ARTICLE

Genetic variation, agronomic potential, and acylsugar content in Santa Cruz dwarf tomato after backcrossings

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Ana Luisa Alves Ribeiro[1], Gabriel Mascarenhas Maciel[1*], Ana Carolina Silva Siquieroli[2], Lucas Medeiros Pereira[1], Nilo Cesar Queiroga Silva[1], Camila Soares de Oliveira[1] and Frederico Garcia Pinto[3]

Abstract: *Tomato cultivation is globally significant, demanding enhanced yields and biotic stress resilience for sustainability. Dwarf plant utilization in tomato genetic enhancement offers underexplored benefits. Yet, Santa Cruz dwarf tomato germplasm is unavailable. This study evaluated genetic dissimilarity, agronomic potential, and acylsugar content of Santa Cruz dwarf tomato plants across three successive backcrossings. Twelve advanced backcrossing populations (BC) and a commercial control (cv. Kada) were assessed, totaling 15 treatments. Agronomic traits and acylsugar content were measured, and analysis techniques were applied to assess genetic dissimilarity and backcrossing superiority. BC3 populations UFU-Sci#8, UFU-Sci#6, UFU-Sci#5, and UFU-Sci#1 excelled. Dwarf plants predominantly exhibited high leaflet acylsugar levels, suggesting potential for acquisition of hybrid with pest resistance. Notably, UFU MC TOM1 (dwarf plant) displayed significant glycine and L-serine presence, associated with various biotic stresses. These findings unveil the promising creation of dwarf Santa Cruz tomato hybrids with a broad spectrum of resistance.*

Keywords: Solanum lycopersicum *L., biotic stress, metabolomic, dwarf plants, genetic improvement*

INTRODUCTION

Increased interest in consuming a healthy diet has greatly increased the consumption of vegetables in Brazil and worldwide. Vegetable farming plays an important role in ensuring food security. New strategies are needed to meet the Sustainable Development Goals, particularly to enable the development of new sustainable agricultural technologies using available genetic resources (Adalja and Lichtenberg 2018, Maggio et al. 2018).

The tomato plant (*Solanum lycopersicum* L.) is considered one of the most important vegetables due to its high nutritional value and high levels of vitamins, minerals, and antioxidants (Flores et al. 2017). This plant is also socio-economic relevant in terms of job creation and marketing.

In Brazil, the fruit can be classified as mini tomato, round, beefsteak, saladette and Santa Cruz. Santa Cruz stands out for its high yield potential and post-harvest durability (Alvarenga 2013).

***Corresponding author:**
E-mail: gabrielmaciel@ufu.br
ORCID: 0000-0002-3004-9134

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[1] Universidade Federal de Uberlândia, Instituto de Ciências Agrárias, Rua Acre, 1004, Umuarama, 38405-302, Uberlândia, MG, Brazil
[2] Universidade Federal de Uberlândia, Instituto de Biotecnologia, Rodovia LMG 746, km 01, 38500-000, Monte Carmelo, MG, Brazil
[3] Universidade Federal de Viçosa, Campus Rio Paranaíba, Rodovia BR 230, km 7, 38810-000, Rio Paranaíba, MG, Brazil

Tomato production is a high-risk activity due to the susceptibility of tomatoes to pest attacks and diseases. Thus, the main challenge for breeders is identifying biofortified and highly productive individuals with broad resistance to pests and diseases (Peixoto et al. 2020). Crossbreeding of dwarf tomato plants and mini tomato strains has resulted in the production of compact and promising hybrids (Maciel et al. 2015, Finzi et al. 2017). To obtain Santa Cruz tomato hybrids from dwarf tomato populations, it is necessary to have a detailed understanding of these plants.

Backcrossing is used to obtain progenies with high agronomic performance. This technique enables the introgression of a specific characteristic, of the donor parent (Finzi et al. 2020, Oliveira et al. 2022). After the first backcrossing, dwarf tomato plants of the Santa Cruz type were identified and selected for the propagation of the next generations (Gomes et al. 2022, Gomes et al. 2023). We obtained hybrid dwarf populations from additional backcrossings and evaluated their agronomic performance and acyl-sugar levels in the leaves. The aim of this study was to evaluate genetic dissimilarity, agronomic potential, and acylsugar content of Santa Cruz dwarf tomato plants obtained through three successive backcrossings.

