melhoramento interpopulacional. Os compostos biparentais derivados das combinações 2255A x 319A e 2255 x 2276A, o composto triplo 2255A x 2276A x 2029A, e os compostos quádruplos 2255A x 741B x 2276A x 319A e 2255A x 2276A x 2029A x 319A são os mais indicados para a formação de populações compostas, visando o aumento da qualidade química dos grãos, a partir de um processo cíclico de seleção recorrente.

Palavras-chave: Zea mays L.; Amido; Açúcares solúveis totais; Capacidade de combinação.

Resumen
Las variedades locales de maíz dulce cultivadas en el extremo oeste de Santa Catarina, Sur de Brasil, muestran notable potencial para varias características agronómicas importantes en el mejoramiento genético del maíz dulce. Sin embargo,
no existen datos en la literatura sobre las capacidades combinatorias general y específica de estas variedades para la calidad química de los granos, así como sobre los efectos de sus interacciones con el ambiente. El porcentaje de azúcares solubles totales, porcentaje de almidón y la relación azúcares y almidón de los granos se evaluaron en experimentos diseñados en bloques completos al azar, con dos repeticiones, en dos ambientes de esta región. La división del análisis dialélico para capacidad combinatoria general y específica mostró predominancia de efectos no aditivos para todos los rasgos evaluados y no presente significancia (p ≤ 0.05) de las interacciones de las capacidades combinatorias general y específica x ambiente. Las variedades 2255A y 2276A presentan mayor concentración de genes favorables para incrementar la calidad química de los granos. Los híbridos inter variedades P1’S 2255A x 319A, 2255A x 2029A, 2255A x 2276A, Cubano x 2276A, 2276A x 2029A y 2255A x 741B se destacaron para el mejoramiento inter poblacional. Los compuestos biparentales derivados de las combinaciones 2255A x 319A y 2255A x 2276A, el compuesto triple 2255A x 2276A x 2029A y los compuestos cuádruples 2255A x 741B x 2276A x 319A y 2255A x 2276A x 2029A x 319A son los más adecuados para la formación de poblaciones compuestas, seguidas de selección poblacional, dirigido al aumento de la calidad química de los granos.

Palabras clave: Zea mays L.; Almidón; Azúcares solubles totales; Capacidad combinatoria.

1. Introduction

Sweet corn is a special type of corn intended exclusively for human consumption (Pereira Filho & Teixeira, 2016). In Brazil, the cultivated area is not very representative (40 thousand hectares) but expanding (Teixeira et al., 2013).

Sweet corn differs from other types of corn due to the presence of at least one of the mutant genes that affects the expression of enzymes involved in starch anabolism. Thus, they cause an increase in the concentration of sugars in the endosperm of the grains and wrinkling when they reach physiological maturity (Boyer & Shannon, 1984). Among the mutated genes best known for conferring this trait are: sugary1 (su1); dull (du) e amiloase-extender (ae); shrunken-2 (sh2); brittle1 (bt1); sugary enhancer (se); brittle-2 (bt2) e waxy (wx) (Boyer & Shannon, 1984).

Although there are several mutant genes, the genetic basis of sweet corn is narrow. It is believed that in the world there are only 300 open-pollinated varieties of this type of corn. In Brazil, the genetic base is even smaller, as only 20 accessions are kept in the Maize Active Gene Bank (Maize BAG) of the Brazilian Agricultural Research Corporation (Embrapa), most of them imported or derived from breeding programs (Teixeira et al., 2019). There are few commercial sweet corn cultivars in the Brazilian seed market, which restricts the expansion of cultivation in Brazil (Pereira et al., 2019).

However, an important genetic pool of sweet corn is conserved in the diversity microcenter of Zea mays L. of the far west region of the State of Santa Catarina (FWSC), in southern Brazil (Costa et al., 2016). Thirteen genotypes with wrinkled grains were identified in this region (Souza et al., 2020). Of these, seven have the sugary1 gene and one has the shrunken2 gene for the sweet phenotype (Souza et al., 2021a). The FWSC sugary1 local sweet corn varieties show genetic diversity between and within populations, excellent performance in several desirable agronomic traits and are promising to be used in genetic breeding programs (Souza et al., 2021b). The temperature amplitude due to the different altitudes in FWSC influences the agronomic performance of these varieties (Souza et al., 2021b). However, there is no information on the performance of these varieties regarding the chemical quality of the grains, especially for the percentage of soluble sugars and starch in the dry matter of the grains, when cultivated at different altitudes, nor on the interactions of the general and specific combining ability with environment for these characteristics.

