

Combining agronomic performance and pest resistance in Santa Cruz-type dwarf tomato germplasm

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Abstract: Dwarf tomato plants offer distinct advantages for hybrid development, including superior agronomic performance, fruit quality, and pest resistance. However, Santa Cruz-type dwarf tomato germplasm remains undercharacterized. This study evaluated morphological traits on seven breeding lines of Santa Cruz-type dwarf tomatoes, the donor parent UFU MC TOM 1, the recurrent parent UFU-TOM-MOTHER-2, and the control cultivar Caniati. Additionally, the wild accession *Solanum pennellii* was included to quantify acylsugar content. Pest resistance was evaluated through acylsugar quantification and analyses of herbivory caused by *Tuta absoluta* and *Liriomyza huidobrensis*. Breeding lines UFU-Sci#6.12-2.1.5, UFU-Sci#6.12-2.1.7, and UFU-Sc#8.3.2-2.1.2 emerged as superior, exhibiting elevated acylsugar levels, reduced pest damage, and improved fruit quality. Importantly, acylsugar content was strongly associated with increased pest resistance, particularly against *T. absoluta* and *L. huidobrensis*, mimicking the defensive profile of the wild *S. pennellii* accession. These findings support the development of pest-resilient, productive tomato cultivars aligned with sustainable agriculture goals.

Keywords: *Solanum lycopersicum*, dwarfism-associated genes, acylsugars, *Tuta absoluta*, *Liriomyza huidobrensis*

INTRODUCTION

Tomato (*Solanum lycopersicum*, Solanaceae) is a crop of major economic and nutritional relevance worldwide, with fruits consumed in various forms and rich in bioactive compounds such as lycopene, known for its role in disease prevention (Jiménez Bolaño et al. 2024). However, its domestication has made it highly susceptible to a wide range of arthropod pests, especially those affecting leaves and fruits, causing substantial yield losses (Jaiswal et al. 2020). In Brazil, tropical conditions further intensify pest pressure (Bacci et al. 2021), and pest control remains heavily dependent on chemical pesticides, raising concerns about environmental contamination and human health risks (Pignati et al. 2022).

For decades, efforts have been directed toward developing pest-resistant tomato cultivars through genetic improvement. Transgenic approaches, such as the insertion of *Bacillus thuringiensis* (Bt) genes encoding Cry proteins,

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have shown high efficacy in controlling *T. absoluta* and other lepidopteran pests (Vendemiatti et al. 2024). Indeed, several resistance genes have been utilized in breeding programs, including *Mi-1*, which confers resistance to root-knot nematodes and some insects such as whiteflies and aphids, and *Sw-5*, which provides resistance to Tomato Spotted Wilt Virus (TSWV). More recently, genes involved in acylsugar biosynthesis—such as *ASAT1*, *ASAT2*, *ASAT3*, and *ASAT4*—have gained prominence due to their role in producing defensive metabolites in glandular trichomes (Mutschler et al. 2023). However, the adoption of transgenic tomatoes remains restricted, with approvals for cultivation granted only in Canada and the United States. In Brazil, transgenic pest-resistant tomato cultivars are not yet authorized for commercial use (CTNBio 2024).

In contrast, conventional breeding approaches have shown promising results, particularly utilizing the wild relative *Solanum pennellii*. The presence of acylsugars in *S. pennellii* leaves has been associated with satisfactory levels of pest resistance (Mutschler et al. 2023). However, the use of *S. pennellii* for generating F1 hybrids may be limited by unfavorable traits such as reduced fruit size (Semel et al. 2006).

Among the innovative strategies in tomato breeding, the use of dwarf tomato plants as parental lines for hybrid development has gained traction (Pereira et al. 2024). The development of hybrids with standard plant architecture can be efficiently achieved through the direct combination of a dwarf male parent with a standard female parent. The inheritance of the dwarf architecture trait in tomato (*S. lycopersicum*) follows a monogenic pattern, governed by recessive alleles (Maciel et al. 2015). Hybrids derived from dwarf male parents have demonstrated higher productivity, compact growth, increased inflorescence density per linear meter, and enhanced pest resistance (Pereira et al. 2024). However, there is limited information on the morpho-agronomic traits and pest resistance of dwarf tomatoes with a Santa Cruz genetic background. This study aimed to characterize Santa Cruz-type dwarf tomato breeding lines, focusing on plant morphology, productivity, fruit quality, and pest resistance.

