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Performance of double-haploid tropical super sweet corn lines in a partial diallel

Desempenho de linhagens duplo-haploides de milho superdoce tropical em dialelo parcial

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Highlights

The commercial checks were outperformed by 38% of the diallel hybrids.
Two DH lines from the SD3005 population hold potential for use as new testers.
Useful phenotypic correlations to guide selection were observed.
The additive and dominant parts were important for most traits.

Abstract

Brazilian super sweet corn production is predominantly directed toward the canning industry, which demands high yields, uniformity, and production quality, characteristics provided by hybrid cultivars derived from inbred lines. Double-haploid (DH) technology is being employed to reduce the production time for completely homozygous lines and to enhance the exploitation of heterosis in hybrid combinations for common corn. However, its application remains underexplored in super sweet corn. The objectives of this study were to evaluate the potential of DH super sweet corn lines in hybrid synthesis, identify elite DH lines for use as testers in top crosses, and determine the predominant type of gene action for key traits in super sweet corn breeding, along with their correlations. Twenty-nine combinations of DH lines derived from four super sweet populations and six checks were evaluated at the School Farm/UEL during the 2019/2020 and 2020/2021 harvest seasons using a randomized block design with three replicates. The following traits were evaluated: husked and dehusked ear yields, grain yield, plant and ear

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heights, ear length and diameter, number of grain rows per ear, agronomic performance, and Brix degree. Significant differences were observed between harvest seasons for all traits, with the 2020/2021 harvest season yielding superior results. Treatment × Harvest Season interactions were significant only for ear diameter and agronomic performance. On average, across both harvest seasons, 38% of the diallel hybrids outperformed the commercial checks, which were grouped with the average performance of the remaining hybrids. Lines L_1 and L_5 showed the highest general combining ability (GCA) estimates for husked and dehusked ear and grain yields, with values of 2244 and 2627; 1260 and 1388; and 811 and 1000 kg ha^{-1}, respectively, making them candidates for use as testers in future studies. Among the most productive hybrids, the highest specific combining ability (SCA) estimates for husked and dehusked ear and grain yields were observed in hybrids H_{A5}, H_{B2}, and H_{C12}, with values ranging from 4685 to 1947, 2829 to 1329, and 1680 to 1095 kg ha^{-1}, respectively. Both additive and non-additive gene actions were found to be important for most of the evaluated traits. Dehusked ear yield exhibited the strongest correlation with grain yield, suggesting its potential use as a selection criterion for identifying more productive genotypes suitable for canned corn production.

Key words: Combining ability. Elite lines. Breeding. *Zea mays* L. var. saccharata.

Resumo

A produção de milho superdoce brasileira é preponderantemente destinada as indústrias de conservas, que necessitam de elevada produtividade, uniformidade e qualidade de produção, oferecidas pelas cultivares híbridas de linhagens. A tecnologia duplo-haploide (DH) está sendo utilizada para reduzir o tempo de produção de linhagens completamente homozigotas e melhor explorar a heterose em combinações híbridas em milho comum, mas ainda pouco estudada em milho superdoce. Os objetivos foram determinar o potencial de linhagens DHs de milho superdoce na síntese de híbridos; identificar linhagens DHs elites para uso como testadoras em cruzamento top crosses; determinar o tipo predominante de ação gênica para características importantes no melhoramento de milho superdoce e suas correlações. As 29 combinações entre linhagens DHs de quatro populações superdoce e seis testemunhas foram avaliadas na Fazenda Escola/UEL, durante as safras 2019/2020 e 2020/2021, empregando o delineamento de blocos casualizados, com 3 repetições. As características avaliadas foram: produtividades de espigas com e sem palha, produtividadede grãos; alturas de plantas e de espigas; comprimento e diâmetro de espigas; número de fileiras de grãos nas espigas; padrão agronômico e grau Brix. Houve efeito significativo de safras todas as características, sendo a safra 2020/2021 a melhor para produtividade. A interação tratamento x safra foi observada apenas para diâmetro de espiga e padrão agronômico. Na média das duas safras, 38% dos híbridos do dialelo foram superiores em relação às testemunhas comerciais, que ficaram agrupadas junto à média do restante dos híbridos avaliados. As linhagens L_1 e L_5 apresentaram as maiores estimativas de capacidade geral de combinação para as características de produtividades de espigas com palha, sem palha e de grãos, com valores iguais a 2244 e 2627; 1260 e 1388; 811 e 1000 kg ha^{-1}, respectivamente, sendo candidatas para uso como testadoras em trabalhos futuros. Entre os híbridos mais produtivos, as maiores estimativas de capacidade específica para produtividades de espigas com palha, sem palha e de grãos foram observadas para os híbridos H_{A5}, H_{B2} e H_{C12}, com valores entre 4685 e 1947, 2829 e 1329, 1680 e 1095 kg ha^{-1}, respectivamente. Foi verificado que as ações gênicas aditivas e não aditivas foram importantes para a maioria das características avaliadas. A característica produtividade de espigas sem palha é a que mais se correlaciona com produtividade de grãos, podendo ser utilizada para a seleção de genótipos mais produtivos para a produção de milho em conserva.

Palavras-chave: Capacidade de combinação. Linhagens elites. Melhoramento genético. *Zea mays* L. var. saccharata.

Introduction

Super sweet corn (*Zea mays* L. var. saccharata) is a specialized type of corn characterized by grains with a higher sugar concentration than common corn at the milk stage. Recessive homozygosity for the brittle (*bt1* and *bt2*) or shrunken (*sh1* and *sh2*) genes results in super sweet corn (15% to 25% sugars), whereas the sugary (*su*) gene produces sweet corn (9% to 14% sugars) (Teixeira et al., 2013).

The United States of America is the leading producer of super sweet corn, which is the second most commonly used crop in industrial processing in the country, surpassed only by tomatoes. In the 2021 harvest, super sweet corn generated $774 million in revenue, with 75% of the production destined for fresh consumption and 25% used for processing (Agricultural Marketing Resource Center [AGMRC], 2022).