The diallel analysis allows inferences about parameters useful in breeding (Cruz & Regazzi, 2001). The diallel analysis methodology proposed by Griffing (1956) allows obtaining estimates of the effects of general and specific combining ability and inferring the type of predominant genetic action in character control (Hallauer et al., 2010). The general and specific combining ability studies have been frequently used in the genetic breeding of sweet corn (Hossain & Lakhera, 2010; Khanduri et al., 2008; Sadaiah et al., 2013; Souza, 2019; Suzukawa et al., 2018; Teixeira et al., 2013). Souza (2019) used diallel analysis to study the genetic basis of phenological, morphological and agronomic characters of the FWSC sugary1 sweet corn local varieties and proved the existence of variability resulting from the action of additive effects for most of the characters evaluated. However,
there is no information about the combining ability and the predominant genetic effects in the determination of the characters related to the chemical quality of the grains of these varieties. Therefore, the present work aimed at evaluating the combining ability of local varieties of sugary1 sweet corn for total soluble sugars, starch content, and relationship sugars/starch, aiming to identify the type of predominant gene action in the determination of these related characters and to define breeding strategies for sweet corn in the FWSC.

2. Methodology

Samples of grains in milky grain stage of 21 genotypes were obtained, being: six varieties of sweet corn sugary1 (five local varieties from FWSC and the access Cubano from Embrapa’s Maize BAG) and 15 intervarietal hybrids F1’s resulting from the crossing between these varieties, following the complete diallel scheme.

The local varieties evaluated in the present study are part of the total set of 13 sweet corn varieties conserved in situ-on farm at the FWSC, which were collected by members of the Nucleus of Studies in Agrobiodiversity (NEABio) of the Federal University of Santa Catarina (UFSC), in farms of the municipalities of Anchieta and Guaraciaba, between 2013 and 2016 (Vidal et al., 2020). These varieties were characterized for some morphological and agronomic characters and were stored in the UFSC’s Maize BAG (Souza 2019; Souza et al., 2021a). The five local varieties selected to be part of this research represent the genetic diversity of sweet corn conserved on farm in the FWSC (with a 90% confidence level) for the following quantitative grain characteristics: ear weight; ear length; grain volume; and grain weight. This result was obtained using the formula: n = \frac{t(0.05;GL)^2 \cdot S^2}{\bar{y} - \mu e}, being S²: population variance; μ: population average; e \bar{y}: sample average (Cochran, 1977). The result was adjusted for a finite population, using the formula: n' = \frac{n}{1 + \frac{n}{N}}, where N: finite population size (Bartlett, Kotrlik & Higuins, 2001).

The 21 genotypes were evaluated in two experiments carried out at FWSC, in the municipalities of Guaraciaba (624 m of altitude) and Anchieta (717 m of altitude). The cultivation sites represent, in terms of altitude, the conditions under which local sweet corn varieties are grown in that micro-region, given that the cultivation altitude of the varieties varies from 515 to 833 m (Souza, 2019).

The experimental design was complete randomized blocks, containing two replications and plots represented by two rows of four linear meters in length, at 1.0 m spacing between rows and under a plant density of 50,000 plants ha⁻¹ after thinning. The useful plot area of 2.0 m² was constituted by the central part of the two rows and from which the grain sample was obtained from five random ears of each genotype, manually pollinated, and harvested on the 21st day after manual pollination.

The grain samples were freeze-dried, fragmented, and submitted to the procedures of quantification of total soluble sugars and starch in triplicates.

The extraction of total soluble sugars was performed according to the methodology proposed by Shannon (1968). 2 mL of the MCW solution (methanol: chloroform: water) (12:5:3, v/v) were added to a sample of 50 mg of dry mass. The solution was centrifuged (4000 rpm for 10 minutes) and then the supernatant was collected. The residue was diluted again with 2 mL of the MCW solution, centrifuged (4000 rpm for 10 minutes) and the supernatant removed. 80 μL of the supernatants were diluted in 3920 μL of MCW (adjusted according to the sample). Subsequently, 1 mL of chloroform and 1.5 mL of water were added, and the extract was centrifuged again (4000 rpm for 5 minutes). After centrifugation, the extract formed two phases, the upper phase being collected and used for sugar quantification, according to the method of Umbreit and Burris (1964). 1 mL aliquots of the extract plus 2 mL of 0.2% Anthrone solution (200 mg of Anthrone in 100 mL of concentrated Sulfuric Acid) were vortexed and heated in a water bath at 100°C for three minutes. With the samples cooled, 300 μL were transferred to a microplate for reading the absorbance (620 nm), in a microplate reader, model Spectramax Paradigm. The quantification of total soluble sugars was performed using the glucose standard curve (5; 10; 25; 50; 75; 100 mg/mL; R² = 0.99; y = 0.0081x). Results were expressed
as milligrams of total soluble sugars per gram of dry mass.

