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PLANT BREEDING

Enhancing fruit quality and stress resilience: Genetic advancements in dwarf tomato populations

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ABSTRACT. This study investigated the enhancement of fruit-related traits in dwarf tomato populations through advanced hybridisation strategies, employing UFU MC TOM1 as the donor parent. This experiment was conducted at the Federal University of Uberlândia's experimental station over 3 production cycles from 2019 to 2021. Crossbreeding and backcrossing were performed using UFU-57 as the recurrent parent and UFU MC TOM1 as the donor parent, and dwarf plants were selected in the BC1F2 and BC2F2 generations. This research focused on improving key fruit quality attributes, including size, acidity, and phytonutrient levels, such as β-carotene and lycopene. Notable improvements were observed, particularly in the second backcrossing generation, which produced salad-type fruit with enhanced traits. Promising populations, including UFU × DTOM 8#2-3, UFU × DTOM 22#1-17, and UFU × DTOM 4#4-14, demonstrated significant potential for further lineage development and hybrid breeding programs. Metabolomic analysis identified increased levels of glycine, myo-inositol, acetamide, and dodecanoic acid in the dwarf salad-type tomato line, which were likely associated with improved stress resilience, enhancing its potential for breeding robust cultivars. These results provide a crucial understanding of the genetic mechanisms underlying fruit quality improvement and stress resistance in dwarf tomato. These findings highlight the potential for developing superior cultivars that combine improved nutritional quality with enhanced resilience to biotic and abiotic stressors, thereby contributing to sustainable agricultural practices and food security.

Keywords: genetic improvement; plant breeding, abiotic stress; acylsugars.

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Introduction

Tomato (*Solanum lycopersicum* L.) is widely cultivated in various regions of the world and has significant socioeconomic importance (Alvarenga, 2013). In 2022, Brazil produced 3,809,986 tonnes of tomatoes in an area of 54.7 thousand hectares, with an average yield of 69.9 tonnes per hectare (Instituto Brasileiro de Geografia e Estatística [IBGE], 2022). Fresh tomatoes for consumption are divided into four categories: cherry tomatoes, Santa Cruz, saladette, and salad (Alvarenga, 2013). In the Brazilian market, the salad segment stands out in the commercialisation of table tomatoes. However, the production cost per hectare is high, exceeding 180 thousand BRL (Cepea, 2023).

Several studies have investigated different tactics to increase tomato productivity, such as irrigation, spacing, plant training, cultivation lighting, and plant nutrition (Singh et al., 2023; Nkansah et al., 2021; Schipper et al., 2023; Massimi et al., 2023). Furthermore, genetic advancements have enabled sustainable productivity gains, benefitting society (Wang et al., 2019).

Solanum pennellii is a wild tomato species native to the arid regions of South America. This species has evolved to thrive under extreme environmental conditions, making it a valuable genetic resource for stress tolerance. Introgression lines (ILs) incorporating segments of the *S. pennellii* genome into cultivated *S. lycopersicum* have been used in breeding programs. The species' ability to maintain physiological function in arid environments is linked to genetic mechanisms, including a wax-rich cuticle that minimises water loss and genes associated with stress responses (Bolger et al., 2014).

A promising alternative to enhancing productivity and optimising resources can be achieved using dwarf plants in genetic improvement programs (Wang et al., 2023). The quest for more compact plants of commercial interest can yield several advantages. Harvesting becomes more agile and streamlined, optimising space utilisation (Würschum et al., 2017; Ke et al., 2021), simplifying spraying operations, enhancing pest control efficiency (Kumar et al., 2021), and enabling increased plant density per hectare (Ke et al., 2021, Karpe et al., 2024). The regulation of plant stature is intricately governed by phytohormone interactions (Liu et al., 2020). Investigations have identified mutations (Schrager-Lavelle et al., 2019) and genes governing height in tomato plants, such as the SlGID1a gene (Liu et al., 2020), which affects internode elongation. Although research on tomato dwarfism has been extensively undertaken as a model system (Liu et al., 2020; Rajendran et al., 2022), its commercial application remains in its nascent stages. Finzi et al. (2017) presented a methodological proposal for obtaining hybrids with agronomic potential in cherry tomatoes. This strategy resulted in a reduction in internode distance in the normal-sized phenotype, leading to a higher number of clusters per linear meter of the plant (Finzi et al., 2017). However, this methodology cannot yet be used to obtain salad hybrids due to the lack of genetic background for dwarf tomato germplasm available for the segment.

The aim of this study was to obtain and characterise the agronomic potential, fruit quality, pest resistance, and metabolite presence of a salad-type dwarf tomato population.

Material and methods

Experimental site and conditions

This experiment was conducted at the Vegetable Experimental Station of Universidade Federal de Uberlândia (UFU), located at the Monte Carmelo Campus in Minas Gerais State, Brazil (18°42'43.19" S, 47°29'55.8" W, altitude 873 m). Hybridisation and backcrossing processes were implemented over 3 consecutive production cycles from January 2019 to June 2021.

Plant material and breeding strategy

Dwarf tomato populations were sourced from the germplasm repository of UFU. Initially, crossbreeding was performed using UFU-57♀ (recurrent parent) and UFU MC TOM 1♂ (donor parent). UFU-57 represents a homozygous salad-type line characterised by normal plant architecture and indeterminate growth habit, but it is vulnerable to pests. Conversely, UFU MC TOM 1, a dwarf tomato line (dd), has an indeterminate growth pattern, yields mini-tomato fruit, and exhibits pest resistance due to the elevated acylsugar content in its leaflets.

Following the acquisition of the F1 generation, the first backcrossing (BC1F1) was conducted, followed by self-pollination to produce the BC1F2 population. Dwarf plants were selected from the BC1F2 generation, and a second backcrossing BC2F1 was performed, followed by self-pollination to generate BC2F2. In the BC1F2 and BC2F2 populations, only dwarf plants with a salad-type genetic background were selected (Figure 1).