In Brazil, limited information exists regarding the importance of sweet or super sweet corn. Nearly all production is allocated to the canning industry, which generated approximately R$1.44 billion in 2016 (Instituto Brasileiro de Geografia e Estatística [IBGE], 2016). Generally, the Brazilian population and farmers are unaware of the differences between regular and super sweet green corn, despite their frequent consumption of canned corn.

The industries responsible for processing super sweet corn require cultivars with uniform ripening as well as consistent ear size and shape. Therefore, hybrid cultivars are best suited to meet industrial demands (Kwiatkowski & Clemente, 2007; Luz et al., 2014). However, regarding the breeding and development of new cultivars, only 127 sweet corn cultivars and 10 super sweet corn cultivars were registered by 2024, compared to 5,937 cultivars registered for common corn (Ministério da Agricultura, Pecuária e Abastecimento [MAPA], 2024).

The first step in developing new hybrid cultivars is obtaining homozygous lines. DH technology is widely used in common corn as it enables the production of 100% homozygous lines in two to three generations, making it more efficient than conventional methods, which require six to seven cycles of manual self-pollination and still do not achieve complete homozygosity. The production of DH lines involves the following steps: haploidy induction, identification of haploid seeds or seedlings, chromosome duplication, self-pollination of fertile plants to produce DH lines, and seed multiplication (Chaikam et al., 2019; Khulbe & Pattanayak, 2021).

There are limited studies in the literature on the production of DH lines in sweet and super sweet corn (Zhang et al., 2008; Khulbe & Pattanayak, 2021; Sekiya et al., 2020), as well as on the performance of these lines in hybrid combinations, diallels, and top crosses. Existing research highlights greater difficulty obtaining putative haploid seeds from sweet corn genotypes compared to common corn (Trentin et al., 2022). The *R1-nj* gene, present in haploidy inducers, is responsible for the selection of haploid seeds by inducing anthocyanin expression in the endosperm and embryo of diploid seeds, resulting in a purple endosperm. However, Tracy (2001) reported that the presence of the *C1-I* allele is common in sweet corn genotypes, which inhibits anthocyanin synthesis in the seed aleurone. This inhibition makes it impossible to select haploid seeds in these genotypes when they are used as donor populations in crosses with haploidy-inducing lines.

Through DH technology, breeding programs can generate large numbers of lines. However, these lines must demonstrate their value both individually and in crosses to be classified as elite. The individual value of the lines is important for seed production, while their value in crosses is essential for identifying superior hybrid combinations. Top cross and diallel crossing schemes are employed to select elite lines and the best hybrid combinations. These approaches are also useful for inferring the types of gene action controlling traits of interest and for defining the populations to be used as basic germplasm in breeding programs (Carena et al., 2010; Kwiatkowski et al., 2011; Senhorinho et al., 2015; Xavier et al., 2019).

Diallel and top crosses use the concepts of general combining ability (GCA) and specific combining ability (SCA) introduced by Sprague and Tatum (1942). The GCA of a given line represents the deviation of the average performance of the hybrids in which it participates in relation to the overall mean of the hybrids evaluated in the diallel or top crosses. The SCA represents the part of the hybrid performance resulting from the specific crossing of two lines, which cannot be explained by the sum of the effects of the overall mean and the GCAs of each line. Higher magnitudes of mean squares and GCA estimates indicate the predominance of additive genetic effects and the frequency of favorable alleles in the genotypes. On the other hand, the SCA is associated with non-additive effects. Superior hybrids are expected to show high SCA and GCA estimates for at least one of the parental lines (Cruz, 2006).

The objectives of this study were to evaluate the potential of super sweet corn DH lines for synthesizing hybrids with high agronomic performance through GCA and SCA estimates in a partial diallel; to identify elite DH lines suitable as testers in top cross schemes; and to determine the predominant type of gene action governing key traits in super sweet corn breeding, along with their correlations.

Material and Methods

The doubled-haploid lines used in this study were obtained from four synthetic populations of super sweet corn (SD3006, SD3004, SD3005, and SD3007) developed by the Plant Breeding Laboratory (LMG) of the Department of General Biology at the State University of Londrina (UEL).

The populations were pollinated with the inducing genotype PI4003, belonging to LMG, which carries the *R1-nj* gene responsible for expressing purple pigmentation in the embryo and endosperm. The F_1 seeds resulting from these crosses were classified based on the expression of the *R1-nj* gene, with seeds exhibiting purple pigmentation in both the endosperm and embryo considered diploids, while those with purple pigmentation only in the endosperm were classified as putative haploids.

Putative haploid seeds were sown in trays filled with sphagnum peat and kept in a greenhouse for germination. Once the seedlings reached the V2 stage, those clearly identified as diploids were removed based on their greater vigor and the purple pigmentation of the first leaf sheath, which distinguishes them from haploid seedlings (Sekiya et al., 2020).

The haploid seedlings were treated by injecting 100 µL of a 0.125% colchicine and 0.5% dimethyl sulfoxide (DMSO) solution into the meristematic region of the stem, 0.6 to 1.2 cm above the substrate, to induce chromosome duplication and restore fertility, following the method proposed by Eder and Chalyk (2002). The treated seedlings were transplanted to the field to complete their growth cycle and were self-pollinated to produce doubled-haploid lines.

Resulting lines were multiplied through self-pollination and phenotypically selected based on individual agronomic potential. The selected lines were then crossed using an incomplete partial diallel scheme. This involved crossing a tester line from each of the populations SD3004, SD3006, and SD3007 with 12 lines from population SD3005 (Table 1), based on prior knowledge of heterotic groups, as described by Oliveira (2018).

The hybrid combinations were obtained at the UEL School Farm (FAZESC), Paraná, Brazil (23°20’32” S, 51°12’34” W, 550 m above sea level), on eutroferric Red Latosol soil. The lines were arranged in side-by-side rows measuring 4.00 m in length, with a spacing of 0.80 × 0.20 m.

The 29 diallel hybrids and six checks (commercial hybrids AF505 and Thunder, along with four experimental hybrids developed by LMG) were evaluated at FAZESC, following technical recommendations for corn cultivation. The experiments were conducted using a randomized block design with three replicates, in single-row plots measuring 4.00 m, with a spacing of 0.80 × 0.20 m, during the 2019/2020 and 2020/2021 harvest seasons. The first experiment was sown on 11/17/2019, and the second on 09/27/2020.