MATERIAL AND METHODS

Experimental location and genotypes used

The experiment was performed at the Horticultural Experimental Station of the Federal University of Uberlândia (UFU) (lat 18° 42' 43.19" S, long 47° 29' 55.8", alt 873 m asl). The region has a tropical altitude climate (Köppen's classification Cwa), with a rainy summer and dry winter, and an average annual temperature of approximately 22 °C. The plants were grown in an arched greenhouse with ceiling height of 4 m and anti-aphid net side curtains.

Seven Santa Cruz-type dwarf tomato breeding lines (UFU-Sci#6.1,2-2.1.1 to UFU-Sc#8,3.2-2.1.2) were evaluated, along with the donor parent (UFU MC TOM1), recurrent parent (UFU-TOM-MOTHER-2), and a commercial control (cv. Caniati), totaling 10 genotypes. The wild accession *S. pennellii* was also included to assess acylsugar content related to pest resistance (Maciel and Silva 2014). The donor UFU MC TOM1 carries a monogenic recessive dwarf allele (*d*), distinct from the self-pruning (*sp*) mutation, and exhibits indeterminate growth with reduced height. This line, developed from local germplasm at the Federal University of Uberlândia (Maciel et al. 2015), is genetically independent from the MicroTom lineage. The BC₃F₃ dwarf lines were derived by hybridizing UFU MC TOM1 with UFU-TOM-MOTHER-2, followed by three backcrosses and two selfing generations. The recurrent parent UFU-TOM-MOTHER-2 was derived from Santa Cruz-type commercial cultivars. Thus, the term 'Santa Cruz genetic background' refers to the genetic base represented by UFU-TOM-MOTHER-2. The commercial cv. Caniati, used as a control, is a Santa Cruz-type tomato widely adopted in Brazilian agriculture. Its inclusion allows for the benchmarking of the dwarf breeding lines against a standard Santa Cruz cultivar currently in use.

Seeds were sown in polystyrene trays. After 40 days, healthy dwarf plants with typical morphology and no visible damage from pests or diseases were selected and transplanted into 5-L pots. Each genotype was represented by three pots per block (one plant per pot), totaling nine plants per genotype. Pots were arranged in double rows with 0.3 × 0.3 m spacing.

Plant morphology evaluation

Plant morphology was evaluated using the following descriptors: PH (plant height), IL (internode length), FS (flower size), FW (fruit weight), FL (fruit length), FD (fruit diameter), PT (pulp thickness), LF (locules per fruit), and °BRIX (soluble

solids content). Plant height was measured 50 days after transplanting, from base to apex. IL was measured between the 4th and 6th nodes using a digital caliper. FS and PT were recorded from at least four flowers or fruits per plant. FW, FL, and FD were calculated from 10 mature fruits per plant. LF was determined by counting internal compartments in cross-sections. °BRIX was measured with a digital refractometer (Atago PAL-13810) using a homogenized sample from 10 fruits, blended with a stainless-steel blade mixer.

Acylsugar quantification

Acylsugar levels (nmol cm^{-2} of leaf area) were determined 30 days after transplanting. For the analysis, samples of eight leaf discs (equivalent to 4.2 cm^2) were collected from the upper third of each plant within the plot. Extraction and quantification of acylsugars were performed according to the methods described by Maciel and Silva (2014).

Reaction of plants to infestation of leafminer *Tuta absoluta* (Meyrick) and *Liriomyza huidobrensis* (Blanchard)

The same plants used for acylsugar quantification were assessed for *T. absoluta* and *L. huidobrensis* herbivory. Temperature and humidity were monitored throughout (Figure 1). Infestation began 18 days after transplanting, with insect releases in a greenhouse using Santa Clara cv. pots every 50 cm. Eight days later, six assessments at two-day intervals rated plant and leaflet injuries (Oliveira et al. 2022). Ratings were summed after seven assessments. Injury levels (scale 1-5) followed Akhtar et al. (2018). Herbivory area was then measured via ImageJ using ten scanned leaflets per plot (Schneider et al. 2012).