The seeds were sown in polyethylene trays (200 cells) filled with commercial coconut fibre substrates. Seedlings were produced in a hoop-type greenhouse with white anti-aphid mesh on the sides and UV-resistant polyethylene film on the cover. Transplanting occurred 30 days after sowing into 5-L plastic pots containing the same substrate. The experiment was conducted in a twin-arch greenhouse with anti-aphid side curtains and a polyethylene cover. Cultural practices followed tomato cultivation recommendations.

Experimental design and phenotypic and fruit quality evaluations

The experiment followed a randomised complete block design with four replications, with each plot consisting of six plants. Seven dwarf BC1F2 populations with a salad-type background and 15 dwarf BC2F2 populations with a salad-type background were analysed as described below. The donor parent (UFU MC TOM 1), recurrent parent (UFU-57), and commercial control (Paronset hybrid) were included, totalling 25 treatments. For variables related to indirect pest resistance, a wild accession of *Solanum pennellii* was used.

After fruit maturation, fruit was harvested, counted, weighed, and analysed for various parameters, including length (cm), diameter (cm), morphology, pulp thickness (cm), and number of locules. Fruit quality characteristics, such as titratable acidity, soluble solids content (°Brix), and carotenoids (β-carotene and lycopene) (mg 100 mg^{-1}) were evaluated.

Figure 1. Comparison between the phenotypes of the parents (donor and recurrent) and the dwarf populations BC1F2 and BC2F2. Legend: BC2F2 populations (1 = UFU-DTOM 22#1-7; 2= UFU-DTOM 22#1-8; 3 = UFU-DTOM 22#1-17; 4 = UFU-DTOM 8#2-3; 5 = UFU-DTOM 21#2-1; 6 = UFU-DTOM 21#2-2; 7 = UFU-DTOM 8#4-2; 8 = UFU-DTOM 8#4-5; 9 = UFU-DTOM 8#1-1; 10 = UFU-DTOM 8#1-2; 11 = UFU-DTOM 19#1-3; 12 = UFU-DTOM 19#1-4; 13 = UFU-DTOM 4#4-2; 14 = UFU-DTOM 4#4-11; 15 = UFU-DTOM 4#4-14); BC1F2 populations (16 = UFU-DTOM 19#1; 17 = UFU-DTOM 4#4; 18 = UFU-DTOM 8#1; 19 = UFU-DTOM 22#1; 20 = UFU-DTOM 8#2; 21 = UFU-DTOM 8#4; 22 = UFU-DTOM 21#2); RP = Recurrent parent UFU-57; DP = Donor parent UFU MC TOM 1.

Pest resistance assessment

For pest resistance, acylsugars in the leaflets were quantified 90 days post-sowing using a composite sample of leaf discs (Maciel & Silva, 2014). Metabolite analysis via gas chromatography-mass spectrometry (GC-MS) was used to compare the dwarf tomato variety UFU MC TOM 1 and the commercial hybrid Paronset ($p < 0.01$).

Statistical analyses

The data were subjected to residual normality testing, variance homogeneity assessment, and block additivity examination. Analysis of variance was conducted, and means were compared using the Scott–Knott test and the Dunnett test. Genetic parameters were evaluated, and genetic dissimilarity was assessed using a generalised Mahalanobis distance matrix.

Selection gains were estimated using the Mulamba and Mock rank sum index and the genotype–ideotype distance index. All analyses were performed using GENES software integrated into R and Matlab (Cruz, 2013).

Results

Agronomic characteristics

The backcrossed dwarf tomato populations (BC1F2 and BC2F2), the Paronset hybrid, the recurrent parent UFU-57, and the donor parent UFU MC TOM1 showed statistically significant differences in agronomic characteristics, demonstrating variability among treatments. As expected, the recurrent parent and the commercial hybrid Paronset exhibited superior characteristics (Table 1).

The effectiveness of gene transfer related to fruit mass was clearly evident when the backcross populations (BC1F2 and BC2F2) were compared with the donor parent (UFU MC TOM1). Notable increments in fruit mass were observed, ranging from 374 to 1137% in BC1F2 populations and from 519 to 956% in BC2F2 populations (Table 1). The BC2F2 population UFU-DTOM 8#2-3 was particularly promising, showing a 956% increase in fruit mass, closely approaching the genetic standard for salad-type fruits.

Regarding fruit shape, 59% of the dwarf populations exhibited a fruit shape index smaller than 1, indicative of similarity to the salad fruit type. This underscores the significance of backcrossing in integrating the traits of the recurrent parent, UFU-57, into dwarf plants. Compared to the donor parent, the remaining dwarf plants displayed thicker fruit pulp and diverged in fruit shape. UFU-DTOM 8#2-3 (BC2F2) demonstrated a notable 136% increase in pulp thickness, a crucial trait aligning the fruits of these populations with the recurrent parent.

Table 1. Agronomic characteristics evaluated in dwarf salad tomato populations.