MATERIAL AND METHODS

Experimental location and genotypes used

The experiment was performed from April 2021 to August 2022 at the Horticultural Experimental Station of the Federal University of Uberlândia (UFU), Monte Carmelo Campus, MG, Brazil (lat 18° 42’ 43.19” S, long 47° 29’ 55.8’’, alt 873 m asl). The plants were grown in an arched greenhouse (7 × 21 m) with ceiling height of 4 m, anti-aphid net side curtains, and a transparent polyethylene cover protective against ultraviolet rays.

Twelve populations of Santa Cruz dwarf tomato plants were evaluated: two populations from the first backcrossing (BC_1 = UFU-Sci#11 and UFU-Sci#12), two populations from the second backcrossing (BC_2 = UFU-Sci#9 and UFU-Sci#10), eight populations from the third backcrossing (BC_3 = UFU-Sci#1, UFU-Sci#2, UFU-Sci#3, UFU-Sci#4, UFU-Sci#5, UFU-Sci#6, UFU-Sci#7, and UFU-Sci#8), donor parent (UFU MC TOM 1), recurrent parent (UFU-TOM-Mother 2) and the commercial control Santa Cruz Kada, totaling 15 populations. The wild accession *Solanum pennellii* was used to examine acylsugar content, a variable related to pest resistance (Maluf et al. 2010).

Santa Cruz-type dwarf tomato populations belonging to the UFU tomato germplasm bank were obtained after hybridizing a homozygous pre-commercial strain with Santa Cruz-type fruit patterns (UFU-TOM-Mother-2) *versus* the UFU MC TOM1 dwarf strain (Maciel et al. 2015). This homozygous dwarf strain (UFU MC TOM1) was used as a donor parent as it expresses the dwarf-bearing phenotype of recessive, monogenic origin, and mini tomato-type fruit (Maciel et al. 2015).

The populations of BC_1 were obtained by crossing the F_1 generation (UFU-TOM-Mother-2 *versus* UFU MC TOM1) *versus* UFU-TOM-Mother-2, followed by self-pollination. BC_2 was formed through hybridization of segregating plants selected in BC_1 *versus* UFU-TOM-Mother-2 followed by self-fertilization. Subsequently, populations of BC_3 were obtained from segregating plants selected in BC_2 *versus* UFU-TOM-Mother-2. In the segregating populations of each backcrossing (BC_1, BC_2, and BC_3), normal plants were eliminated, and only dwarf plants were selected, based on previous studies of dwarfism inheritance in tomato plants (Maciel et al. 2015, Oliveira et al. 2022).

The seeds were sown in polystyrene trays with a commercial coconut fiber substrate. At 40 days after sowing, the dwarf plants were selected and transplanted into 5-L plastic pots. The experiment was conducted in a randomized block design with four replications, totaling 60 plots. Each plot consisted of six plants distributed in double rows with 0.3 × 0.3 m spacing.

Cultivation was performed as recommended for tomato growing in protected cultivation (Filgueira 2013). Harvest began 65 days after transplant and was performed weekly, totaling eight harvests. For agronomic assessment, the fruits were harvested when they were fully ripe.

Characteristics evaluated

The following characteristics were analyzed in agronomic assessments: *Fruit shape (cm) (FS)*: ratio between the transverse and longitudinal diameter, measured using a caliper; *Number of locules (locules fruit^{-1}) (NL):* number of locules after cutting the fruit horizontally; *Flesh thickness (cm) (FT):* measurement with a caliper of the length between the skin of the fruit and beginning of the locules after cutting the fruit horizontally; *Mean weight (g) (MW):* ratio between the mass and number of fruits in each experimental plot; and *Number of internodes per linear meter (m) (ITM):* ratio between the number of internodes and total plant height.

Acylsugar content (nmol cm^{-2} leaf) was determined at 50 days after transplanting, using a sample of eight leaf disks (equivalent to 4.2 cm^2) from the upper third of each plant in the plot. Extraction and quantification were performed as described by Resende et al. (2002) and adapted by Maciel and Silva (2014).