In both experiments, the following traits were evaluated: a) Stand (ST): the number of plants present in each plot; b) Plant height (PH, in cm): measured from the soil surface to the insertion of the flag leaf; c) Ear height (EH, in cm): measured from the soil surface to the insertion of the ear; d) Agronomic performance (AP): visual performance of the genotypes, graded from 1 (low) to 10 (excellent); e) Husked ear yield (HEY, in g $plot^{-1}$); f) Dehusked ear yield (DEY, in g $plot^{-1}$); g) Ear length (EL, in cm); h) Ear diameter (ED, in cm); i) Number of grain rows per ear (NR); j) Grain yield (GY, in g $plot^{-1}$); k) Soluble solids content (BRIX, in %). Evaluations of ears and yield traits were performed at the milk stage. The averages of PH and EH were calculated based on observations of three representative plants per plot. The averages of EL, ED, and NR were calculated based on observations of five representative ears per plot.

Table 1
Partial diallel crossing scheme between two groups of DH lines (L) obtained from four super sweet corn populations and the hybrid checks

Genotype tested		SD3004(D17) -2	SD3006(D17) -2	SD3007(D17)
		LT-A	LT-B	LT-C
SD3005(D16)-2	L1	---	HSE$_{B1}$	HSE$_{C1}$
SD3005(D16)-8	L2	HSE$_{A2}$	HSE$_{B2}$	HSE$_{C2}$
SD3005(D16)-9	L3	HSE$_{A3}$	HSE$_{B3}$	---
SD3005(D16)-10	L4	HSE$_{A4}$	---	HSE$_{C4}$
SD3005(D17)-3	L5	HSE$_{A5}$	---	HSE$_{C5}$
SD3005(D17)-9	L6	HSE$_{A6}$	HSE$_{B6}$	HSE$_{C6}$
SD3005(D17)-11	L7	HSE$_{A7}$	HSE$_{B7}$	HSE$_{C7}$
SD3005(D17)-13	L8	HSE$_{A8}$	HSE$_{B8}$	HSE$_{C8}$
SD3005(D16)-3	L9	HSE$_{A9}$	---	HSE$_{C9}$
SD3005(D16)-7	L10	HSE$_{A10}$	---	HSE$_{C10}$
SD3005(D17)-2	L11	---	HSE$_{B11}$	HSE$_{C11}$
SD3005(D17)-10	L12	HSE$_{A12}$	HSE$_{B12}$	HSE$_{C12}$
Checks				
Tester 1	AF505 (SAKATA SEED SUDAMERICA LTDA)			
Tester 2	Thunder (SYNGENTA SEEDS LTDA)			
Tester 3	H$_{AB}$ (LMG)			
Tester 4	H$_{BC}$ (LMG)			
Tester 5	H$_{C14}$ (LMG)			
Tester 6	H$_{A13}$ (LMG)			

The yield traits HEY, DEY, and GY were adjusted to an ideal stand of 20 plants per plot, following the methodology of Vencovsky and Barriga (1992), and extrapolated to kg per hectare (kg ha^{-1}) for an ideal stand of 62,500 plants ha^{-1}. Based on these data, the HEY/DEY, GY/DEY, and EH/PH (RPE) ratios were calculated to indicate the proportion of husk and cob weight contributing to yield and the position of the ear in relation to the plant, respectively.

Analyses of variance were performed using the Statistical Analysis System, while the Scott-Knott mean test was conducted using the GENES program. Based on the treatment means, Pearson correlations were estimated between HEY, DEY, GY, and the other agronomic traits, using the t-test at a 5% significance level.

The treatment effects from the analysis of variance were decomposed into the effects of diallel hybrids, checks, and the contrast between diallel hybrids and checks. The degrees of freedom for diallel hybrids were further broken down through partial diallel analysis into the effects of general combining ability for tester lines (GCA-T) and tested lines (GCA-L), as well as specific combining ability (SCA). The statistical model adopted was based on Griffing (1956), adapted for partial diallel crosses involving only F$_1$ generations, expressed as: $Y_{ij} = m + \hat{g}_i + \hat{g}_j + \hat{s}_{ij} + e_{ij}$, where Y_{ij} =

mean value of the hybrid combination between tester line i and tested line j; m = overall mean of the experimental hybrids; $\hat{g}_i$ = effect of the general combining ability of tester line i; $\hat{g}_j$ = effect of the general combining ability of tested line j; $\hat{s}_{ij}$ = effect of the specific combining ability between parents i and j; and e_{ij} = mean experimental error.

The effects of general and specific combining abilities, as well as their sums of squares, were estimated using the least squares method with the equations X'Xβ = X'Y, derived from the linear model Y = Xβ + ε , where Y is the vector of observed mean data (experimental hybrids); X is the matrix of constants (values of 0 and 1) related to the parameters m, $\hat{g}_i$, $\hat{g}_j$, and $\hat{s}_{ij}$; β is the vector of these parameters; and ε is the vector of errors associated with the means (e_{ij}) (Cruz, 2006).

Results and Discussion

Typically, super sweet corn genotypes are homozygous recessive for the *sh2* and *a1* genes, which prevents the expression of anthocyanin in plant tissues (Tracy, 2001). The *A1* allele is part of the structural genes involved in anthocyanin biosynthesis (Trentin et al., 2020). Thus, the absence of anthocyanin expression in the first leaf sheath of seedlings originating from F_1 seeds resulting from crosses between donor populations and homozygous inducers for the *R1-nj* gene confirms that they are haploid. This is because these seedlings carry only the genome of the super sweet donor population, which does not express purple anthocyanin in the first leaf sheath (Sekiya et al., 2020). On the other hand, diploid F_1 seedlings express the purple pigment in the first leaf sheath, indicating the presence of inducer chromosomes containing the *R1-nj* and *A1* genes. All donor populations used in this study lack genes that inhibit the expression of the *R1-nj* gene in seeds and have a green first leaf sheath, facilitating the selection of haploids and the production of DHs.