Genotypes	Generations	FW	FL	FD	FS	PT	NL
UFU-DTOM 22#1-7	BC2F2	52.00 d*	4.40 c*	4.86 b*	0.91 e*	0.63 d*	3.50 c*
UFU-DTOM 22#1-8	BC2 F2	47.25 e*	4.16 d*	4.52 c*	0.91 e*	0.56 d*	4.00 b*
UFU-DTOM 22#1-17	BC2 F2	57.42 d*	4.92 c*	4.67 c*	1.05 d*	0.66 c*	4.00 b*
UFU-DTOM 8#2-3	BC2 F2	61.83 d*	4.71 c*	4.99 b*	0.94 e*	0.71 c*	4.00 b*
UFU-DTOM 21#2-1	BC2 F2	41.69 e*	4.06 d*	4.29 d*	0.94 e*	0.55 d*	3.25 c*
UFU-DTOM 21#2-2	BC2 F2	42.91 e*	4.59 c*	4.30 d*	1.06 d*	0.61 d*	2.25 e
UFU-DTOM 8#4-2	BC2 F2	40.69 e*	4.69 c*	4.27 d*	1.10 d*	0.55 d*	2.50 e
UFU-DTOM 8#4-5	BC2 F2	42.84 e*	4.78 c*	4.19 d*	1.14 d*	0.62 d*	3.00 d*
UFU-DTOM 8#1-1	BC2 F2	57.11 d*	4.65 c*	4.83 b*	0.96 e*	0.69 c*	3.50 c*
UFU-DTOM 8#1-2	BC2 F2	56.75 d*	4.47 c*	4.68 c*	0.95 e*	0.67 c*	3.75 b*
UFU-DTOM 19#1-3	BC2 F2	46.61 e*	5.59 a*	4.18 d*	1.33 b*	0.62 d*	2.25 e
UFU-DTOM 19#1-4	BC2 F2	36.25 f*	4.74 c*	4.19 d*	1.13 d*	0.61 d*	2.25 e
UFU-DTOM 4#4-2	BC2 F2	46.85 e*	4.30 d*	4.51 c*	0.95 e*	0.58 d*	3.25 c*
UFU-DTOM 4#4-11	BC2 F2	43.70 e*	4.31 d*	4.50 c*	0.96 e*	0.58 d*	3.25 c*
UFU-DTOM 4#4-14	BC2 F2	56.96 d*	4.47 c*	4.87 b*	0.92 e*	0.65 c*	3.50 c*
UFU-DTOM 19#1	BC1 F2	30.55 g*	4.26 d*	3.77 e*	1.14 d*	0.55 d*	3.00 d*
UFU-DTOM 4#4	BC1 F2	34.98 f*	4.10 d*	4.23 d*	0.97 e*	0.60 d*	3.00 d*
UFU-DTOM 8#1	BC1 F2	44.07 e*	4.03 d*	4.59 c*	0.87 e*	0.68 c*	3.50 c*
UFU-DTOM 22#1	BC1 F2	72.40 c*	5.34 b*	4.32 d*	1.23 c*	0.63 d*	4.00 b*
UFU-DTOM 8#2	BC1 F2	40.67 e*	4.08 d*	4.59 c*	0.89 e*	0.68 c*	4.00 b*
UFU-DTOM 8#4	BC1 F2	45.56 e*	3.96 d	4.44 c*	0.89 e*	0.67 c*	3.75 b*
UFU-DTOM 21#2	BC1 F2	27.74 g*	4.09 d*	3.79 e*	1.08 d*	0.60 d*	2.25 e
CHECK	HB	130.19 a*	5.79 a*	6.71 a*	0.86 e*	0.90 a*	3.25 c*
UFU-57	RP	115.62 b*	5.73 a*	6.42 a*	0.89 e*	0.75 b*	4.75 a*
UFU MC TOM 1	DP	5.85 h	3.50 e	2.00 f	1.75 a	0.30 e	2.00 e
Average		45.56	4.47	4.51	0.96	0.63	3.25
CV (%)		9.85	4.96	4.65	5.59	8.72	13.68
DMS Dunnett		10.65	0.47	0.44	0.12	0.11	0.94
h^2		99	96.11	98.45	97.72	92.7	90.08
CVg/Cve		4.97	2.48	3.98	3.27	1.78	1.50

FW: Average fruit weight (g); FL: Fruit length (cm); FD: Fruit diameter (cm); FS: Fruit shape; PT: Pulp thickness (cm); NL: Number of locules per fruit; RP: Recurrent parent; DP: Donor parent; CHECK: Commercial check (Paronset hybrid); CV (%): Coefficient of variation; h^2: Genotypic determination coefficients; CVg/CVe: Ratio between genetic and environmental coefficients of variation. Means followed by different letters within a column differ from each other by the Scott–Knott test at a 0.05 level. *Means in the column differ from the donor parent UFU MC TOM 1 dwarf line by the Dunnett test at a 0.05 level of probability.

Fruit quality

Significant disparities in fruit quality were observed between the populations (BC1F2 and BC2F2) and the donor parent (UFU MC TOM1), which exhibited superior outcomes for total titratable acidity, soluble solids content, and β-carotene and lycopene levels (Table 2).

Table 2. Quality characteristics of fruit evaluated in BC1F2 and BC2F2 populations of dwarf salad tomato plants.

Genotypes	Generation	ATT	SS (°Brix)	βC	LI
UFU-DTOM 22#1-7	BC2F2	0.21 d*	5.20 c*	4.09 b*	2.79 c*
UFU-DTOM 22#1-8	BC2F2	0.20 d*	5.22 c*	3.20 d*	2.40 d*
UFU-DTOM 22#1-17	BC2F2	0.21 d*	5.67 b*	3.73 c*	2.75 c*
UFU-DTOM 8#2-3	BC2F2	0.27 b*	5.40 c*	3.67 c*	2.43 d*
UFU-DTOM 21#2-1	BC2F2	0.26 c*	5.32 c*	4.03 b*	2.85 c*
UFU-DTOM 21#2-2	BC2F2	0.25 c*	5.47 c*	4.36 b*	3.13 b*
UFU-DTOM 8#4-2	BC2F2	0.20 d*	5.52 c*	4.06 b*	2.87 c*
UFU-DTOM 8#4-5	BC2F2	0.27 b*	5.40 c*	4.16 b*	2.94 c*
UFU-DTOM 8#1-1	BC2F2	0.25 c*	5.55 c*	3.34 d*	2.42 d*
UFU-DTOM 8#1-2	BC2F2	0.22 d*	5.40 c*	3.70 c*	2.73 c*
UFU-DTOM 19#1-3	BC2F2	0.25 c*	5.30 c*	3.95 b*	2.89 c*
UFU-DTOM 19#1-4	BC2F2	0.24 c*	5.37 c*	4.48 b*	3.28 b*
UFU-DTOM 4#4-2	BC2F2	0.22 d*	5.02 c*	3.62 c*	2.79 c*
UFU-DTOM 4#4-11	BC2F2	0.27 b*	5.47 c*	3.64 c*	2.65 c*
UFU-DTOM 4#4-14	BC2F2	0.26 c*	5.35 c*	3.96 b*	2.79 c*
UFU-DTOM 19#1	BC1F2	0.26 c*	6.10 b*	3.91 b*	2.77 c*