The quantification of starch content was performed using the residue from the total soluble sugar extraction, following the method by McCready, Guggolz and Owens (1950); 2 mL of 30% Perchloric Acid were added and the extract was centrifuged (4000 rpm for 10 minutes). The supernatant was collected, and the residue was again extracted with 2 mL of 30% Perchloric Acid and centrifuged (4000 rpm for 10 minutes). 80 μL of the supernatants were diluted in 3920 μL of MCW (adjusted according to the sample). 1 mL aliquots of the extract, plus 2 mL of 0.2% Anthrone solution, were vortexed and heated in a water bath at 100 °C for three minutes. With the samples cooled, 300 μL were transferred to a microplate for reading the absorbance (620 nm), in a microplate reader, model Spectramax Paradigm. Starch quantification was performed using the standard starch curve (5; 10; 25; 50; 75; 100 mg/mL; R² = 0.98; y = 0.0065x). Results were expressed as milligrams of starch per gram of dry mass.

The data were submitted to individual preliminary examinations for normality and homogeneity of variances. The diallel analysis was performed according to Model II by Griffing (1956), in which the parents and the F1’s hybrids are included in the analysis, without considering the reciprocal hybrids. The following random statistical-modeling model was Yijkl = μ + gi + gj + sij + lz + lgi + ljsij + bk(z) + cijkz being: Yijkl = average value to hybrid combination (i ≠ j) or parent (i=j); μ = overall average of treatments; gi e gj = effect of the general combining ability of the i-th or j-th parent (i,j = 1.2 ...6); sij = effect of specific combining ability for crosses between parents of order i and j; lz = environment effect (1, 2); lgi and ljs = effect of the interaction of the general combining ability of parents i and j with the z-th environment; asij = effect of the interaction of the specific combining ability of parents i and j with the z-th environment; b(z) = effect of blocks within environments, and eijkz = average experimental error associated with order observation ijkz.

The estimates of the variance components associated with the general combining ability (GCA) were obtained by the formula: \( \sigma^2g = \frac{QMG - QMS}{ra} \) and the estimates of the components of variance associated with specific combining ability (SCA) were obtained by the formula: \( \sigma^2s = \frac{QMS - QMR}{ra} \), where: QMG = mean square of general combining ability; QMS = mean square of specific combining ability; QMR = mean square of the residue; QMA = mean square of environments; QMg = mean square of genotypes; p: number of parents; r: number of repetitions; and a: number of environments (Cruz & Regazzi, 2001).

The estimates of \( \hat{g}_i \) associated with the effects of the general combining ability were obtained by the formula: \( \hat{g}_i = \frac{1}{p+2} [Yii + Yi. + \frac{2}{p} Y..] \), where: p: number of parents; Yi.: sum of combinations of parent i with the other parents; and Y..: total sum of combinations ij. The estimates of \( \hat{s}_{ij} \) associated with the effects of specific combining ability were obtained by the formula: \( \hat{s}_{ij} = Yi.j - \frac{1}{p+2} [Yii + Yi.j + Yi.+Y.j] + \frac{2}{(p+1)(p+2)} Y.. \), where: p: number of parents; Yi.: sum of combinations of parent i with the other parents; and Y..: total sum of combinations ij.

The predicted values (VP) for the compounds were estimated for compounds type A x B (VP2) with two parents, type A x B x C (VP3) with three parents, and type A x B x C x D (VP4) with four parents, given by the formulas: \( VP_2 = \frac{Yii+Yij+2Yij}{4} \), \( VP_3 = \frac{Yii+Yij+Ykk+2(Yik+Yij+Yjk)}{9} \) and \( VP_4 = \frac{Yii+Yij+Ykk+Ymm+2(Yij+Yik+Yjm+Yjk+Yjm+Ykm)}{16} \), where: Yi: mean of the parent, when i = j, or of the hybrid, when i ≠ j, of the selected variable.

All statistical and genetic analyzes were performed with the aid of the computer software GENES (Cruz, 2013).

3. Results and Discussion

In the unfolding of the effects of treatments on GCA and SCA of the diallel analysis, significant differences (p ≤ 0.05) were detected in the estimates of the effects of SCA for all characters and in the estimates of the effects of GCA for starch content.
and relationship sugars/starch. There was no significant effect of the GCA x Environment interaction (CGC x E) and the SCA x Environment interaction (SCA x E) (Table 1).

The coefficients of variation (CVs) were 9.56% for total soluble sugars, 4.89% for starch content and 11.21% for the relationship sugars/starch (Table 1). According to the classification by Pimentel Gomes (1978), CVs were considered low for total soluble sugars and starch content (CV < 10%) and medium for the relationship sugars/starch (CV < 20%). These values were lower than those reported by Scapim et al. (1996), who reported CVs of 16.47% and 27.27% when evaluating the content of total sugars and reducing sugars in sweet corn grains, respectively.