Statistical analyses

Statistical assumptions were checked for normality (Lilliefors test), homogeneity (Oneill- Matheus test) and additivity (Tukey test). The data were analyzed using F test ($p < 0.05$), and means were compared using Scott-Knott test ($p < 0.05$).

Genetic dissimilarity between populations of dwarf plants from the first, second, and third backcrossings was determined from the generalized Mahalanobis (D^2) distance matrix. This matrix was represented by a heat map and dendrogram obtained using the maximum and minimum distances with R software version 3.6.3 (R Core Team 2020).

The selection index was calculated using the genotype-ideotype distance only for dwarf populations. To estimate selection gains, 33% of the populations were selected. The selection criterion was based on the magnitude of the genetic distance using an ideotype. The ideal ideotype was defined as the lowest mean ITM and highest means for the other characteristics. Dwarf plant populations were classified according to the Mahalanobis distance (D^2) in relation to the ideotype. Those with the smallest distances were considered more favorable.

Kohonen's self-organizing map (SOM) was obtained using the unsupervised artificial neural network technique. Different training sessions were performed for each possible combination to select the best architecture. The combination that best represented genetic dissimilarity between the dwarf tomato populations had three rows and two columns (six neurons) with a neighbor radius pattern of 1, architecture referring to 2000 seasons, hexagonal topology, and based on Euclidean distance to form the groups. All analyses were performed using Genes software, integrated with R software version 3.6.3 (R Core Team 2020) and Matlab (Cruz 2016).

Chromatographic analysis and metabolomic profile

Leaflet samples (n = 6) were collected from the middle portion of the plant and crushed with liquid nitrogen using a mortar and pestle until a fine powder was obtained. The analysis of metabolite by gas chromatography-mass spectrometry (GC-MS) was performed using 100 mg of freeze-dried samples. Extraction, derivatization and GC-MS analysis were carried out as described by Lisec et al. (2006).

RESULTS AND DISCUSSION

The genotypes differed in the agronomic characteristics assessed for FS, NL, FT, MW, and ITM (F test, $p < 0.05$) (Figure 1). The dwarf tomato populations BC_1, BC_2, and BC_3 were similar to the recurrent parent (UFU-TOM-Mother-2) and commercial control Kada, with slightly oblong fruit shapes smaller than 1.5. The relationship between the transverse and longitudinal diameter of the fruit indicates that the dwarf tomato populations belong to the Santa Cruz-type segment. The consumer market determines the preference for FS, and this segment has satisfactory acceptability for fresh consumption (Peixoto et al. 2017, Costa et al. 2020).

The recurrent parent (UFU-TOM-Mother-2) showed the highest value for NL, with an average of five locules. The fruits of the dwarf donor parent (UFU MC TOM1) had the smallest NL with two locules. The dwarf tomato populations evaluated showed intermediate values that differed from those of the recurrent and donor parents, except for the UFU-Sci#12 population.

FT and NL strongly influence fruit quality, with thicker flesh and fewer locules indicating greater firmness (Vieira et al. 2019). The dwarf tomato populations showed a mean increase of 105% in FT compared to that of the donor parent (UFU MC TOM1), with the populations UFU-Sci#1 from the BC_3 generation, UFU-Sci#9 from the BC_2 generation, and UFU-Sci#11 and UFU-Sci#12 from the BC_1 generation showing the highest mean thickness of 3.75 mm.