The experimental coefficients of variation ranged from 2.5% to 18.6% (Table 2), similar to values reported in the literature for the same traits in super sweet corn evaluated in this study, indicating appropriate experimental precision (Xavier et al., 2019; Gava et al., 2021).

Significant effects of the mean squares for harvest seasons were observed across all traits. In the 2020/2021 harvest season experiment, increases of 30.6%, 22.1%, and 9.3% were recorded for HEY, DEY, and GY, respectively, along with better performance for most evaluated traits compared to the 2019/2020 harvest season experiment. Slightly higher means were observed only for BRIX degree and AP in the 2019/2020 harvest season. These findings indicate that differences in harvest seasons and sowing times resulted in significant environmental variations for treatment evaluations. However, no interaction between treatments and environments was detected for yield and most evaluated traits, except for ED and AP.

Analysis of variance revealed that the treatments and diallel hybrids did not exhibit uniform performance across all evaluated traits. The checks showed no significant effect for the variables DEY, GY, GY/DEY, ED, BRIX, or AP. Using the Scott-Knott clustering test, it was observed that the hybrid checks developed by LMG-UEL had higher yields (HEY, DEY, and GY) compared to the commercial checks Thunder and AF505. Among these, the H_{BC} hybrid demonstrated the highest average husked and dehusked ear yields, at 26,725 kg ha^{-1} and 16,926 kg ha^{-1}, respectively (Table 3).

Table 2

Analysis of variance with respective degrees of freedom (DF), mean squares, F-test significance levels, and coefficients of variation (CV) for different agronomic traits and their correlations with yield, assessed over two harvest seasons (2019/2020 and 2020/2021). UEL, Londrina

SV	DF	HEY	DEY	GY	DEY/HEYτ	GY/DEYτ	NR	ED	EL	BRIX	AP	RPEτ	MAL	FEM
	Mean square													
Harvest	1	1722689275*	405749048*	16740926*	130.97*	92.322*	33.002*	1.5198*	62.582*	254.59*	10.965*	16.528*	691.52*	494.75*
Treatment	34	39924566*	17194523*	6954509*	3.3602*	10.4470*	19.556*	0.3091*	15.049*	3.1325*	2.5471*	3.5917*	31.357*	18.099*
Checks	5	24532456*	8257873^{ns}	2016173^{ns}	2.9880*	2.5663^{ns}	13.223*	0.0956^{ns}	2.6480*	1.204^{ns}	1.477^{ns}	5.4823*	14.237*	17.753*
Diallel	28	35930819*	15678797*	6442845*	2.7736*	9.8596*	17.200*	0.2535*	15.304*	3.0312*	2.4312*	2.4631*	30.679*	15.584*
GCA -T	2	88666568*	55759309*	13910969*	4.6305*	5.8691*	77.080*	0.0720^{ns}	153.81*	10.116*	8.7603*	10.127*	314.21*	106.42*
GCA-L	11	27893634*	10827170*	6434496*	4.5685*	15.977*	23.344*	0.4163*	9.6596*	4.4878*	1.069^{ns}	2.5714*	8.9515*	8.4285*
SCA	15	34793321*	13892588*	5453218*	1.209^{ns}	5.9059*	4.7103*	0.1582*	0.9767*	1.018^{ns}	2.5857*	1.3618^{ns}	8.8084*	8.7193*
Diallel vs Check	1	12909936^{ns}	11867778^{ns}	12656898*	4.0168*	28.317*	40.509*	1.3824*	10.043*	2.134^{ns}	2.669^{ns}	0.0545^{ns}	44.831*	11.11^{ns}
Treat. x Harvest	34	11251884^{ns}	5807049^{ns}	1870164^{ns}	1.173^{ns}	1.932^{ns}	0.544^{ns}	0.0723*	0.309^{ns}	1.526^{ns}	1.2503*	1.3864^{ns}	2.794^{ns}	4.370^{ns}
Error	134	8818419	4125249	1411933	0.9365	1.3562	0.5678	0.0450	0.4107	1.3610	0.7794	0.9765	2.6639	4.1381
2019/20		18558	12700	6112	0.69	0.47	17.2	5.1	17.6	16.9	7.3	0.57	63.0	64.1
2020/21		24329	15501	6681	0.64	0.43	18.0	5.0	18.7	14.7	6.8	0.55	66.6	67.2
Mean		21430	14090	6386	0.66	0.45	17.6	5.0	18.1	15.8	7.0	0.56	64.8	65.6
CV%		13.9	14.4	18.6	4.6	8.2	4.3	4.2	3.5	7.4	12.6	5.6	2.5	3.1
	Correlations													
HEY		1.00*	0.96*	0.81*	-0.14^{ns}	0.30^{ns}	0.08^{ns}	0.42*	0.62*	-0.50*	0.66*	-0.38*	-0.26ns	-0.17ns
DEY		0.96*	1.00*	0.90*	0.13^{ns}	0.45*	0.08^{ns}	0.54*	0.61*	-0.49*	0.73*	-0.38*	-0.35*	-0.28ns
GY		0.81*	0.90*	1.00*	0.35*	0.78*	0.21^{ns}	0.80*	0.45*	-0.49*	0.71*	-0.37*	-0.40*	-0.40*

^{ns} and *: not significant and significant at the 5% probability level, respectively. τ = mean squares multiplied by 10^{-3}. SV = source of variation; HEY = husked ear yield (kg ha^{-1}); DEY = dehusked ear yield (kg ha^{-1}); GY = grain yield (kg ha^{-1}); DEY/HEY = ratio between DEY and HEY; GY/DEY = ratio between GY and DEY; NR = number of rows; ED = ear diameter (cm); EL = ear length (cm); BRIX = soluble solids content; AP = visual assessment of agronomic performance (1 = low and 10 = excellent); RPE = relative position of the ear; MAL = days to male flowering; FEM = days to female flowering.