Table 1. Mean square estimates from the joint diallel analysis of six parents and 15 intervarietal F1's hybrids of sweet corn (sugary1), evaluated in Anchieta and Guaraciaba, Santa Catarina, 2017/2018 harvest.

| Variation factor                        | Degrees of freedom | Mean squares                  |
|-----------------------------------------|--------------------|-------------------------------|
|                                         |                    | Total soluble sugars<sup>1</sup> | Starch content<sup>1</sup> | Total soluble sugars / starch content |
| Block<sup>2</sup>/ Environments         | 2                  | 10.46                         | 9.40                         | 0.05                     |
| Environments                            | 1                  | 0.35<sup>ns</sup>             | 0.13<sup>ns</sup>           | 0.0010<sup>ns</sup>     |
| Genotype                                | 20                 | 59.24**                      | 68.65**                      | 0.1043**                |
| General Combination Ability             | 5                  | 110.01<sup>ns</sup>          | 147.33*                      | 0.2423**                |
| Specific Combination Ability            | 15                 | 42.31**                      | 42.29**                      | 0.0584**                |
| Genotype x Environment                  | 20                 | 5.07<sup>ns</sup>            | 4.84<sup>ns</sup>           | 0.0070<sup>*</sup>      |
| General Combination Ability x Environment | 5              | 9.90<sup>ns</sup>            | 6.88<sup>ns</sup>           | 0.0135<sup>ns</sup>    |
| Specific Combination Ability x Environment | 15             | 3.46<sup>ns</sup>            | 4.16<sup>ns</sup>           | 0.0048<sup>ns</sup>    |
| Residue                                 | 40                 | 2.86                         | 2.93                         | 0.0034                  |
| General mean                            |                    | 17.66                        | 34.97                        | 0.52                    |
| CV (%)                                  |                    | 9.56                         | 4.89                         | 11.21                   |
| Components<sup>2</sup>                  |                    |                               |                              |
| gi                                      | 2.12               | 3.28                         | 0.006                        |
| sij                                     | 9.15               | 9.11                         | 0.013                        |

<sup>1</sup> Percentage in grain dry matter. <sup>2</sup> Variance components associated with the general ability (gi) and the specific ability (sij) of combination; ns: not significant; ** and * significant at 1% and 5%, respectively, by the F Test. Source: Authors.

With the exception of total soluble sugars, significant effects were detected for the general combining ability, indicating the differences between genotypes regarding the additive effects for starch and for the sugar/starch ratio (Table 1). Estimates of variance components associated with GCA effects (σ<sup>2</sup>gi), SCA (σ<sup>2</sup>sij), and the ratio between them (σ<sup>2</sup>sij/σ<sup>2</sup>gi) of 4.32 for total soluble sugars, 2.78 for starch content, and 2.17 for relationship sugars/starch, indicate that non-additive gene effects are the most important for these characters, mainly due to the starch content. When comparing the relative contribution of the components of σ<sup>2</sup>gi and σ<sup>2</sup>sij in the character control, for the characters that presented significance, the contribution was greater for the non-additive part. These results are in line with those reported in several studies carried out with sweet corn (Khanduri et al., 2010; Kumari et al., 2008; Sadaiah et al., 2013). When studying the genetic effects involved in the concentration of total sugars in sweet corn grains, Kumari et al. (2008) and Sadaiah et al. (2013) reported the predominance of non-additive gene action. Khanduri et al. (2010) also reported the greater importance of non-additive gene action for the concentration of total sugars.
sugars, reducing sugars, non-reducing sugar, and grain yield in sweet corn. According to Cruz and Regazzi (2001), the significance of variations attributed to non-additive effects enables interpopulational breeding to obtain hybrids and the significance of variations attributed to additive effects enables the indication of populations to be used in intrapopulational breeding programs.

Although the environments where the experiments were conducted are at different altitudes, in two municipalities in the state of Santa Catarina, the differences between the environments were not enough to detect significance for the interactions G x E, GCA x E and SCA x E, possibly because Anchieta and Guaraciaba are located in the same agroecological micro-region. The non-significant effects of the GCA x E and SCA x E interaction allowed the estimation of the GCA effects (ĝi) and SCA (ŝij), as well as the prediction of compounds based on the average of the sites.

For the total soluble sugars character, the greatest positive effect of ĝi was presented by the local variety 2276A (2.14%) and the greatest negative effect was presented by the variety Cubano (-2.66%). For the character starch content, the greatest negative effect was presented by 2255A (-3.00%) and the greatest positive effect was presented by Cubano (2.53%). For the relationship sugars/starch, the greatest positive effect of ĝi was presented by 2255A (0.11) and the greatest negative effect was presented again by the variety Cubano (-0.12) (Table 2). The values obtained indicate the increase (positive) or reduction (negative) of the chemical quality indicators of the grains, according to the cross of diallel analysis. Considering that significant genetic differences between the local varieties associated with the general combining ability were due to starch content, the most promising genotypes on the basis of this parameter would be the ones whose estimated values of ĝi were negative for this trait and positive for the relationship sugars/starch.