Statistical analysis

Statistical assumptions were tested for normality, homogeneity, and additivity (Tukey). Data underwent ANOVA (F test, $p < 0.05$), with means compared using Scott-Knott and Dunnett tests ($p < 0.05$). The cv. Caniati was used as a

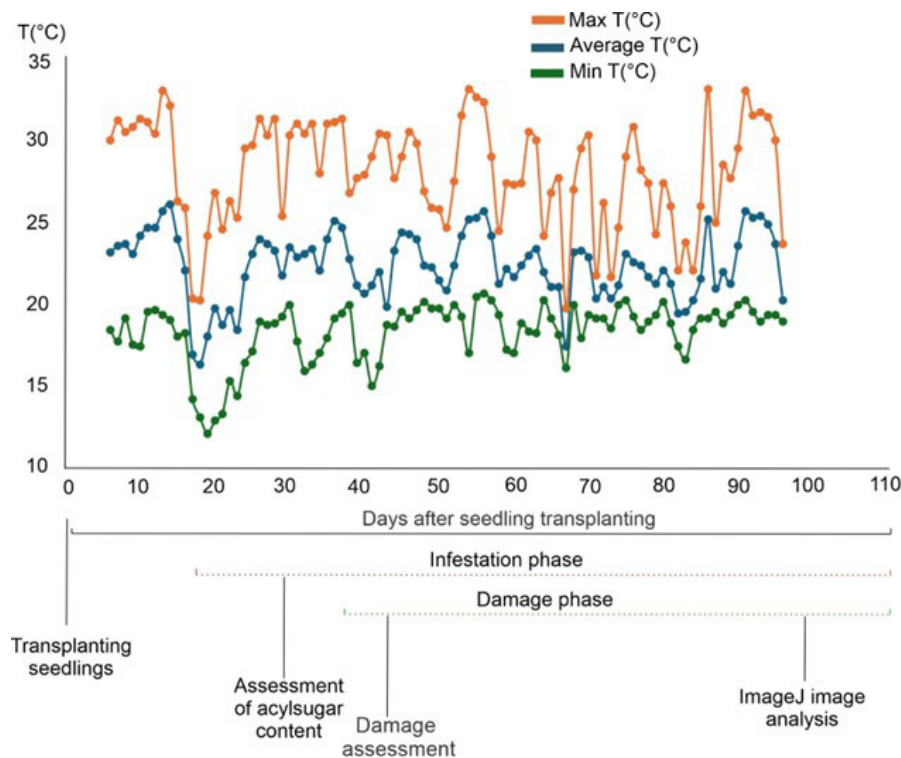


Figure 1. Climate conditions during the execution of the experiment. Maximum temperature (Max T), Average temperature (Average T) (Minimum temperature (Min T).

phenotypic control for agronomic comparisons, while the donor parent UFU MC TOM1, which expresses the desired resistance traits, served as a statistical reference in analyses related to acylsugar content and herbivory.

Morphological and production traits were used to classify genotypes using a Self-Organizing Map (SOM), an unsupervised neural network for clustering and dimensionality reduction. Input data were mapped onto a two-dimensional hexagonal grid, where each neuron (node) represents a cluster of genotypes with similar profiles. The SOM was trained under different configurations to optimize the hidden layer and minimize quantization and topographic errors (Haldorai et al. 2024). Genotypes were assigned to neurons based on minimum Euclidean distance, and inter-neuron distances were used to infer neighborhood relationships. A UPGMA dendrogram was generated from the SOM distance matrix to visualize genotype grouping (Khaki et al. 2020). Outputs included: Counts plot (genotype distribution), Codes X (trait profiles per neuron), and Neighbour distances (Euclidean distance between adjacent neurons).

Genotype performance was also evaluated using the genotype–ideotype distance index. The ideotype was defined by desirable traits: reduced height, short internodes, high flower production, and superior fruit quality. Standardized Euclidean distances were calculated, and a weighted average across traits determined genotype ranking (Olivoto and Nardino 2021). Analyses were performed using GENES (Cruz 2016) and R (R Core Team 2021).