Table 3

Means of different performance-related agronomic traits of experimental single-cross hybrids (H_{ij}) and chekcs, evaluated over two harvest seasons (2019/2020 and 2020/2021). UEL, Londrina

H_{ij}	HEY	DEY	GY	DEY/HEY	GY/DEY	NR	ED	EL	BRIX	AP	RPE	MAL	FEM
H_{C12}	27319^a	18045^a	8330^a	0.67^a	0.46^a	16.9^c	5.1^b	21.2^a	15.5^a	8.2^a	0.57^a	61.7^c	64.2^b
H_{BC}	26725^a	16926^a	7667^a	0.64^a	0.46^a	20.5^a	5.3^a	19.8^b	15.0^a	7.3^a	0.49^a	64.2^c	65.5^a
H_{A5}	25135^a	16091^a	8084^a	0.64^a	0.50^a	21.2^a	5.4^a	18.3^d	15.3^a	7.7^a	0.54^a	65.2^c	65.8^a
H_{C1}	24961^a	16302^a	8064^a	0.66^a	0.50^a	16.1^d	5.3^a	20.8^a	15.1^a	7.7^a	0.55^a	62.7^c	63.8^b
H_{C9}	24614^a	15643^a	6624^a	0.63^a	0.42^b	16.1^d	4.9^b	20.4^b	15.9^a	8.0^a	0.52^a	62.5^c	65.7^a
H_{B2}	24503^a	15146^a	7225^a	0.62^a	0.48^a	17.7^c	5.2^a	16.7^e	15.5^a	7.0^a	0.54^a	66.3^b	65.8^a
H_{C4}	24432^a	16176^a	6940^a	0.67^a	0.43^b	13.9^e	5.0^b	19.3^c	13.8^a	7.2^a	0.55^a	63.7^c	65.2^b
H_{C5}	23396^a	15105^a	6658^a	0.64^a	0.43^b	16.8^c	5.1^b	21.1^a	14.4^a	7.2^a	0.53^a	67.0^b	67.0^a
H_{AB}	22860^a	15250^a	7468^a	0.67^a	0.49^a	22.0^a	5.5^a	17.8^e	15.1^a	8.3^a	0.57^a	65.4^c	66.0^a
H_{C6}	22820^a	15572^a	7658^a	0.68^a	0.51^a	16.5^c	5.1^b	19.4^c	15.6^a	7.7^a	0.57^a	63.3^c	64.0^b
H_{B1}	22793^a	14543^a	6111^b	0.63^a	0.39^b	17.4^c	4.8^b	17.4^e	16.2^a	6.2^a	0.58^a	69.3^a	68.3^a
H_{C8}	22341^a	15831^a	7643^a	0.72^a	0.48^a	17.4^c	5.4^a	19.3^c	15.9^a	7.0^a	0.54^a	63.2^c	63.8^b
H_{C14}	22298^a	16033^a	8218^a	0.72^a	0.52^a	18.6^b	5.5^a	18.5^d	16.1^a	8.2^a	0.53^a	62.2^c	62.8^b
H_{A13}	22226^a	14667^a	7225^a	0.66^a	0.50^a	19.3^b	5.4^a	18.3^d	16.2^a	7.0^a	0.55^a	64.7^c	66.3^a
H_{A7}	22145^a	14585^a	6378^b	0.66^a	0.43^b	17.5^c	4.9^b	16.8^e	16.5^a	7.2^a	0.55^a	63.0^c	63.3^b
H_{C11}	21388^b	14303^a	6227^b	0.67^a	0.43^b	16.7^c	5.0^b	19.1^c	16.4^a	7.5^a	0.56^a	64.2^c	65.2^b
AF505	21367^b	13977^b	6134^b	0.66^a	0.44^b	17.4^c	5.0^b	20.1^b	15.9^a	7.0^a	0.62^a	64.3^c	67.7^a
H_{A4}	21317^b	14170^a	6547^b	0.67^a	0.46^a	16.8^c	5.0^b	16.9^e	15.3^a	6.7^a	0.56^a	65.0^c	65.7^a
H_{C10}	21060^b	14270^a	6418^b	0.69^a	0.45^a	14.4^e	5.0^b	18.2^d	15.1^a	7.5^a	0.52^a	62.5^c	63.2^b
H_{B6}	20908^b	13922^b	6394^b	0.67^a	0.46^a	18.8^b	5.1^b	15.7f	16.4^a	7.0^a	0.58^a	68.8^a	69.2^a
H_{A12}	20247^b	13067^b	5429^b	0.65^a	0.41^b	19.9^b	4.8^b	18.1^d	16.4^a	7.2^a	0.58^a	64.3^c	67.0^a
H_{A6}	20132^b	13830^b	6865^a	0.69^a	0.50^a	18.9^b	5.3^a	16.1^f	16.7^a	7.0^a	0.59^a	64.3^c	66.0^a
H_{A8}	19937^b	12838^b	6087^b	0.65^a	0.48^a	19.3^b	5.2^a	16.6^e	16.1^a	6.8^a	0.56^a	63.3^c	64.0^b
H_{B11}	19930^b	13093^b	5736^b	0.66^a	0.43^b	19.5^b	5.1^b	16.3^f	16.4^a	7.3^a	0.55^a	68.3^a	67.2^a
H_{C7}	19822^b	12951^b	5249^b	0.66^a	0.40^b	16.9^c	4.8^b	19.1^c	16.1^a	6.8^a	0.55^a	63.7^c	65.0^b
H_{A9}	19711^b	12410^b	4449^b	0.64^a	0.34^b	16.1^d	4.5^b	18.6^d	17.1^a	6.0^a	0.59^a	66.2^b	67.7^a
H_{A3}	19205^b	12256^b	4825^b	0.64^a	0.38^b	17.5^c	4.8^b	17.8^e	15.4^a	6.7^a	0.60^a	64.0^c	66.0^a
H_{C2}	19178^b	12407^b	5561^b	0.65^a	0.44^b	15.4^d	5.0^b	19.0^c	15.7^a	6.2^a	0.54^a	63.7^c	65.0^b
H_{A10}	19099^b	12448^b	5722^b	0.66^a	0.46^a	15.9^d	5.0^b	16.7^e	15.7^a	6.8^a	0.57^a	65.3^c	65.3^b
H_{B3}	19002^b	12208^b	4789^b	0.64^a	0.39^b	15.8^d	4.8^b	16.8^e	16.7^a	7.2^a	0.55^a	65.8^b	65.5^a
H_{B12}	18638^b	12262^b	5524^b	0.65^a	0.41^b	18.5^b	4.8^b	17.2^e	16.3^a	5.5^a	0.56^a	68.2^a	67.8^a
H_{B7}	18105^b	11635^b	4659^b	0.64^a	0.39^b	18.9^b	4.9^b	16.1^f	16.6^a	5.7^a	0.56^a	68.8^a	66.8^a
Thunder	17810^b	12185^b	6248^b	0.70^a	0.50^a	16.1^d	5.2^a	18.2^d	14.7^a	6.5^a	0.57^a	59.5^c	61.2^b
H_{B8}	17686^b	12115^b	5729^b	0.69^a	0.47^a	19.8^b	5.1^b	15.3^f	16.4^a	6.5^a	0.54^a	68.5^a	68.2^a
H_{A2}	17412^b	11259^b	4992^b	0.65^a	0.44^b	15.9^d	4.9^b	17.0^e	16.5^a	6.5^a	0.57^a	65.2^c	66.2^a