Table 2. Estimates of the effects of the general combining ability (ĝi) and standard deviations (SD) for three grain traits of six sweet corn varieties (sul/sul) cultivated in Anchieta and Guaraciaba, Santa Catarina, 2017/2018 harvest.

| Genotype   | Total soluble sugars¹ | Starch content¹ | Total soluble sugars/Starch content |
|------------|-----------------------|-----------------|-------------------------------------|
|            | Anchieta  | Guaraciaba | Mean | Anchieta  | Guaraciaba | Mean | Anchieta  | Guaraciaba | Mean |
| Cubano     | -2.36     | -2.97      | -2.66 | 2.49      | 2.57      | 2.53 | -0.11     | -0.12      | -0.12 |
| 2255A      | 2.93      | 1.31       | 2.13  | -3.12     | -2.88     | -3.00 | 0.14      | 0.09       | 0.11  |
| 741B       | -1.35     | -0.35      | -0.85 | 1.09      | -0.20     | 0.45 | -0.06     | -0.01      | -0.04 |
| 2276A      | 1.68      | 2.59       | 2.14  | -1.97     | -1.57     | -1.77 | 0.08      | 0.10       | 0.09  |
| 2029A      | -0.10     | -0.75      | -0.43 | -0.93     | 0.42      | -0.26 | 0.01      | -0.03      | -0.01 |
| 319A       | -0.80     | 0.17       | -0.32 | 2.43      | 1.66      | 2.05 | -0.06     | -0.02      | -0.04 |
| SD (ĝi)    | 0.35      | 0.42       | 0.39  | 0.35      | 0.39      | 0.010 | 0.015     | 0.013      |
| SD (ĝi - ĝi)| 0.54     | 0.65       | 0.60  | 0.54      | 0.66      | 0.60 | 0.016     | 0.024      | 0.02  |

¹ Percentage in grain dry matter. Source: Authors.

The results of the present study show that the varieties 2255A and 2276A were the ones that contributed the most, on average, to the desirable increase in the relationship sugars/starch, while Cubano was the one that contributed the least to this characteristic, having the greatest contribution to the undesirable increase in starch content. In a diallel study of several phenological, morphological and agronomic characteristics of local sweet corn varieties from FWSC, Souza (2019) reported that varieties 2276A and 2255A present positive estimates of ĝi for yield (t ha⁻¹), indicating them as favorable parents to increase sweet corn productivity through selection. Souza (2019) also reported that the 2276A population exhibits negative ĝi estimates for the crop cycle, indicating it as a favorable parent for selection to reduce the vegetative cycle of sweet corn.
According to Cruz and Vencovsky (1989), the most favorable hybrid is the one with the highest SCA, in which one of the parents has the highest GCA. Therefore, we discussed the hybrid combinations with the best estimates of $\hat{s}_{ij}$ and that involve at least one of the parents that have presented the favorable effect of GCA. The best estimates of $\hat{s}_{ij}$ for total soluble sugars and relationship sugars/starch were from the hybrid combinations 2255A x 319A, 2255A x 2029A, 2255A x 2276A, Cubano x 2276A, 2276A x 2029A and 2255A x 741B (Table 3). In these cases, the estimates of $\hat{s}_{ij}$ for starch content result in negative values. This indicates that the combinations that have the highest positive effect for total soluble sugars and relationship sugars/starch have the opposite effect for starch content. The positive values of $\hat{s}_{ij}$ and away from zero for the variable total soluble sugars and relationship sugars/starch of the mentioned combinations indicate that the parent divergence is greater in relation to the average frequency of favorable alleles for this trait, compared to the other parents involved in the diallel cross. Other combinations with the parent 2276A and 2255A, which showed positive effects closer to zero, as in the case of the hybrid 741B x 2276A (for total soluble sugars), or negative values, as in the case of the combination 2276A x 319A (for sugars/starch), indicate the same or lower than expected for the GCA.

Based on the set of characteristics evaluated, it is concluded that the hybrids that stood out from the other combinations were 2255A x 319A, 2255A x 2029A, 2255A x 2276A, Cubano x 2276A, 2276A x 2029A and 2255A x 741B. Souza (2019) also highlighted the combinations 2255A x 319A, 2255A x 2276A and 2255A x 741B, due to their potential for productivity (t ha$^{-1}$) of sweet corn.