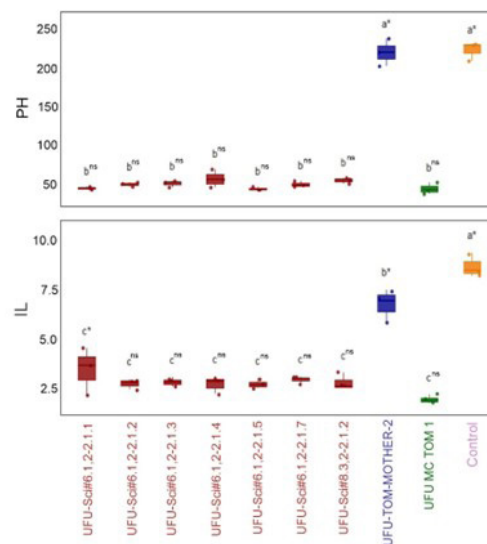
RESULTS AND DISCUSSION

In this study, we conducted a comprehensive evaluation of seven dwarf tomato breeding lines derived from backcrosses, focusing on the identification of valuable morphological and agronomic traits for genetic improvement programs. Morphological characterization of the dwarf tomato breeding lines revealed significant differences in several key traits critical for the selection of superior genotypes.

Plant morphology and growth characteristics

The dwarf lines showed an average height of ~50 cm, similar to the donor UFU MC TOM1 (Figure 2). In contrast, the controls Caniati and UFU-TOM-MOTHER-2 reached 150 cm and 160 cm, respectively. Internode length was also significantly shorter in the dwarf genotypes compared to controls, with no differences among the dwarf lines, indicating uniformity for this trait. Internode length varied considerably among the breeding lines (Figure 2). The donor parent UFU MC TOM 1 exhibited the shortest internodes, with an average length of 2.5 cm. In contrast, the commercial cultivar Caniati had the longest internodes, averaging 7.5 cm. The recurrent parent UFU-TOM-MOTHER-2 displayed an intermediate internode length, with an average of 5.3 cm.

A.



B.

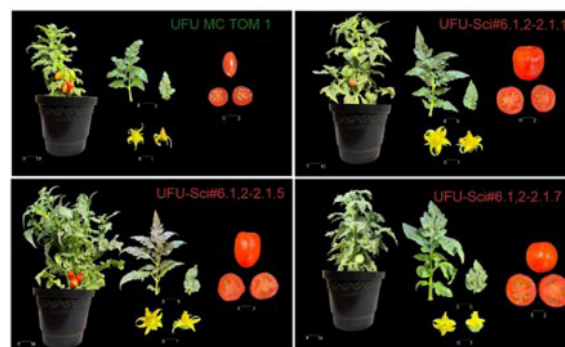


Figure 2. Morphological Characterization of BC₃F₃ Dwarf Tomato breeding lines and Parental Lines. **A.** BC₃F₃ breeding lines, recurrent parent (UFU-TOM-Mother 2), donor parent (UFU MC TOM 1), and control (cv. Caniati). Means followed by distinct letters differ significantly. Asterisk means differ from the dwarf donor parent UFU MC TOM 1 according to the Dunnett test at 0.05 probability level. IL: internode length (cm); PH: plant height (cm). **B.** Leaf, flower, and fruit morphology of the three standout breeding lines compared to the donor parent UFU MC TOM 1.

The leaves of the selected breeding lines exhibited significant variations in size and shape (Figure 2B). The breeding line UFU-Sci#6.1,2-2.1.1 stood out for having larger leaves with less serrated leaflets compared to the donor parent UFU MC TOM 1. Flower size also varied, with the UFU-Sci#6.1,2-2.1.1 lineage exhibiting larger flowers with more intense coloration (Figure 2B). The variation in leaf size and morphology among the evaluated breeding lines, as shown in Figure 2B, suggests that larger leaves with less serrated leaflets can directly influence photosynthetic efficiency and plant yield. These morphological traits likely enhance light interception and photosynthetic efficiency, particularly in controlled environments where maximizing photosynthetic activity can increase productivity. Previous studies have indicated that larger and less serrated leaves improve light interception, optimizing light use efficiency for photosynthesis, which ultimately leads to higher yields per plant (Zhang et al. 2024). Moreover, less serrated leaflets may reduce water loss through transpiration, making these genotypes better adapted to conditions of high light intensity or water limitation (Li et al. 2021). The integration of these traits into breeding programs is essential for developing more efficient and resilient cultivars.