UFU-DTOM 4#4	BC1F2	0.29 b*	5.20 c*	4.51 b*	3.20 b*
UFU-DTOM 8#1	BC1F2	0.23 d*	6.10 b*	3.13 d*	2.33 d*
UFU-DTOM 22#1	BC1F2	0.27 b*	5.45 c*	3.61 c*	2.62 c*
UFU-DTOM 8#2	BC1F2	0.25 c*	5.50 c*	4.16 b*	2.89 c*
UFU-DTOM 8#4	BC1F2	0.25 c*	5.70 b*	3.75 c*	2.66 c*
UFU-DTOM 21#2	BC1F2	0.30 b*	5.45 c*	4.38 b*	3.25 b*
CHECK	HB	0.25 c*	5.65 b*	3.69 c*	2.73 c*
UFU-57	RP	0.20 d*	5.90 b*	3.93 b*	2.89 c*
UFU MC TOM 1	DP	0.37 a	7.92 a	6.05 a	4.13 a
Average		0.25	5.58	3.96	2.85
CV (%)		8.61	5.31	8.97	9.44
DMS Dunnett		0.04	0.62	0.75	0.56
h^2		91.73	92.73	90.07	86.48
CVg/Cve		1.66	1.78	1.50	1.26

ATT: Titratable acidity; SS: Soluble solids content (°Brix); βC: β-carotene content (mg 100 mg^{-1}); LI: Lycopene content (mg 100 mg^{-1}); RP: Recurrent parent; DP: Donor parent; CHECK: Commercial control (Paronset hybrid); CV (%): Coefficient of variation; h^2: Genotypic determination coefficients; CVg/CVe: Ratio between genetic and environmental coefficients of variation. Means followed by different letters in the column differ significantly at the 0.05 level by the Scott–Knott test. *Means in the column differ from the donor parent control UFU MC TOM 1 by the Dunnett test at a probability level of 0.05.

The donor parent, UFU MC TOM 1, showed notable superiority in terms of titratable acidity. Additionally, populations UFU-DTOM 21#2, UFU-DTOM 22#1, and UFU-DTOM 4#4 from a single backcross and UFU-DTOM 4#4-11, UFU-DTOM 8#4-5, and UFU-DTOM 8#2-3 from two backcrosses exhibited higher titratable acidity compared to both the recurrent parent and the commercial hybrid.

Sugar and phytochemical content

In our study, the donor parent (UFU MC TOM1) outperformed the commercial hybrid by 63 and 51% in terms of β-carotene and lycopene contents, respectively (Table 2). Furthermore, 60% of the salad-type dwarf tomato populations exhibited β-carotene and lycopene levels higher than those of the commercial hybrid. These results indicate significant potential for developing nutritionally superior varieties.

Metabolism and acylsugars

Notably, *S. pennellii*, the donor parent, and the UFU-DTOM 22#1 population exhibited elevated levels of acylsugars compared to the recurrent parent, commercial hybrid, and other treatments (Figure 2).

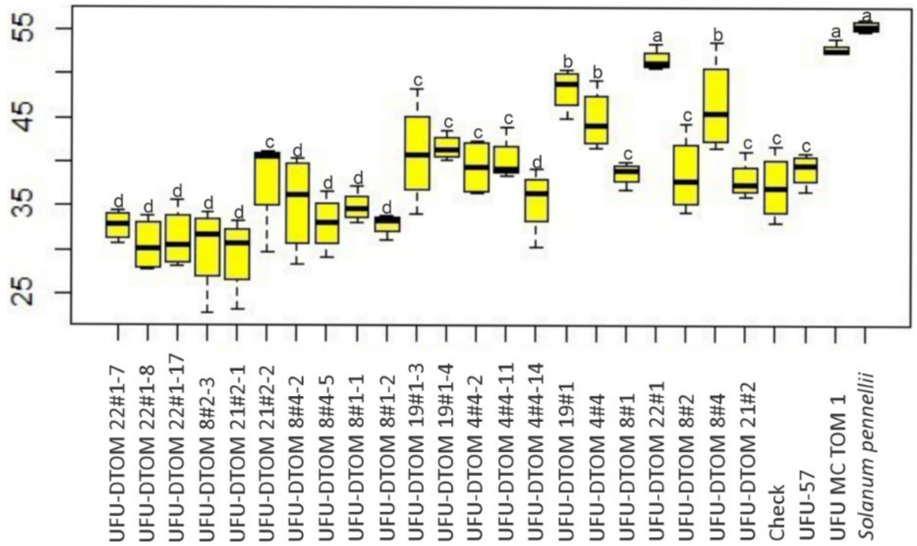

Figure 2. Comparative boxplot regarding the mean values of acylsugar contents (nmols·cm^{-2} of leaf area). The x-axis represents the different tomato genotypes evaluated, while the y-axis indicates the acylsugar content (nmols·cm^{-2}). Means followed by different letters differ significantly according to the Scott–Knott test at a 0.05 significance level. Check: Commercial control (Paronset hybrid); UFU 57: Recurrent parent; UFU MC TOM 1: Donor parent.

The donor parent (UFU MC TOM1) exhibited elevated levels of acylsugars in its leaves, comparable to *S. pennellii*, with no statistical differences observed (Scott–Knott at 0.05). Additional populations, including UFU-DTOM 19#1, UFU-DTOM 4#4, and UFU-DTOM 8#4, also showed superiority in this trait compared to the recurrent parent and the commercial hybrid Paronset.

Multivariate analysis and genetic selection

To explore and prioritise promising populations, an additional approach involving genetic analysis and selection indices was employed. The heat map accompanied by a dendrogram generated through the Unweighted Pair-Cluster Method using Arithmetic Averages (UPGMA) method from the generalised Mahalanobis matrix was instrumental in visualising the genetic dissimilarity among the assessed individuals (Figure 3).