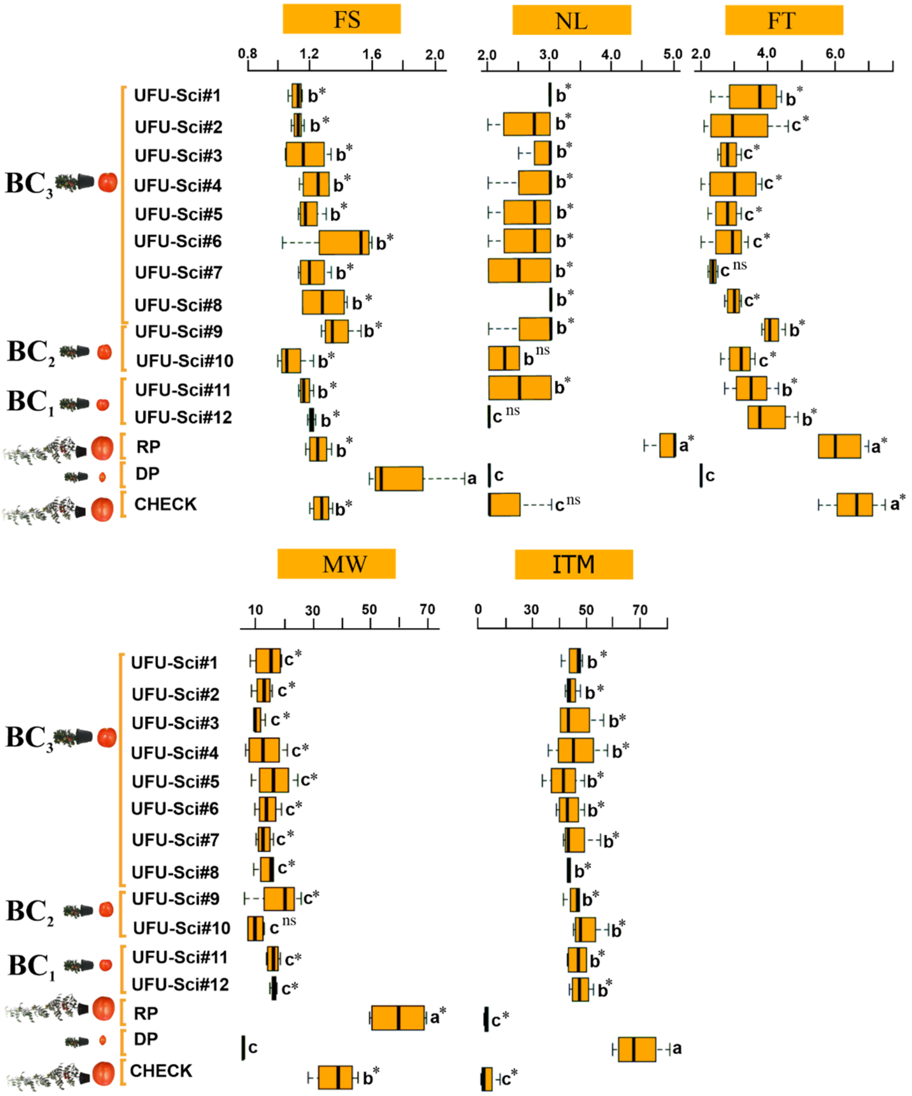

Figure 1. Boxplot comparing the mean values of agronomic characteristics for fruit shape (FS), number of locules (NL), flesh thickness (FT), mean weight (MW), and number of internodes per linear meter (ITM). BC1: first backcrossing, BC2: second backcrossing, BC3: third backcrossing, RP: recurrent parent UFU-TOM-Mother 2, DP: donor parent UFU MC TOM1, Check: Santa Cruz Kada. Means followed by different letters in the column differed in Scott-Knott test at the 0.05 significance level. *Means in the column differed from the dwarf donor parent UFU MC TOM1 in Dunnett's test at the 0.05 probability level.

Compared to the donor parent (UFU MC TOM1), the dwarf tomato populations BC1, BC2 and BC3 showed a mean increase of 161.98% in fruit MW. The populations UFU-Sci#5 (BC3), UFU- Sci#9 (BC2), and UFU-Sci#12 (BC1) showed the highest fruit production, with MW of 18.28 g. As expected, the recurrent parent (UFU-TOM-Mother-2) and commercial control Kada showed the highest mean values for AW and FT.

For the fruit traits AW, FT, and NL, the dwarf tomato populations obtained through backcrossing were superior to the donor parent (UFU MC TOM1). The increases in BC2 and BC3 demonstrated the effectiveness of the crossing method used in this study. The results agree with those of Gomes et al. (2021), who showed that Santa Cruz-type dwarf tomato populations showed significant increases in mean fruit weight and flesh thickness after the first and second backcrossings. Backcrossing enables the transfer of genes of interest to other parents and confers desirable agronomic characteristics

(Finzi et al. 2020, Oliveira et al. 2021). In the BC2 and BC3 generations, the populations are expected to contain means of 87.5% and 93.75%, respectively, of the recurrent parent's genome (Borém et al. 2021). There are reports that the gene action for AW, FT, and NL is of the additive x additive type, enabling increments in the advancement of generations (Mukherjee et al. 2024).