Fruit characteristics

The analyzed breeding lines showed significant variation in fruit weight, size, pulp thickness, locule number, and °BRIX, key traits for tomato breeding. The donor parent UFU MC TOM1 averaged 6.6 g, while UFU-Sci#6.1,2-2.1.5 reached 49 g, a 642% increase. The commercial control (cv. Caniati) weighed 330 g (Figure 3A).

Fruit diameter ranged from 1.7 cm in UFU MC TOM1 to 6.2 cm in UFU-TOM-MOTHER-2. The UFU-Sci#6.1,2-2.1.1 population reached a diameter of 4.3 cm, nearly tripling the value observed in the donor parent UFU MC TOM1 (Figure 3A). Fruit length also varied significantly, from 3.7 cm in UFU MC TOM1 to 7.6 cm in UFU-TOM-MOTHER-2. The UFU-Sci#6.1,2-2.1.3 population exhibited a length of 5.1 cm, representing an increase of approximately 50% (Figure 3A). Pulp thickness ranged from 0.21 cm (UFU MC TOM1) to 0.55 cm (UFU-Sci#8.3,2-2.1.2), reflecting a more than 100% increase in certain genotypes (Figure 3A).

UFU-TOM-MOTHER-2 had the highest locule number (4.71), while UFU MC TOM1 had the lowest (2.05). Backcross breeding lines ranged from 2.55 (UFU-Sci#6.1,2-2.1.2) to 3.41 (UFU-Sci#6.1,2-2.1.5), and Caniati averaged 2.33. The Scott-Knott test grouped the recurrent parent separately, while others formed a single class; Tukey's test placed UFU-Sci#6.1,2-2.1.5 in an intermediate group. UFU MC TOM1 had the highest °BRIX (7.93), with UFU-Sci#6.1,2-2.1.4 leading backcrosses (6.25) (Figure 3A). The selection index highlighted UFU-Sci#6.1,2-2.1.1, UFU-Sci#6.1,2-2.1.7, and UFU-Sci#6.1,2-2.1.5 as the most promising for breeding (Figure 3B).

The selected breeding lines showed significant gains in fruit diameter, fruit weight, and pulp thickness compared to the donor UFU MC TOM1 (Figure 3A). These traits are key for both fresh consumption and processing, as larger fruits