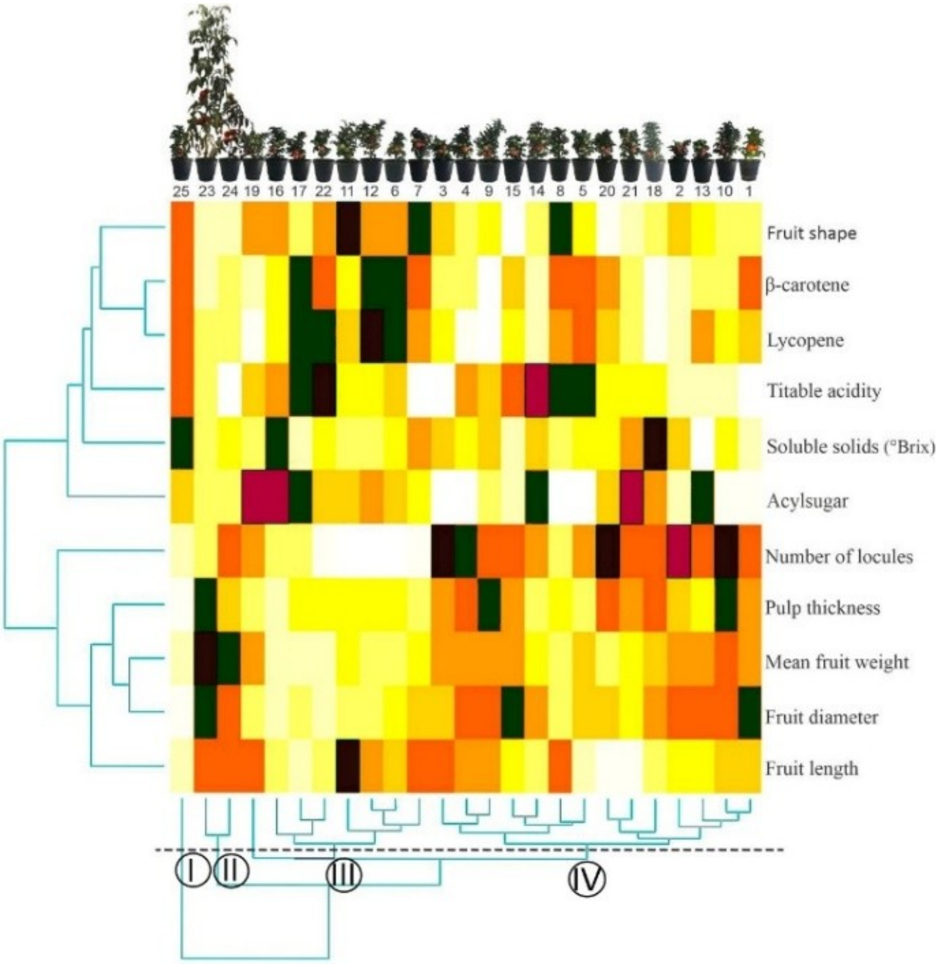

Figure 3. Dendrogram and heat map of genotypes. Legend: 1 - UFU-DTOM 22#1-7; 2- UFU-DTOM 22#1-8; 3 - UFU-DTOM 22#1-17; 4 - UFU-DTOM 8#2-3; 5 - UFU-DTOM 21#2-1; 6 - UFU-DTOM 21#2-2; 7 - UFU-DTOM 8#4-2; 8 - UFU-DTOM 8#4-5; 9 - UFU-DTOM 8#1-1; 10 - UFU-DTOM 8#1-2; 11 - UFU-DTOM 19#1-3; 12 - UFU-DTOM 19#1-4; 13 - UFU-DTOM 4#4-2; 14 - UFU-DTOM 4#4-11; 15 - UFU-DTOM 4#4-14; 16 - UFU-DTOM 19#1; 17 - UFU-DTOM 4#4; 18 - UFU-DTOM 8#1; 19 - UFU-DTOM 22#1; 20 - UFU-DTOM 8#2; 21 - UFU-DTOM 8#4; 22 - UFU-DTOM 21#2; 23 - Paronset commercial hybrid; 24 - Recurrent parent UFU-57; 25 - Donor parent UFU MC TOM 1. Intense colouring indicates a greater contribution of the response variable in each evaluated plant population.

The analysis revealed the formation of five distinct clusters due to genetic heterogeneity among individuals. Group I was characterised by the donor parent, while Group II encompassed the recurrent parent and the commercial check, both exhibiting typical normal plant stature traits. Group III was distinguished by population UFU-DTOM 22#1 (BC1F2), demonstrating the most substantial enhancements in average fruit weight and fruit morphology, similar to those of the donor parent, UFU MC TOM 1. Groups IV and V confirmed the genetic diversity among dwarf tomato populations post-backcrossing.

In summary, backcrosses proved efficient in obtaining dwarf tomato populations with fruit characteristics similar to the salad segment. Contrasts between BC1F2 populations versus the donor parent (UFU MC TOM1), BC2F2 populations versus the donor parent (UFU MC TOM 1), and BC1F2 populations versus BC2F2, tested by the Scheffé test (α = 0.01 and 0.05), demonstrated successful enhancement through backcrossing. Both the first (BC1F2) and second (BC2F2) backcrossing allowed the fruit shape to resemble the salad type compared to the donor parent, resulting in improvements in the average fruit weight and pulp thickness (Figure 4).