There was no significant difference in the fruit MW between BC1, BC2, and BC3, despite the significant difference between the backcrossed dwarf tomato populations and donor parent (UFU MC TOM1). This result may be related to the fact that the dwarf plant does not have the morphological structure or produce photoassimilates capable of generating the expected increases, thus limiting the increase in fruit MW. Because fruit MW is a quantitative trait (Kouam et al. 2018), the third backcrossing can introduce as many effective alleles as possible into future lineages to maximize the probability of obtaining productive hybrids.

ITM in tomato plants is directly related to the plant architecture. Mini tomato hybrids from dwarf tomato populations have short internodes and large numbers of bunches per linear meter (Finzi et al. 2017). The donor parent (UFU MC TOM1) showed the highest ITM, whereas the dwarf populations showed higher values in the BC3 generation, highlighting the importance of successive backcrossing. However, as the backcrossing progressed, no significant variation was observed in ITM. Thus, hybrids with different backcrossing populations should be obtained to achieve the expected results.

The allelochemical acylsugar is highly correlated with resistance to arthropod pests in tomato plants through antixenosis and antibiosis mechanisms (Marinke et al. 2022). There were significant differences in the acylsugar content between the genotypes evaluated (Figure 2A).

The average levels of acylsugars in the dwarf tomato populations were 70% higher than those in the commercial control Kada and in the recurrent parent. The results agree with those of Oliveira et al. (2022) and Gomes et al. (2022), who found higher acylsugar values in dwarf tomato populations. The wild accession *S. pennellii* is used for comparison of the acylsugar content (Maluf et al. 2010). In interspecific crossbreeding, tomato breeding programs currently use *S. pennellii* to introduce genes responsible for a high sugar content into commercial lines. However, successive backcrossings with the recurrent parent are necessary to re-establish desirable characteristics (Marinke et al. 2022).

Given the preliminary nature of research on the potential use of dwarf tomatoes for biotic stress resistance, the existence of other compounds in the leaflets of BC3 lines is suggested. In this regard, chromatographic analysis and metabolomic profiling have contributed to advancing knowledge. It was possible to observe the presence of other compounds of interest for further investigations. Notably, we highlight two of these compounds that showed a considerable increase in dwarf tomatoes compared to commercial ones. For instance, glycine exhibited an increase of over 24 times, while L-serine showed a significant