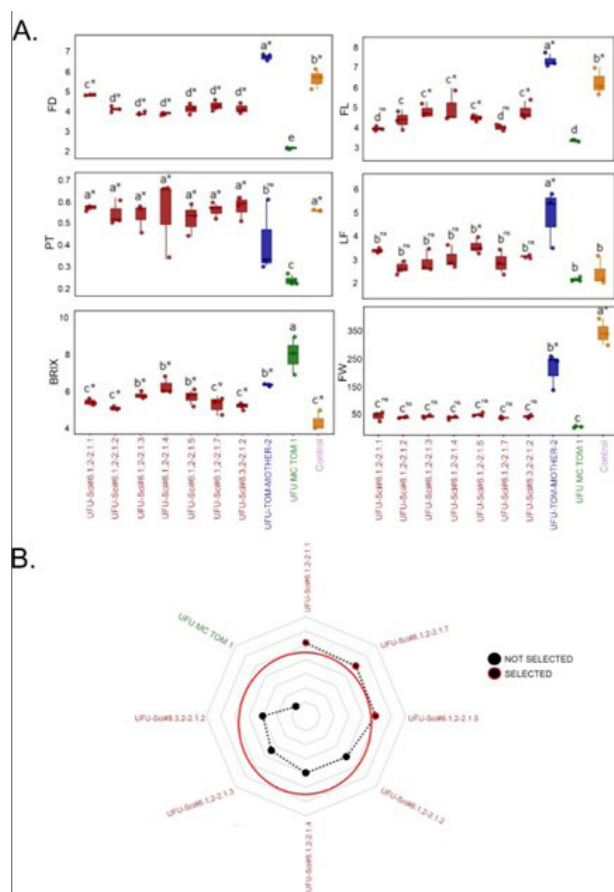


Figure 3. Morphological and Agronomic Traits of BC₃F₃ Dwarf Tomato Breeding Lines and Parental Lines with Selection Index Based on Genotype-Ideotype Distance. **A.** BC₃F₃ breeding lines of dwarf tomato, recurrent parent (UFU-TOM-MOTHER-2), donor parent (UFU MC TOM 1), and control (cv. Caniati). Means followed by distinct letters differ significantly according to the Scott-Knott test at 0.05 probability level. * Means differ from the dwarf donor parent UFU MC TOM 1 according to the Dunnett test at 0.05 probability level.; FD: fruit diameter (cm); FL: fruit length (cm); PT: pulp thickness (cm); LF: locules per fruit; °BRIX: soluble solids content; FW: average fruit weight (g). **B.** Selection Index - Genotype-Ideotype Distance Based on Morphological and Agronomic Traits.

with thicker pulp improve yield and efficiency (Bhandari et al. 2023). Their positive correlation with market value reinforces the importance of selecting genotypes aligned with consumer demand (Ni et al. 2024). In addition, higher °BRIX levels in the selected lines enhance flavor and nutritional quality—attributes strongly influenced by metabolic modulation in tomato cultivars (Zhu et al. 2018). Although fruit weight increased relative to the donor, it remained below that of the recurrent parent UFU-TOM-MOTHER-2 (~250 g), suggesting a possible pleiotropic effect of the dwarfing gene (*d*), which may limit both vegetative growth and fruit expansion. Similar associations between compact architecture and reduced organ size have been reported in other Solanaceae species and should be considered in breeding strategies targeting productive dwarf ideotypes.

Acylsugar content and plant response to infestation by *Liriomyza huidobrensis* and *Tuta absoluta*

Acylsugar content and herbivory in UFU MC TOM-1 were similar to wild *S. pennellii*. Even after three backcrosses for the Santa Cruz fruit type, UFU-Sci#6.1,2-2.1.2, UFU-Sci#6.1,2-2.1.5, UFU-Sci#6.1,2-2.1.7, and UFU-TOM-MOTHER-2 and Caniati (Figure 4).

The observed increase in acylsugar levels in the selected breeding lines, which correlates with greater resistance to pests such as *T. absoluta* and *L. huidobrensis*, underscores the importance of these metabolites in integrated pest management strategies. Acylsugars, synthesized primarily in the glandular trichomes of Solanaceae species, function as defense compounds due to their chemical diversity and bioactivity (Fiesel et al. 2024). The correlation between high acylsugar levels and reduced insect-induced damage, as shown in Figure 5, highlights the role of these compounds in pest resistance. Breeding lines such as UFU-Sci#6.12-2.1.5 and UFU-Sci#6.12-2.1.7, which exhibited the highest acylsugar concentrations, consistently showed lower pest injury scores. This suggests that breeding strategies aimed at enhancing acylsugar synthesis could be pivotal for developing cultivars with intrinsic pest resistance.

The results of this study confirm the efficacy of acylsugars in reducing insect damage, aligning with previous studies that suggest that selecting genotypes with high levels of these compounds can significantly contribute to resistance against multiple pests, thereby improving cultivar durability in the field (Resende et al. 2022).

Genetic dissimilarity and selection of superior breeding lines

UPGMA and self-organizing map (SOM) analysis identified six genetic groups (Figure 5). The donor parent UFU MC TOM1 was in Group III, while UFU-Sci#6.1,2-2.1.5, UFU-Sci#8.3,2-2.1.2, UFU-Sci#6.1,2-2.1.7, and UFU-Sci#6.1,2-2.1.2 clustered in Group IV. Genetic dissimilarity analysis is an essential tool for identifying genotypes with desirable phenotypic and genetic traits for breeding programs. In this study, we utilized the UPGMA method and a self-organizing map (SOM) to assess genetic dissimilarity among dwarf tomato genotypes, resulting in the formation of six distinct groups