Mean predicted values for compounds derived from double, triple, and quadruple combinations for three characters of grains from six sweet corn parents in two FWSC environments are shown in table 4. The compound derived from 2255A x 2276A showed mean predicted values of 21.53% for total soluble sugars, 29.65% for starch content and 0.73% for 319A relationship sugars/starch, while the compound derived from 2255A x 319A had mean predicted values of 19.88% for total soluble sugars, 31.42% for starch content and 0.64 for relationship sugars/starch. When carrying out the prediction of compounds for the sweet corn varieties of the FWSC, Souza (2019) also highlighted the biparental compound derived from the 2255A x 319A combination, as being the compound with the good estimates for the traits of ear weight without straw, plant height and stem diameter.

The compound formed from the combination of three parents (type A x B x C), such as 2255A x 2276A x 2029A, would be the most suitable to increase total soluble sugars and relationship sugars/starch, due to the averages of 21.04% of total soluble sugars and 0.67 for relationship sugars/starch (Table 4). The superiority of the 2255A x 2029A combination corroborates the SCA estimate presented above. The combinations 2255A x 741B x 2276A x 319A and 2255A x 2276A x 2029A x 319A had higher predicted averages for total soluble sugars and relationship sugars/starch. The first presented 19.82% for total soluble sugars, 32.10% for starch content and 0.63 for relationship sugars/starch, and the second presented 19.83% for total soluble sugars, 33.60% for starch content and 0.62 for relationship sugars/starch. These combinations differ mainly due to the starch content variable and may be indicated for the formation of four-parent compounds (type A x B x C x D) to increase total soluble sugars and relationship sugars/starch.
Table 3. Estimates of specific combining ability (sij) and standard deviations (SD) for three grain characters of 15 intervarietal hybrids F1’s (su/su) cultivated in Anchiesta and Guaraciaba, Santa Catarina, 2017/2018 harvest.

| Genotypes           | Total soluble sugars¹ | Starch content¹ | Total soluble sugars/ Starch content |
|---------------------|------------------------|----------------|--------------------------------------|
|                     | Anchieta | Guaraciaba | Mean | Anchieta | Guaraciaba | Mean | Anchieta | Guaraciaba | Mean |
| Cubano              | -0.79    | -2.58      | -1.69 | -3.96    | -3.27      | -3.62 | 0.04     | -0.02      | 0.01 |
| Cubano x 2255A      | -2.05    | -3.35      | -2.70 | 7.12     | 6.06       | 6.6   | -0.16    | -0.17      | -0.17 |
| Cubano x 741B       | -1.24    | -1.65      | -1.45 | -0.81    | 0.12       | -0.35 | -0.01    | -0.04      | 0.03 |
| Cubano x 2276A      | 1.47     | 4.5        | 2.99  | -0.01    | -0.98      | -0.48 | 0.03     | 0.13        | 0.08 |
| Cubano x 2029A      | 0.29     | 3.43       | 1.86  | 3.39     | 0.79       | 2.09  | -0.03    | 0.08        | 0.03 |
| Cubano x 319A       | 3.13     | 2.24       | 2.69  | -1.79    | 0.55       | -0.62 | 0.11     | 0.06        | 0.09 |
| 2255A               | -6.77    | -4.80      | -5.79 | -0.02    | 0.16       | 0.07  | -0.22    | -0.17       | -0.20 |
| 2255A x 741B        | 2.45     | 0.56       | 1.51  | -2.92    | -1.64      | -2.28 | 0.12     | 0.04        | 0.08 |
| 2255A x 2276A       | 3.61     | 3.54       | 3.58  | -0.12    | -0.18      | -0.15 | 0.13     | 0.12        | 0.13 |
| 2255A x 2029A       | 5.27     | 3.82       | 4.55  | -0.66    | -2.00      | -1.33 | 0.18     | 0.14        | 0.16 |
| 2255A x 319A        | 4.27     | 5.04       | 4.66  | -3.40    | -2.56      | -2.98 | 0.17     | 0.20        | 0.19 |
| 741B                | -1.66    | 0.71       | -0.48 | -1.14    | -3.02      | -2.08 | -0.03    | 0.07        | 0.02 |
| 741B x 2276A        | 0.41     | 0.67       | 0.54  | 4.00     | 4.50       | 4.26  | -0.06    | -0.06       | -0.06 |
| 741B x 2029A        | 0.19     | -0.62      | -0.22 | 1.10     | 0.28       | 0.69  | -0.02    | -0.03       | -0.03 |
| 741B x 319A         | 1.52     | -0.39      | 0.56  | 0.90     | 2.77       | 1.84  | 0.03     | -0.05       | -0.01 |
| 2276A               | -2.01    | -3.84      | -2.93 | -2.41    | -1.58      | -2.00 | -0.02    | -0.09       | 0.06 |
| 2276A x 2029A       | 1.60     | 1.61       | 1.61  | -2.02    | -4.64      | -3.33 | 0.08     | 0.14        | 0.11 |
| 2276A x 319A        | -3.06    | -2.64      | -2.85 | 2.94     | 4.46       | 3.7   | -0.14    | -0.15       | -0.15 |
| 2029A               | -3.31    | -3.19      | -3.25 | -3.00    | 0.88       | -1.06 | -0.07    | -0.11       | -0.09 |
| 2029A x 319A        | -0.73    | -1.86      | -1.30 | 4.21     | 3.80       | 4.00  | -0.08    | -0.10       | -0.09 |
| 319A                | -2.57    | -1.19      | -1.88 | -1.43    | -4.51      | -2.97 | -0.05    | 0.02        | -0.02 |
| SD (sii)            | 0.80     | 0.95       | 0.88  | 0.8      | 0.97       | 0.89  | 0.02     | 0.04        | 0.03 |
| SD (sij)            | 0.97     | 1.15       | 1.06  | 0.96     | 1.17       | 1.07  | 0.03     | 0.04        | 0.04 |
| SD (sii-sij)        | 1.09     | 1.29       | 1.19  | 1.09     | 1.32       | 1.21  | 0.03     | 0.05        | 0.04 |
| SD (sij-šik)        | 1.44     | 1.71       | 1.57  | 1.44     | 1.74       | 1.59  | 0.04     | 0.06        | 0.05 |
| SD (šij – škl)      | 1.33     | 1.58       | 1.46  | 1.33     | 1.62       | 1.48  | 0.04     | 0.06        | 0.05 |