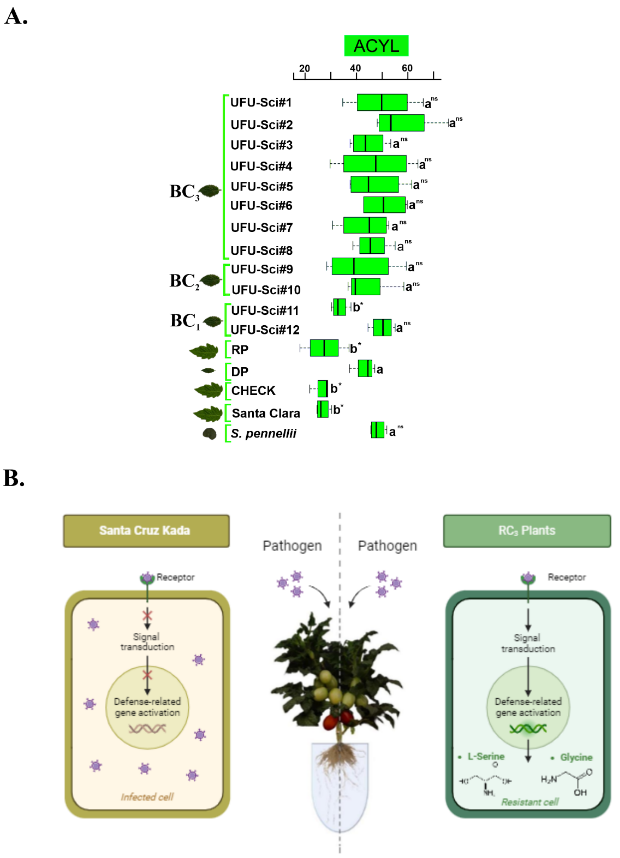

Figure 2. Acylsugar Comparison and Pathogen Resistance Enhancement. **A**. Boxplot comparing the average acylsugar values (ACYL) of the genotypes evaluated. BC1: first backcrossing, BC2: second backcrossing, BC3: third backcrossing, Gr: recurrent parent UFU-TOM-Mother 2, Gd: donor parent UFU MC TOM1, Check: Santa Cruz Kada. Means followed by different letters in the column differed in Scott-Knott test at the 0.05 significance level. *Means in the column differed from the control dwarf donor line UFU MC TOM1 in Dunnett's test at 0.05 probability. **B**. Potential enhanced resistance to pathogens in BC3 plants attributed to the elevated levels of glycine and L-serine.

increase of 3.8 times at $p < 0.01$. These results not only suggest the presence of these specific compounds but also underscore their potential role in the resistance mechanisms of the BC3 lineage, providing valuable insights for future genetic improvement approaches.

Besides the presence of acylsugar, there are reports indicating that specific amino acids, such as glycine and L-serine, play a crucial role in promoting resistance to various types of stresses, both biotic and abiotic, in plants (Hildebrandt et al. 2015). These biochemical compounds are not only associated with defense against pathogens but also have a substantial impact on essential physiological processes for plant development and survival. Their influence spans from protein synthesis to intracellular pH regulation, metabolic energy generation, and resistance to a wide range of abiotic and biotic stresses (Hildebrandt et al. 2015). The accumulation of these amino acids, especially in locally infected leaves, can be seen as an adaptive strategy of the plant to strengthen its defense response by providing the necessary substrates for the rapid synthesis of proteins and other compounds related to immunity against pathogens (Schwachtje et al. 2018).