Means followed by the same letters belong to the same group according to the Scott-Knott test, at a 5% probability level. HEY = husked ear yield (kg ha^{-1}); DEY = dehusked ear yield (kg ha^{-1}); GY = grain yield (kg ha^{-1}); DEY/HEY = ratio between DEY and HEY; GY/DEY = ratio between GY and DEY; NR = number of rows; ED = ear diameter (cm); EL = ear length (cm); BRIX = soluble solids content; AP = visual assessment of agronomic performance (1 = low and 10 = excellent); RPE = relative position of the ear; MAL = days to male flowering; FEM = days to female flowering.

In the contrast between Diallel and Checks, the means of the two hybrid groups did not differ significantly for the traits HEY, DEY, BRIX, AP, RPE, and FEM. However, through the clustering of means using the Scott-Knott test, approximately 38% of the hybrids in the diallel were found in the best-performing group for HEY, DEY, and GY, along with the four LMG checks. The remaining diallel hybrids were grouped with the commercial checks AF505 and Thunder for these traits. This result indicates that the diallel hybrids developed from DH lines exhibit high performance and are competitive with commercial checks.

The diallel hybrids with the best performance for yield and other evaluated traits were H_{C12}, H_{A5}, H_{C1}, H_{C9}, H_{B2}, H_{C4}, H_{C5}, H_{C6}, and H_{C8}, with HEY values ranging from 22,341 to 27,319 kg ha⁻¹, DEY from 15,105 to 18,045 kg ha⁻¹, and GY from 6,624 to 8,330 kg ha⁻¹. With the exception of H_{A2}, the other hybrids met the standards required by the super sweet corn processing industries, as cited by Pereira et al. (2002) and Souza et al. (2013). These standards include dehusked ear yield exceeding 12,000 kg ha⁻¹, a minimum of 14 rows of grains per ear, and ear length and diameter greater than 15 cm and 3 cm, respectively. In the literature, husked ear yields of up to 24.38 t ha⁻¹ (Luz et al., 2014), 25.72 t ha⁻¹ (Xavier et al., 2019), and 23.9 t ha⁻¹ (Gava et al., 2021) are reported, with grain yields of up to 7.40 t ha⁻¹ (Xavier et al., 2019) and 8.13 t ha⁻¹ (Gava et al., 2021). These values are slightly lower than those observed in this study.

Based on the performance of the evaluated experimental hybrids, it is possible to estimate 177 triple hybrids (HT) and 72 double hybrids (HD) using the average prediction method presented by Vencovsky (1987). Hybrids $HT_{(C)(1\ \ 12)}$, $HT_{(C)(4\ \ 12)}$, $HT_{(C)(6\ \ 12)}$, $HT_{(C)(8\ \ 12)}$, and $HT_{(C)(12\ \ 14)}$ stood out, with estimates ranging from 24,809 to 26,140 kg ha⁻¹ for HEY, 16,575 to 17,174 kg ha⁻¹ for DEY, and 7,635 to 8,274 kg ha⁻¹ for GY. Hybrid $HD_{(AC)(45)}$ was also prominent, showing means of 23,570, 15,386, and 7,057 kg ha⁻¹ for HEY, DEY, and GY, respectively. The mean estimates of these HTs and HDs fall within the group of superior single-cross hybrids for yield, as determined by the Scott-Knott test. In super sweet corn, the identification of triple and double hybrids with high performance is particularly important, as single-cross hybrids, which are generated by crossing two lines, naturally produce smaller seeds. Moreover, since super sweet corn cultivars are homozygous for genes that limit starch production in the endosperm, they have fewer reserves to ensure good germination and plant stand.

The traits HEY, DEY, and GY showed a strong positive correlation with each other, with estimates ranging from 0.81 to 0.96 (Table 2). These results are consistent with those obtained by Xavier et al. (2019) and emphasize the importance of at least dehusking the ears for yield assessment to improve super sweet corn genotypes intended for the green corn grain canning industry. Additionally, a positive association was observed between GY and the traits GY/DEY, ED, EL, and AP, which can be used for indirect selection of super sweet corn grain yield. On the other hand, similar to the findings of Xavier et al. (2019), the traits DEY/HEY, NR, days to male flowering (MAL), and FEM did not show significant correlations with yield. Significant negative correlations were observed between BRIX and yield traits, with estimates ranging from -0.49 to -0.50, indicating that higher BRIX values were associated with lower productivity. This differs from the results of Xavier et al. (2019), who did not observe a significant correlation for soluble solids content.

The GCA effects for tester and tested lines, as well as SCA, were significant for most traits, except for ED in GCA-T, AP in GCA-L, and DEY/HEY, BRIX, and RPE in SCA. These significant effects for husked and dehusked ear yields, grain yield, and ear length align with the findings of Lemos et al. (2002), Solomon et al. (2012), Elayaraja et al. (2014), and Xavier et al. (2019), demonstrating that both additive and dominant gene actions are important for the expression of these traits. However, in the study by Solomon et al. (2012), the ear diameter trait exhibited only additive gene action, and no GCA or SCA effects were detected for BRIX, differing from the findings of this study and the other cited works.