¹ Percentage in grain dry matter. Source: Authors.
Table 4. Predicted values derived from double, triple and quadruple combinations for three characters of the grains in compounds from six sweet corn parents (*suIsu*) in two environments, in the municipalities of Anchieta (E1) and Guaraciaba (E2), Santa Catarina, 2017/2018 harvest.

| Compounds                      | Total soluble sugars¹ | Starch content⁴ | Total soluble sugars/ Starch content |
|-------------------------------|-----------------------|-----------------|-------------------------------------|
|                               | E1                      | E2 | Mean | E1 | E2 | Mean | E1 | E2 | Mean |
| 1 4 (Cubano x 2276A)          | 17.07                   | 17.86 | 17.47 | 33.87 | 34.31 | 34.09 | 0.51 | 0.53 | 0.52 |
| 2 3 (2255A x 741B)            | 18.43                   | 17.86 | 18.15 | 36.83 | 30.39 | 33.61 | 0.67 | 0.59 | 0.63 |
| 2 4 (2255A x 2276A)           | 21.95                   | 21.1  | 21.53 | 29.18 | 30.12 | 29.65 | 0.75 | 0.7  | 0.73 |
| 2 5 (2255A x 2029A)           | 20.67                   | 18.06 | 19.37 | 29.79 | 31.80 | 30.80 | 0.69 | 0.58 | 0.64 |
| 2 6 (2255A x 319A)            | 19.65                   | 20.1  | 19.88 | 32.18 | 31.42 | 31.8  | 0.63 | 0.64 | 0.64 |
| 3 4 (741B x 2276A)            | 17.35                   | 19.38 | 18.37 | 35.17 | 34.35 | 34.76 | 0.5  | 0.57 | 0.54 |
| 4 5 (2276A x 2029A)           | 18.78                   | 18.47 | 18.63 | 29.67 | 31.36 | 30.52 | 0.63 | 0.61 | 0.62 |
| 1 2 4 (Cubano x 2255A x 2276A) | 18.83                 | 18.01 | 18.42 | 34.33 | 34.33 | 34.33 | 0.55 | 0.55 | 0.55 |
| 1 4 5 (Cubano x 2276A x 2029A) | 17.27                 | 17.89 | 17.58 | 34.44 | 34.44 | 34.44 | 0.54 | 0.53 | 0.54 |
| 2 3 4 (2255A x 741B x 2276A)  | 20.19                   | 20.14 | 20.17 | 32.01 | 32.01 | 32.01 | 0.63 | 0.63 | 0.63 |
| 2 3 5 (2255A x 741B x 2029A)  | 19.17                   | 17.76 | 18.47 | 32.27 | 32.27 | 32.27 | 0.56 | 0.56 | 0.56 |
| 2 3 6 (2255A x 741B x 319A)   | 18.85                   | 18.92 | 18.89 | 32.93 | 32.93 | 32.93 | 0.59 | 0.59 | 0.59 |
| 2 4 5 (2255A x 2276A x 2029A) | 21.72                   | 20.36 | 21.04 | 30.74 | 30.74 | 30.74 | 0.67 | 0.67 | 0.67 |
| 2 4 6 (2255A x 2276A x 319A)  | 20.07                   | 20.54 | 20.31 | 32.87 | 32.87 | 32.87 | 0.64 | 0.64 | 0.64 |
| 2 5 6 (2255A x 2029A x 319A)  | 19.63                   | 18.61 | 19.12 | 33.92 | 33.92 | 33.92 | 0.57 | 0.57 | 0.57 |
| 3 4 5 (741B x 2276A x 2029A)  | 17.6                    | 18.24 | 17.92 | 33.73 | 33.73 | 33.73 | 0.55 | 0.55 | 0.55 |
| 3 4 6 (741B x 2276A x 319A)   | 16.46                   | 18.19 | 17.33 | 36.54 | 36.54 | 36.54 | 0.50 | 0.50 | 0.50 |
| 1 2 3 4 (Cubano x 2255A x 741B x 2276A) | 18.05 | 17.76 | 17.91 | 34.63 | 34.58 | 34.61 | 0.54 | 0.53 | 0.54 |
| 1 2 4 5 (Cubano x 2255A x 2276A x 2029A) | 19.27 | 18.48 | 18.88 | 33.55 | 33.92 | 33.74 | 0.59 | 0.56 | 0.58 |
| 1 2 4 6 (Cubano x 2255A x 2276A x 319A) | 18.61 | 18.54 | 18.58 | 33.96 | 35.24 | 34.6  | 0.55 | 0.54 | 0.55 |
| 1 2 5 6 (Cubano x 2255A x 2029A x 319A) | 17.98 | 16.9  | 17.44 | 35.95 | 32.3  | 34.13 | 0.52 | 0.48 | 0.50 |
| 2 3 4 5 (2255A x 741B x 2276A x 319A) | 20.14 | 19.49 | 19.82 | 31.98 | 32.21 | 32.1  | 0.64 | 0.62 | 0.63 |
| 2 3 4 6 (2255A x 741B x 2276A x 319A) | 19.29 | 19.73 | 19.51 | 34.01 | 33.87 | 33.94 | 0.59 | 0.60 | 0.60 |
| 2 3 5 6 (2255A x 741B x 2029A x 319A) | 18.79 | 18.07 | 18.43 | 34.22 | 34.19 | 34.21 | 0.57 | 0.54 | 0.56 |
| 2 4 5 6 (2255A x 2276A x 2029A x 319A) | 20.03 | 19.63 | 19.83 | 33.83 | 33.37 | 33.6  | 0.63 | 0.61 | 0.62 |