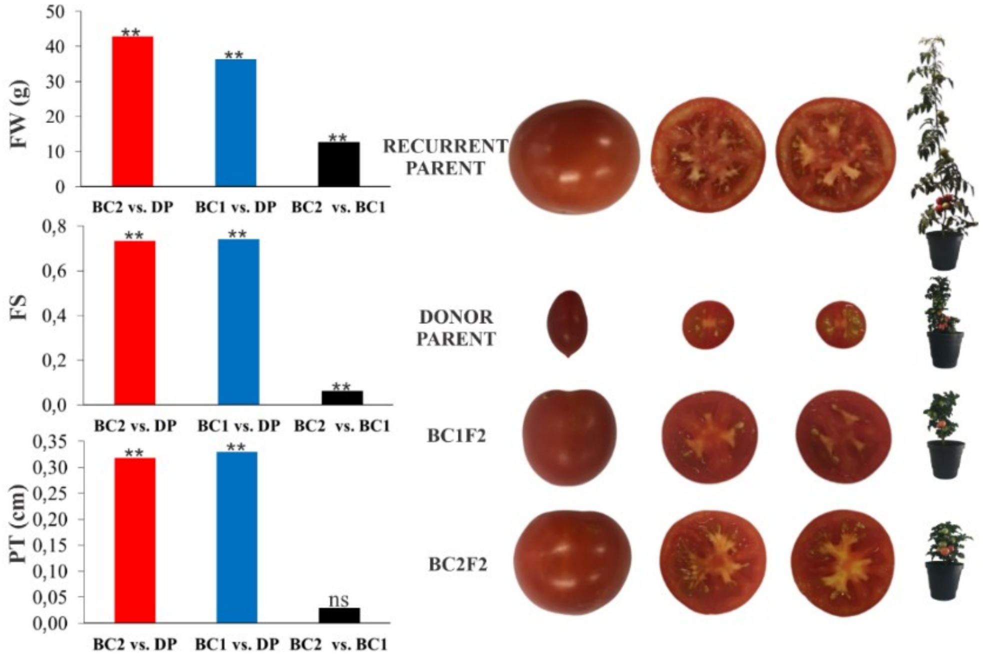

Figure 4. Comparison of BC1F2 (BC1) and BC2F2 (BC2) populations in relation to the donor parent (UFU MC TOM 1) and recurrent parent (UFU TOM 57) based on relevant contrasts. ** = Significant at α = 0.01 by Scheffé's test; ns = Not significant by Scheffé's test; vs.: *versus*; DP = Donor parent; UFU MC TOM 1; RP = Recurrent parent, UFU-57; FW = Fruit mean weight; FS = Fruit shape; PT = Pulp thickness.

Selection gains

The estimates regarding the total selection gains by the Mulamba and Mock (MM) indices and the genotype-ideotype genetic distance (DGI) were 53.34 and 42.31%, respectively (Table 3).

Table 3. Estimates of genetic gains and selection in dwarf tomato populations by different indices.

Variables	Selection indices	
	Mulamba & Mock	Genotype – ideotype
FW	29.71	15.16
FL	6.86	4.82
FD	6.15	1.89
FS	0.59	2.87
NL	14.32	11.66
PT	4.71	2.51
AT	2.31	2.13
βC	-4.41	0.84
LI	-5.07	0.18
SS	0.27	0.14
AA	-2.1	1.01
%GS	53.34	42.31
Selected Genotypes	UFU-DTOM 22#1 UFU-DTOM 8#2-3 UFU-DTOM 22#1-17 UFU-DTOM 4#4-14 UFU-DTOM 8#1-1	UFU-DTOM 22#1 UFU-DTOM 22#1-17 UFU-DTOM 4#4-14 UFU-DTOM 8#4-5 UFU-DTOM 8#2

FW: Average fruit weight (g); FL: Fruit length (cm); FD: Fruit diameter (cm); FS: Fruit shape; NL: Number of locules per fruit; PT: Pulp thickness (cm); AT: Titratable acidity content; βC: β-carotene content (mg·100 mg^{-1}); LI: Lycopene content (mg·100 mg^{-1}); SS: Soluble solids content (°Brix); AA: Acylsugar content (nmols·cm^{-2} leaf).

Through selection using the MM index, greater improvements were observed in all variables related to increased fruit size (average fruit weight, fruit length, fruit diameter, number of locules, and pulp thickness). Selection based on the DGI index showed greater gains in average fruit weight and number of locules. Both selection indices predominantly favoured dwarf tomato populations obtained through the second backcrossing (BC2F2). Specifically, BC2F2 populations UFU-DTOM 22#1-17 and UFU-DTOM 4#4-14 were selected by both indices, showing promise for the development of inbred lines and hybrids with additional advantages.

The differentiated expression of metabolites such as myo-inositol, glycine, acetamide, and dodecanoic acid compared to the commercial cultivar Paronset emphasises the genetic diversity and adaptive capacity inherent among tomato genotypes ($p < 0.01$) (Figure 5).

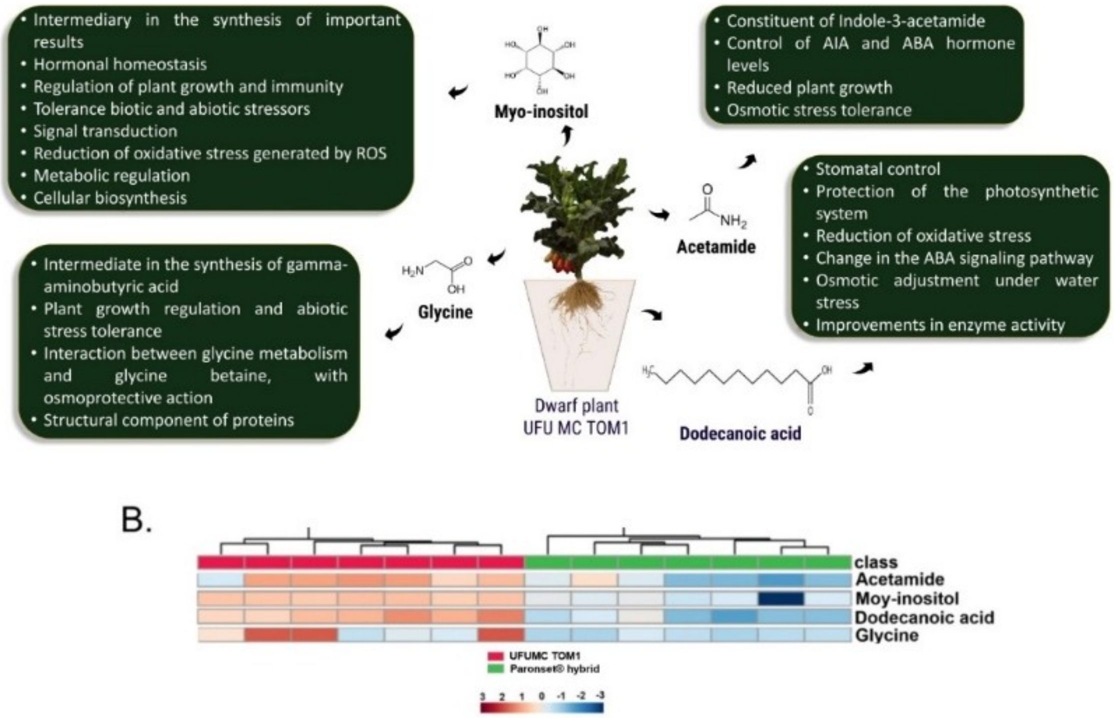

Figure 5. Chromatographic analysis and metabolomic profiling of the dwarf genotype UFU MC TOM 1 compared to the commercial hybrid Paronset ($p < 0.01$). A. The boxes around the plant illustrate the specific roles of each metabolite in plant development and stress response. B. Comparative metabolomic profile between the dwarf genotype UFU MC TOM 1 and the commercial hybrid Paronset. The heatmap shows the differential expression levels of the metabolites, with colour intensity representing the expression levels: red shades indicate higher expression, while blue shades indicate lower expression.