Among the tester lines, LT-C exhibited the highest GCA ($\hat{g}_i$) estimates for yield components and also stood out for EL, increasing ear length by an average of 1.89 cm in the crosses in which it participated (Table 4). The importance of LT-C's GCA can be highlighted by its involvement in seven of the nine hybrids identified as superior for yield. This performance indicates that the SD3007 population belongs to a heterotic group more genetically distant from the SD3005 population compared to the populations that produced the other testers, corroborating the findings of Oliveira (2018). These results are valuable for guiding future crosses within the super sweet corn breeding program.

Table 4

Estimates of the mean (m) general combining ability of three tester ($\hat{g}_i$) and 12 tested ($\hat{g}_j$) lines, specific combining ability ($\hat{s}_{ij}$), and standard deviations (SD) for different agronomic traits, based on the average of two harvest seasons (2019/2020 and 2020/2021). UEL, Londrina

Estimate	HEY	DEY	GY	DEY/ HEY	GY/ DEY	NR	ED	EL	BRIX	AP	RPE	MAL	FEM
m	21275	13900	6181	0.66	0.44	17.32	4.99	17.85	15.87	6.93	0.56	65.4	66.0
$\hat{g}_A$	-714	-526	-192	0.00	0.00	0.66	-0.02	-0.53	0.28	-0.04	0.02	-0.8	-0.3
$\hat{g}_B$	-726	-621	-381	-0.01	-0.01	0.69	-0.02	-1.36	0.20	-0.39	-0.01	2.9	1.6
$\hat{g}_C$	1441	1146	572	0.01	0.01	-1.34	0.04	1.89	-0.48	0.43	-0.01	-2.1	-1.3
$\hat{g}_1$	2244	1260	811	-0.01	0.01	-0.23	0.03	0.95	-0.11	-0.04	0.01	0.2	0.0
$\hat{g}_2$	-911	-963	-255	-0.01	0.02	-0.99	0.04	-0.30	0.01	-0.38	-0.01	-0.4	-0.3
$\hat{g}_3$	-1452	-1095	-1087	-0.01	-0.05	-1.36	-0.20	0.39	-0.07	0.20	0.01	-1.6	-0.9
$\hat{g}_4$	1236	963	372	0.01	0.00	-1.61	-0.01	-0.45	-1.22	-0.21	0.00	0.4	0.2
$\hat{g}_5$	2627	1388	1000	-0.02	0.02	2.02	0.28	1.18	-0.97	0.29	-0.03	2.1	1.2
$\hat{g}_6$	12	541	791	0.02	0.05	0.74	0.17	-0.80	0.36	0.29	0.02	0.1	0.4
$\hat{g}_7$	-1251	-844	-752	0.00	-0.03	0.43	-0.15	-0.55	0.53	-0.38	-0.01	-0.3	-0.9
$\hat{g}_8$	-1287	-306	305	0.03	0.04	1.52	0.23	-0.76	0.24	-0.16	-0.01	-0.4	-0.7
$\hat{g}_9$	524	-184	-835	-0.03	-0.06	-0.88	-0.31	0.98	0.70	-0.13	0.00	0.4	1.5

continue...

continuation...

$\hat{g}_{10}$	-1559	-852	-301	0.01	0.01	-1.85	-0.01	-1.13	-0.39	0.04	-0.01	-0.1	-0.9
$\hat{g}_{11}$	-974	-465	-295	0.01	0.00	1.11	0.03	-0.46	0.70	0.46	0.01	0.4	0.0
$\hat{g}_{12}$	792	558	247	0.00	-0.01	1.10	-0.08	0.97	0.21	0.01	0.01	-0.7	0.3
s_{A2}	-2238	-1153	-743	0.01	-0.02	-1.06	-0.14	-0.02	0.33	-0.02	0.00	0.9	0.8
s_{A3}	96	-24	-76	0.00	-0.01	0.85	-0.02	0.08	-0.67	-0.43	0.01	0.9	1.2
s_{A4}	-479	-167	185	0.01	0.02	0.43	0.07	-0.02	0.40	-0.01	-0.01	0.0	-0.3
s_{A5}	1947	1329	1095	0.01	0.04	1.20	0.18	-0.21	0.06	0.49	-0.01	-1.6	-1.1
s_{A6}	-440	-86	84	0.01	0.01	0.21	0.13	-0.42	0.16	-0.18	-0.01	-0.4	-0.1
s_{A7}	2835	2053	1141	0.00	0.02	-0.95	0.08	-0.02	-0.22	0.65	-0.02	-1.4	-1.4
s_{A8}	663	-231	-207	-0.03	0.00	-0.17	-0.03	0.04	-0.32	0.10	0.00	-0.9	-1.0
s_{A9}	-1374	-781	-706	0.01	-0.04	-1.03	-0.20	0.34	0.24	-0.76	0.02	1.2	0.5
s_{A10}	97	-75	34	-0.01	0.01	-0.27	0.00	0.46	-0.05	-0.10	0.01	0.8	0.6
s_{A12}	-1107	-866	-807	-0.01	-0.02	0.79	-0.07	-0.22	0.06	0.26	0.00	0.4	1.0
s_{B1}	-1	4	-500	-0.01	-0.04	-0.38	-0.19	-0.09	0.24	-0.34	0.02	0.8	0.8
s_{B2}	4865	2829	1680	-0.01	0.04	0.65	0.20	0.49	-0.60	0.84	-0.01	-1.6	-1.5
s_{B3}	-96	24	76	0.00	0.01	-0.85	0.02	-0.08	0.67	0.43	-0.01	-0.9	-1.2
s_{B6}	348	101	-198	0.00	-0.02	0.05	-0.03	-0.03	-0.04	0.17	0.01	0.4	1.2
s_{B7}	-1192	-801	-389	0.00	0.00	0.49	0.03	0.16	0.01	-0.50	0.01	0.7	0.2
s_{B8}	-1576	-859	-377	0.01	0.00	0.27	-0.06	-0.39	0.04	0.12	0.00	0.6	1.2
s_{B11}	355	279	231	0.00	0.01	0.35	0.10	0.22	-0.34	0.33	-0.01	-0.4	-0.5
s_{B12}	-2704	-1576	-523	0.01	0.00	-0.58	-0.07	-0.29	0.02	-1.05	-0.01	0.5	-0.1
s_{C1}	1	-4	500	0.01	0.04	0.38	0.19	0.09	-0.24	0.34	-0.02	-0.8	-0.8
s_{C2}	-2627	-1676	-937	0.00	-0.02	0.41	-0.05	-0.48	0.26	-0.82	0.00	0.7	0.7
s_{C4}	479	167	-185	-0.01	-0.02	-0.43	-0.07	0.02	-0.40	0.01	0.01	0.0	0.3
s_{C5}	-1947	-1329	-1095	-0.01	-0.04	-1.20	-0.18	0.21	-0.06	-0.49	0.01	1.6	1.1
s_{C6}	93	-15	113	-0.01	0.01	-0.26	-0.10	0.45	-0.11	0.01	0.00	0.0	-1.0
s_{C7}	-1643	-1252	-752	0.00	-0.02	0.46	-0.11	-0.14	0.21	-0.16	0.01	0.6	1.3
s_{C8}	912	1090	584	0.02	0.00	-0.10	0.09	0.35	0.28	-0.21	0.00	0.3	-0.2
s_{C9}	1374	781	706	-0.01	0.04	1.03	0.20	-0.34	-0.24	0.76	-0.02	-1.2	-0.5
s_{C10}	-97	75	-34	0.01	-0.01	0.27	0.00	-0.46	0.05	0.10	-0.01	-0.8	-0.6
s_{C11}	-355	-279	-231	0.00	-0.01	-0.35	-0.10	-0.22	0.34	-0.33	0.01	0.4	0.5
s_{C12}	3810	2441	1330	0.00	0.02	-0.21	0.14	0.51	-0.08	0.79	0.01	-0.9	-0.8
$SD(g_i)$	404	276	162	0.00	0.01	0.10	0.03	0.09	0.16	0.12	0.00	0.2	0.3
$SD(g_j)$	948	648	379	0.01	0.01	0.24	0.07	0.20	0.37	0.28	0.01	0.5	0.6
$SD(s_{ij})$	1340	917	536	0.01	0.02	0.34	0.10	0.29	0.53	0.40	0.01	0.7	0.9