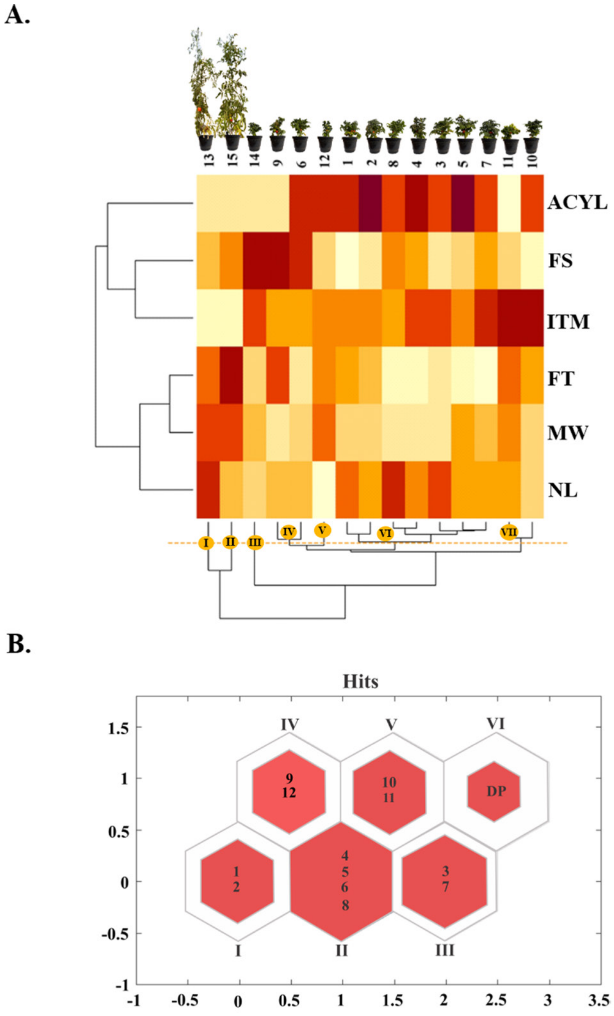

Figure 3. Visualization of Treatment Clusters with Dendrogram and Kohonen Self-Organizing Maps. **A.** Dendrogram and heat map of individuals and the characteristics fruit shape (FS), number of locules (NL), flesh thickness (FT), mean weight (MW), number of internodes per linear meter (ITM), and acylsugar content (ACYL). 1: UFU-Sci#1; 2: UFU-Sci#2; 3: UFU-Sci#3; 4: UFU-Sci#4; 5: UFU-Sci#5; 6: UFU-Sci#6; 7: UFU-Sci#7; 8: UFU-Sci#8; 9: UFU-Sci#9; 10: UFU-Sci#10; 11: UFU-Sci#1; 12: UFU-Sci#12; 13: UFU-TOM-Mother 2 - recurrent parent; 14: UFU MC TOM1 - donor parent; 15: commercial control Santa Cruz Kada. **B.** Kohonen self-organizing map (SOM), with the number of treatments in each neuron, clusters (3 × 2 of radius 1) using an artificial neural network.

Furthermore, another study demonstrated that just 8 hours after infection by *Pseudomonas syringae pv. tomato*, there was a significant increase in some amino acids in Arabidopsis leaves (Ward et al. 2010). These studies also highlight not only the complexity of plant metabolic response to pathogens, but also the dynamic adaptation of primary metabolism to efficiently modulate systemic resistance (Ward et al. 2010, Schwachtje et al. 2018). This intricate biochemical interaction underscores the importance of these amino acids not only in cellular homeostasis, but also as key elements in plants' effective response to environmental challenges. A thorough understanding of the mechanisms by which glycine and L-serine contribute to plant resistance allows for the consideration of strategies aimed at harnessing these amino acids in the development of more resilient tomato varieties. The isolated or combined use of these compounds may represent an innovative approach to reduce pesticide dependence and promote sustainability in agriculture (Figure 2B).

The donor parent (UFU MC TOM1) can transfer resistance genes to the progenies (Maciel et al. 2018, Finzi et al. 2022). The dwarf tomato populations and donor parent (UFU MC TOM1) did not differ from the wild accession in terms of the acylsugar content. Thus, dwarf tomato populations from backcrossings can be used in a similar manner as wild accessions (*S. pennellii*) to obtain populations with a high load of effective alleles. Thus, backcrossings after the initial crossing are not necessary to achieve resistance to arthropod pests. Dwarf tomato populations can be used to quickly and directly obtain hybrids with pest resistance traits.

The backcrossings promoted significant gains for MW, FT and NL compared to those of the donor parent. Thus, genetic dissimilarity and selection indices must be used to select superior dwarf tomato populations. To visualize genetic dissimilarity between the individuals analyzed, a heat map was drawn, with a dendrogram obtained using the unweighted pair group method with arithmetic mean with the generalized Mahalanobis matrix and a Kohonen self-organizing map (SOM) (Figure 3).

A cut-off of 21.68% resulted in the formation of seven distinct groups based on genetic dissimilarity between the individuals. Groups I and II included the recurrent parent and commercial control, respectively. Group III included the donor parent (UFU MC TOM1), group IV included the UFU-Sci#6 (BC3) and UFU-Sci#9 (BC2) populations, and group V included the UFU-Sci#12 (BC1) population. Populations from BC3 formed group VI and the UFU-Sci#10 and UFU-Sci#11 populations from BC1 formed group VII (Figure 3A).

The distances between the dwarf tomato populations and donor parent ranged from 63.27 to 94.58, with the greatest distance observed in the UFU-Sci#2 population from BC3. The distances between the BC1 and BC3 populations showed variability between the dwarf tomato populations after successive backcrossings. The branches for the variables indicated similarity between the characteristics analyzed. In addition, the intense red color revealed a greater contribution to the response variable for the individuals.

When using Kohonen's SOM, the donor parent and dwarf populations were classified into six distinct classes (Figure 3B). Neuron I (row 1 column 1) included the UFU-Sci#1 and UFU-Sci#2 populations; neuron II (row 1 column 2) included the UFU-Sci#4, UFU-Sci#5, UFU-Sci#6, and UFU-Sci#8 populations; neuron III (row 1 column 3) included the UFU-Sci#3 and UFU-Sci#7 populations; neuron IV (row 2 column 1) included the UFU-Sci#9 and UFU-Sci#12 populations; neuron V (row 2 column 2) included the UFU-Sci#10 and UFU-Sci#11 populations; and neuron VI included the donor parent (UFU MC TOM1).