Discussion

Variability and phenotypic improvements

The results of our study revealed significant variability among the evaluated populations, showing substantial improvements in both fruit mass and shape compared to the donor parent (Figure 4). These findings show the efficacy of backcrossing as a valuable method for transferring desirable traits from the donor parent to the progeny, particularly within the context of salad-type tomatoes. Notably, both the recurrent parent and the commercial hybrid exhibited a standard plant architecture, which conferred heightened photosynthetic capacity and a favourable plant morphology conducive to elevated productivity (Figure 1).

However, it is essential to emphasise that the primary objective of this investigation was to verify the increase in production provided by the backcrosses, with a specific focus on the dwarf BC1F2 and BC2F2 populations comparison to the donor parent (UFU MC TOM1). BC2F2 population UFU-DTOM 8#2-3 emerged as particularly promising, demonstrating remarkable increases in fruit mass while also approaching the standard fruit shape for salad-type cultivars. These findings resonate with previous research conducted by Finzi et al. (2020), who similarly highlighted the potential of backcrossing to enhance fruit mass in salad-type tomatoes. In their study, Finzi et al. (2020) reported significant enhancements in fruit mass following backcrossing, with improvements ranging from 341 to 1035%.

Genetic diversity and trait introgression

Through a comprehensive analysis encompassing morphological observations, biochemical assessments, and the utilisation of simple sequence repeats (SSR) markers, Khan et al. (2024) studied the inter- and intra-genetic diversity among various tomato genotypes. Their findings revealed significant differences in agro-morphological traits and biochemical traits among genotypes, indicating considerable variability within the experimental material. SSR profiling identified multiple alleles, and structure analysis unveiled distinct sub-populations, further accentuating the genetic diversity inherent in tomato populations. This observation shows the substantial variability within the experimental material, aligning with our findings of significant variability among the evaluated populations (Figure 3). This suggests the genetic profile and variability within tomato genotypes, providing valuable context to our study's findings on the efficacy of backcrossing in enhancing fruit traits (Khan et al., 2024).

Additionally, the identification of populations with fruit lengths and diameters surpassing those of the donor parent suggests the successful introgression of desirable traits related to fruit size (Figure 4). Fruit characterised by an elongated shape, typical of those from the donor parent, exhibited fewer locules, whereas those with a flattened profile, representative of salad tomatoes, displayed multiple locules (Vazquez et al., 2022). The increase in the number of locules in most backcross-derived dwarf populations compared to the donor parent demonstrates that the fruits align more closely with the salad segment standard (Table 1). Overall, these results contribute to the understanding of genetic variability and trait inheritance in dwarf tomato populations, offering valuable insights for further breeding efforts aimed at developing high-yielding and commercially viable cultivars.

Improvements in fruit characteristics

The success of the backcrossing strategy was demonstrated by the significant improvements observed in fruit characteristics, particularly fruit shape, weight, and pulp thickness. Both the BC1F2 and BC2F2 backcrosses resulted in fruit shapes resembling those of salad tomatoes, indicating successful trait introgression from the donor parent (Figure 4). The substantial increases in fruit mean weight observed in the backcross populations compared to the donor parent further highlight the effectiveness of this breeding approach in enhancing fruit yield-related traits.

The findings of this study reveal the effectiveness of backcrossing as a breeding strategy for enhancing fruit traits in dwarf tomato populations (Bai & Lindhout, 2007). The observed improvements in fruit shape and pulp thickness demonstrate the success of the backcrossing approach in approximating fruit characteristics to the salad standard. Furthermore, the substantial increase in mean fruit weight in BC2F2 populations compared to the donor parent highlights the potential of successive backcrossing generations in achieving the desired enhancements. Although dwarf plants often struggle to attain production levels comparable to normal-sized plants due to their reduced photosynthetic area, hybrid combinations provide a unique opportunity to explore the effects of heterosis and fruit size in normal plants (Finzi et al., 2017).

Related research and comparative analysis

In investigations by Finzi et al. (2020) and Oliveira et al. (2022) focusing on dwarf tomato populations from the salad and cherry tomato segments, respectively, average fruit weight, length, diameter, and pulp thickness surpassed those of the donor parent, demonstrating the success of the conducted backcrosses. In this work, the increments achieved in the populations from the first and second backcrosses, when compared to the donor parent, demonstrated the success of backcrossing in terms of agronomic traits. Additionally, it became apparent that the standard-sized lineage (UFU-57, recurrent parent) exhibited superior means (Table 1) in terms of agronomic traits owing to its phenotype, which was starkly disparate from that of the dwarf plants (Figure 1).

Genome-wide association study has been conducted to identify quantitative trait loci (QTL) for various fruit traits in tomato accessions with diverse genetic backgrounds (Kim et al., 2021). Although our study did not directly identify QTL, the observed increases in fruit mass, β-carotene, and lycopene content as a result of backcrossing in the first and second generations (BC1F2 and BC2F2) significantly improved agronomic fruit traits. Specifically, increases in fruit size, weight, and nutritional quality were noted, with one population showing a 956% increase in fruit mass (Figure 3). This suggests that although specific genetic loci were not identified, the overall improvement in fruit traits supports the potential for marker-assisted selection and genomic selection in future breeding programs aimed at enhancing tomato fruit quality and yield.