¹ Percentage in grain dry matter. Source: Authors.
The concentration of carbohydrates (sugars and starch) is one of the most relevant quality parameters of grains for sweet corn, as it is correlated with sensory attributes, such as sweet taste and grain texture. In a sensory analysis study, Oliveira Jr. et al. (2006) showed that consumers prefer corn with the highest concentration of sugars in the samples. For this reason, the sweet corn industry prefers materials with a high concentration of sugars and low concentration of starch (Kwiatkowski & Clemente, 2007). The greatest commercial potential at the moment is the materials of the super-sweet group, which have between 15% and 25% of sugars in the grains (Pereira Filho & Teixeira, 2016). Thus, the combinations of local sweet corn varieties from the FWSC favor for increasing the percentage of sugars and reducing the percentage of starch and are, therefore, the most promising to be used in genetic improvement programs destined for this region of the Santa Catarina State.

In the context of the FWSC and aiming to support the conservation of the genetic variability of these local varieties, it is opportune that the interpopulation improvement strategy is focused on the identification of genotypes that present superiority of the effects of the specific combining ability and that intervarietal hybrids F1's can be recommended for direct use. On the other hand, compounds involving two, three and four parents can allow the formation of new populations with good prospects to be used in breeding programs with high potential variability available for selection, aiming at developing varieties with wide adaptation in different cultivation conditions in this region.

4. Conclusions

The non-additive genetic effects are more important for the grain chemical quality characteristics, percentage of total soluble sugars, percentage of starch and ratio between sugars and starch in grains.

Varieties 2255A and 2276A have a higher concentration of favorable alleles for increasing the chemical quality of grains. The intervarietal hybrids F1's 2255A x 319A, 2255A x 2029A, 2255A x 2276A, Cubano x 2276A, 2276A x 2029A and 2255A x 741B stood out for interpopulation selection schemes.

The biparental compounds derived from the combinations 2255A x 319A and 2255A x 2276A, the triple compounds 2255A x 2276A x 2029A, and the quadruple compounds 2255A x 741B x 2276A x 319A and 2255A x 2276A x 2029A x 319A are the most suitable for the formation of composite populations followed by recurrent selection, aiming to increase the concentration of sugars in the grains.

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