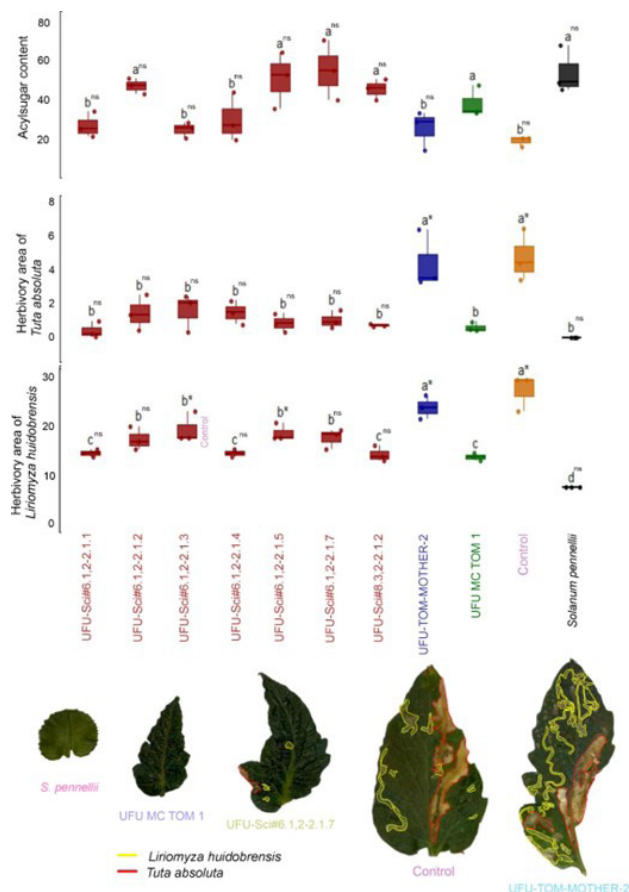


Figure 4. Acylsugar content (nmol cm⁻² of leaf area), cumulative scores from evaluations for *Tuta absoluta*, and herbivory area calculations for *Liriomyza huidobrensis* obtained using ImageJ software. Means followed by distinct letters differ significantly according to the Scott-Knott test at 5% probability level. Significance levels *, **, and ns are based on the Dunnett test in comparison to the donor parent UFU MC TOM1.

(Figure 5). This analysis revealed that the breeding lines UFU-Sci#6.12-2.1.5, UFU-Sci#8.32-2.1.2, UFU-Sci#6.12-2.1.7, and UFU-Sci#6.12-2.1.2 clustered together, sharing genetic proximity and superior phenotypic traits such as larger fruit size. Genetic dissimilarity analysis not only aids in identifying genotypes with desirable attributes but also enhances the understanding of the genetic diversity within the population, which is fundamental for developing new cultivars with multiple desirable traits (Khodadadi and Farokhzadeh 2024). Genetic diversity is crucial for resilience to both biotic and abiotic stresses and facilitates the incorporation of favorable alleles into breeding programs. Thus, genetic dissimilarity analysis is an essential step in selecting superior genotypes that can be utilized to develop cultivars better adapted to diverse environmental conditions and market demands.

Contributions to tomato breeding

This study demonstrates the effective application of advanced methodologies, such as the Selection Index - Genotype-Ideotype Distance, in identifying genotypes with superior traits for use in breeding programs. The genetic dissimilarity among the selected genotypes, as represented in the dendrogram (Figure 5), indicates a diverse genetic base that can be leveraged in future breeding efforts. This diversity is essential for the development of new cultivars that combine multiple desirable traits, high productivity, and superior fruit quality. Harnessing these genetic variations can enhance breeding strategies by incorporating diverse alleles that contribute to complex traits, thereby optimizing genetic gains in breeding programs (Yeon et al. 2024). Similarly, backcross-derived tomato populations carrying the dwarfism gene have proven effective in breeding programs aimed at improving agronomic traits, plant architecture, and fruit quality (Cavasin et al. 2021).