HEY = husked ear yield (kg ha^{-1}); DEY = dehusked ear yield (kg ha^{-1}); GY = grain yield (kg ha^{-1}); DEY/HEY = ratio between DEY and HEY; GY/DEY = ratio between GY and DEY; NR = number of rows; ED = ear diameter (cm); EL = ear length (cm); BRIX = soluble solids content; AP = visual assessment of agronomic performance (1 = low and 10 = excellent); RPE = relative position of the ear; MAL = days to male flowering; FEM = days to female flowering.

The tested lines L_1, L_4, and L_5 stood out with the best GCA estimates, which were generally higher than the $SD(\hat{g}_j)$ for HEY, DEY, and GY, except for L_4 in GY. Nevertheless, L_4 still showed a positive estimate compared to the other lines (Table 4). Among these, L_5 excelled with the best estimates for HEY, DEY, GY, NR, DE, and EL, contributing positively to these variables when used as a parent in crosses. The favorable GCA estimates observed for these lines indicate a high frequency of favorable alleles for various agronomic traits, which highlights the superior performance *per se* of these DH lines (Cruz, 2006).

Regarding the SCA ($\hat{s}_{ij}$) estimates, the best combinations were observed in hybrids H_{A5}, H_{A7}, H_{B2}, and H_{C12}, which had the highest yield estimates. Hybrid H_{B2} exhibited the best SCA estimates for yield, with values of 4865 kg ha^{-1} for HEY, 2829 kg ha^{-1} for DEY, and 1680 kg ha^{-1} for GY, in addition to favorable contributions to NR, DE, EL, and AP. However, despite showing the highest SCA estimates, this hybrid did not achieve the highest yield mean in the experiment, highlighting the importance of selecting combinations with superior $\hat{s}_{ij}$ estimates while ensuring at least one parent has high GCA estimates. Conversely, cases like hybrid HC5 illustrate the opposite: although its parents showed the highest GCA estimates, it ranked as the second-worst combination for $\hat{s}_{ij}$, which contributed to the lower productive performance of this genotype.

For HEY, DEY, and GY, hybrid H_{C12} exhibited the highest means (Table 3), with positive GCA estimates ($\hat{g}_i$ and $\hat{g}_j$) from its parents and the second-highest $\hat{s}_{ij}$ estimates (Table 4). This hybrid also contributed to the prediction of the best estimated triple hybrids. Overall, the high SCA estimates suggest that the donor populations belong to distinct heterotic groups, enabling the extraction of DH lines that maximize heterosis effects an extremely favorable factor for improving super sweet corn hybrids.

Conclusions

The DH lines developed by the LMG breeding program demonstrate potential for producing hybrids with high productive performance and other essential traits for super sweet corn cultivation.

Dehusked ear yield shows a strong correlation with grain yield, making it a viable alternative for selection aimed at producing corn grains for canning, particularly when evaluating a large number of genotypes.

The DH lines L_1 and L_5 exhibited the highest GCA estimates for yield traits, indicating their potential to be used as tester lines.

The traits DEY/HEY, BRIX, and RPE are primarily influenced by additive gene effects, although non-additive effects also are important in the expression of other traits.

Single-cross hybrids H_{C12}, H_{A5}, H_{C1}, H_{C9}, H_{B2}, H_{C4}, H_{C5}, H_{C6}, and H_{C8}, along with triple-cross hybrids $HT_{(C)(1\ 12)}$, $HT_{(C)(4\ 12)}$, $HT_{(C)(6\ 12)}$, $HT_{(C)(8\ 12)}$, and $HT_{(C)(12\ 14)}$, and double-cross hybrid $HD_{(AC)(45)}$, demonstrated superior and competitive performance compared to the commercial hybrids evaluated.

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