Importance of soluble solids and titratable acidity

Previous studies have underscored the pivotal role of titratable acidity in tomato fruit palatability, emphasising its direct correlation with the organic acid concentration and its influence on fruit tanginess and the flavour profile (Anthon & Barrett, 2012; Giordano & Ribeiro, 2000). The critical balance between soluble solids and titratable acidity is essential for tomato taste perception (Raigón et al., 2022). This equilibrium assumes significance, as an excessively diminished acidity relative to the soluble solids content might lead to fruit rejection (Pacco et al., 2014).

The superior performance of the donor parent (UFU MC TOM1) in terms of soluble solids content, evidenced by its highest recorded °Brix value of 7.9 (Table 2), marks a significant advancement in tomato breeding (Meza et al., 2020). This achievement, which surpassed the commercial check by 40%, is crucial, as higher levels of soluble solids are linked to sweeter-tasting fruit and enhanced palatability for fresh consumption. In studies by Vargas et al. (2017) evaluating mini-tomato hybrids under varied management systems, the highest soluble solids content reported was 6.8 °Brix, which is considerably lower than the remarkable performance of UFU MC TOM1. This notable disparity further underscores the advantage of utilising this line as a donor parent in backcrosses.

Genetic improvement strategies

Our study highlights the importance of genetic improvement strategies in enhancing fruit quality attributes in dwarf tomato populations. In fact, there are several methodologies available to evaluate tomato fruit quality; however, they are often complex and require greater investments (Zemach et al., 2023). Our findings demonstrated significant advancements in fruit quality through backcrossing. Specifically, our results highlight the superior performance of the donor parent UFU MC TOM1 and backcrossing in terms of soluble solids content, indicating its potential for yielding fruits with enhanced palatability and nutritional value (Table 2). For fruits intended for industry, a soluble solids content of 5 °Brix or higher is recommended, while for fresh consumption, a minimum of 3 °Brix is preferred (Seabra Junior et al., 2022). All dwarf tomato populations exhibited fruits with a soluble solids content above 5 °Brix, making them promising for this attribute. This aligns with the objectives of tomato breeding programs, where the focus is on improving traits such as soluble solids content, lycopene, and β-carotene levels to enhance fruit pigmentation and nutritional quality (Londonõ-Giraldo et al., 2020).

Although our approach differed from that of Zemach et al. (2023), who identified new associations for complex fruit traits using a phenotype-guided screen of tomato accessions, our study contributes valuable insights into the efficacy of backcrossing in improving fruit quality attributes in dwarf tomato populations. These outcomes emphasise the potential for selecting plants capable of producing fruit with enhanced titratable acidity by utilising the donor parent UFU MC TOM1, offering promising prospects for significant improvements in fruit quality. Furthermore, in tomato breeding programs, the enhancement of lycopene and β-carotene contents stands as a critical objective, given their pivotal roles in fruit pigmentation and their antioxidant properties and provitamin A (Liang et al., 2021). Wild species, such as *S. pennellii*, have been extensively harnessed in tomato breeding endeavours to acquire genes of significant importance for fulfilling desirable traits in commercial plants. The genetic potential exhibited by these dwarf populations for fruit nutritional enrichment shows the importance of considering genotype–environment interactions, reflecting the complexity of carotenoid levels and emphasising the need to integrate environmental contexts into breeding studies.

Pest resistance and acylsugars

Acylsugars are secondary metabolites that may be present in the glandular trichomes of tomato leaflets. The presence of these compounds may confer a lower susceptibility to pests, a highly relevant attribute for crop sustainability and resistance (Resende et al., 2022, Vendemiatti et al., 2024). This study shows the potential of the donor parent (UFU MC TOM1) to contribute to pest resistance traits through its elevated acylsugar content, similar to that found in *S. pennellii* (Figure 2). This aligns with previous research by Finzi et al. (2020), further supporting the notion that the donor parent possesses valuable genetic traits for enhancing pest resistance in its offspring. Additionally, the observed superiority in acylsugar content among certain dwarf tomato populations compared to the recurrent parent and the commercial hybrid Paronset suggests the effectiveness of backcrossing in introducing and enhancing such traits.

Selection gains

Selection gain estimates enabled the selection of superior genotypes in dwarf tomato, aligning with previous studies highlighting the effectiveness of this method in other crops. Pedrozo et al. (2009) efficiently selected superior genotypes in sugarcane populations. Batista et al. (2021) evaluated the efficiency of different selection indices through their estimated gains, highlighting the Mulamba and Mock (1978) rank index as one of the most effective.

Metabolite profiling and stress resistance

Advancements in understanding abiotic stress tolerance in tomato plants can be applied in our study to enhance genotype selection. As demonstrated by Pessoa et al. (2023), the identification of *S. pennellii* introgression lines with abiotic stress tolerance during specific growth stages may be crucial for enhancing the resistance of tomato cultivars to water scarcity. Additionally, the identification of candidate genes associated with abiotic stress tolerance can provide specific targets for genetic improvement, potentially allowing the transfer of these traits to commercially important tomato cultivars. The identification of unique metabolites in genotype UFU MC TOM 1 highlights its potential to impart resistance to various biotic and abiotic stressors in tomato plants (Figure 5).

These findings not only expand our knowledge of the biochemical composition of dwarf tomato plants but also offer insights into their potential roles in sustainable agriculture. Understanding the metabolite profiles of dwarf tomato cultivars can inform breeding programs aimed at developing resilient varieties capable of withstanding environmental challenges while ensuring high-quality fruit production. This study paves the way for further research exploring the molecular mechanisms underlying stress resistance in tomato plants and the development of improved cultivars for future agricultural practices.

Conclusion

The dwarf tomato populations exhibited substantial enhancements in fruit-related variables, which was predominantly attributed to the second backcrossing, facilitating the production of salad-type fruits. Promising prospects for lineage development were observed in populations UFU-DTOM 8#2-3, UFU-DTOM 22#1-17, and UFU-DTOM 4#4-14 resulting from the second backcrossing, potentially contributing to future hybrid breeding endeavours. In addition to the presence of acylsugars in the foliar glands of the dwarf salad-type tomato line, a heightened expression of identified metabolites, including glycine, myo-inositol, acetamide, and dodecanoic acid, was noted. These identified metabolites represent promising avenues for further exploration aimed at bolstering resistance against a spectrum of biotic and abiotic stressors.

Data availability

Not applicable.

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