Multivariate analyses, including genetic dissimilarity (Figure 5), identified the breeding lines UFU-Sci#6.12-2.1.1, UFU-Sci#6.12-2.1.5, and UFU-Sci#6.12-2.1.7 as the most promising. These lines combined favorable fruit traits—such

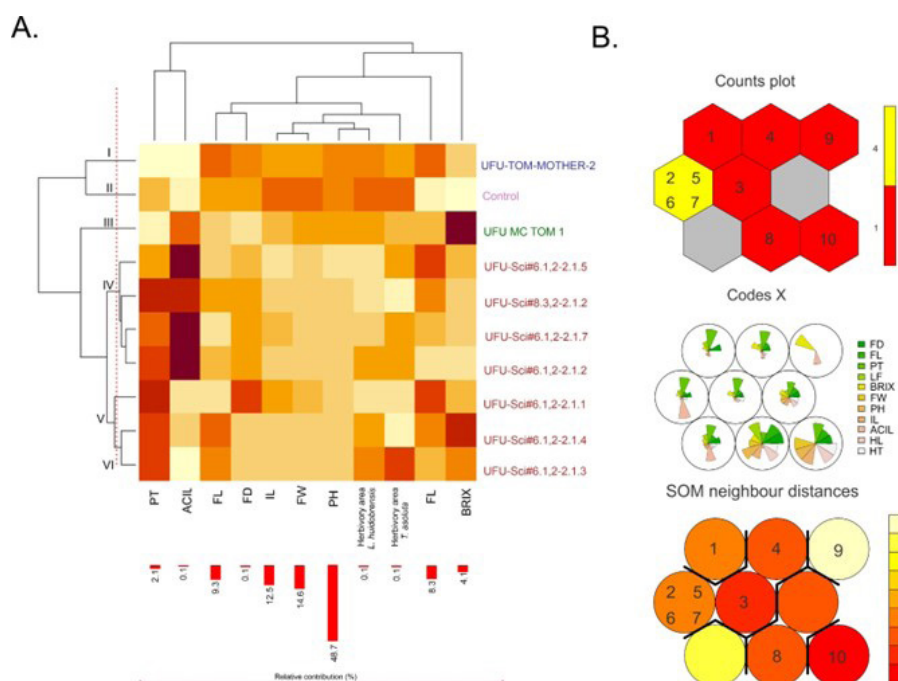


Figure 5. Dendrogram, Heat Map, and Treatment Classification of Dwarf Tomato Breeding Lines Based on Morphological and Agronomic Traits Using the UPGMA Method **A.** Dendrogram and heat map. **B.** Classification of treatments using a Self-Organizing Map (SOM), based on neuron allocation, variable contribution, inter-neuron distances, and UPGMA clustering. Counts plot (top): Each hexagon represents a neuron; numbers indicate neuron IDs. The color scale shows the number of genotypes per neuron (yellow = low, red = high). Codes X (middle): Radar plots summarize the average trait profile of genotypes assigned to each neuron. Neighbour distances (bottom): Euclidean distances between neighboring neurons; darker colors indicate greater dissimilarity. Trait abbreviations: PT = pulp thickness (cm), ACIL = acylsugar content, FL = fruit length (cm), FD = fruit diameter (cm), IL = internode length (cm), FW = fruit weight (g), PH = plant height (cm), LF = locules per fruit, ^aBRUX = soluble solids, HL = herbivory by *L. huidobrensis*, HT = herbivory by *T. absoluta*.

as increased size and weight (Figure 3) - with high acylsugar content (Figure 4) and clustering patterns indicative of distinct phenotypic profiles. Their selection reinforces the relevance of integrated phenotypic evaluation in developing cultivars that meet market standards while offering improved resistance to biotic stresses, as highlighted in previous studies (Cappetta et al. 2020, Zhang et al. 2024).

These findings promote sustainable agriculture by reducing chemical inputs through pest-resistant, high-quality genotypes. Their incorporation into breeding programs improves economic viability and resource use (Cappetta et al. 2020). Integrating phenotypic and genotypic data enhances selection accuracy, efficiency, and adaptability across environments (Cappetta et al. 2020, Yeon et al. 2024), supporting the development of resilient, high-performing cultivars for sustainable production.

CONCLUSION

This study characterized Santa Cruz-type dwarf tomato breeding lines, identifying genotypes with high agronomic potential and pest resistance. The breeding lines UFU-Sci#6.12-2.1.5, UFU-Sci#6.12-2.1.7, and UFU-Sci#8.3,2-2.1.2 stood out for their higher acylsugar content, reduced pest damage, and superior fruit quality.

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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