Dwarf tomato populations belonging to BC3 were organized into groups I, II, and III. The populations belonging to BC1 and BC2 were distributed in neurons IV and V. These results confirmed the increase in dissimilarity between the populations after backcrossing.

SOMs are considered a type of artificial neural network trained to study genetic dissimilarity. This technique is considered an essential tool for multivariate analysis and can organize dimensional data into groups according to similarity. The algorithm can also identify and distinguish close neurons in the network, which indicates greater similarity between individuals (Kohonen 2001, Ferreira et al. 2018). SOM maps were previously used to assess genetic dissimilarity between soybean cultivars in breeding programs (Sá et al. 2022). Additionally, Gomes et al. (2022) demonstrated that the SOM method was efficient in selecting contrasting populations of dwarf tomato with fruits of the Santa Cruz type belonging to BC1 and BC2, aiming to obtain the BC3 population. Dwarf tomato populations belonging to BC3 formed their own clusters, diverging from the populations obtained in other backcrossings and from the donor parent, both by the unweighted pair group method with arithmetic mean clustering method and by the Kohonen self-organizing map (Figure 3). In fact, agronomic improvements in individuals with broad resistance to pests have been obtained through backcrossing. Gonçalves Neto et al. (2010) obtained commercial standard fruit through an interspecific cross between the wild accessions *S. pennellii* and *S. lycopersicum* followed by three backcrossings.

In addition to dissimilarity measures, the selection index is used to select superior individuals with high agronomic performance and elevated acylsugar levels. The dwarf tomato populations were selected based on the genotype-ideotype distance (Figure 4).

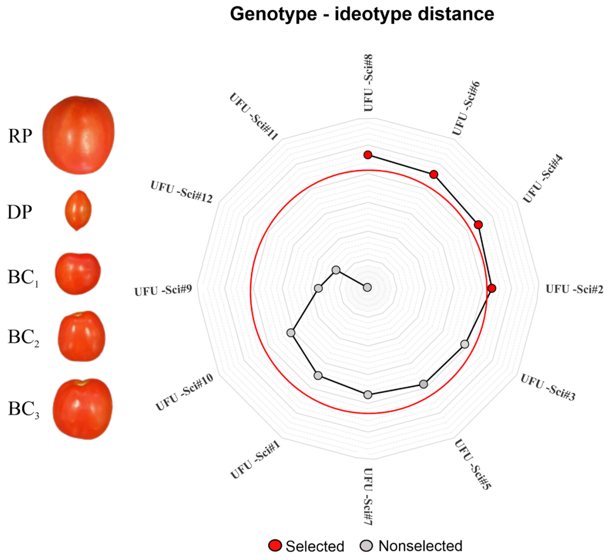

Figure 4. Genotype-ideotype distance for selecting superior dwarf populations after backcrossing.

The genotype-ideotype index selected the UFU-Sci#8, UFU-Sci#6, UFU-Sci#5, and UFU- Sci#1 populations belonging to BC3. Thus, the smallest Mahalanobis distances were found between BC3 populations and defined genotype-ideotype. The other BC3, BC2, and BC1 populations showed intermediate values and greater distances. Ideotypes play a crucial role in achieving different objectives in plant breeding, helping breeders make decisions. In addition, determining an ideotype enables the selection of promising and superior populations (Lessa et al. 2017), as performed in this study.

Dwarf tomato plants showed greatly improved fruit traits and broad resistance to pest arthropods after backcrossing. The selected populations can be used for the genetic improvement of tomato plants, with the potential to obtain compact, productive, and pest-resistant hybrids belonging to the Santa Cruz segment.

In conclusion, dwarf tomato populations showed improved agronomic traits after the three backcrossings. The most prominent populations belonged to BC3 (UFU-Sci#8, UFU-Sci#6, UFU- Sci#5, and UFU-Sci#1). Most dwarf plants had high levels of acylsugars in the leaves; in addition, the significant increase of amino acids, notably L-serine and glycine, suggests the potential for obtaining pest-resistant hybrids.

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DATA AVAILABILITY

The datasets generated and/or analyzed during the current research are available from the corresponding author upon reasonable request.

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