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Saladette-type dwarf tomato introgression lines with agronomic potential, improved fruit quality, and biotic stress tolerance

Linhagens de introgressão de tomateiro anão do tipo saladete com potencial agronômico, qualidade de frutos e tolerante a estresse biótico

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ABSTRACT

Obtaining introgression lines of saladete-type dwarf tomato plants can provide several advantages in breeding programs. In addition to increasing productivity, the dwarf plant can produce metabolites that are important to resistance to biotic stress. However, there are no saladette-type dwarf tomato introgression lines. The objective of this study was to evaluate the agronomic potential, fruit quality, and secondary metabolites associated with pest resistance for the development saladette-type dwarf tomato introgression lines. The experiment was conducted with 23 treatments, including the UFU MC TOM 1 donor parent, the UFU TOM 5 recurrent parent, the Pizzadoro commercial cultivar (control), 5 populations from the first backcross, and 15 populations from the second backcross. Agronomic and nutraceutical characteristics of fruits and the acylsugar content in the leaflets were evaluated. The genetic dissimilarity was calculated using the generalized Mahalanobis distance (D^2). Genetic gain through selection was estimated using the rank sum index and the genotype-ideotype distance index. The selection indices showed the importance of obtaining the second backcross. The populations UFU_13_1, UFU_17_1, UFU_10_1, UFUi_11_3, UFUi_10_3, and UFU_11_2 have the potential to obtain introgression lines as they present good agronomic and fruit quality characteristics and acylsugar content similar to UFU MC TOM 1. The dwarf tomato germplasm obtained has significant genetic variability and a saladette-type genetic background with the potential to develop introgression lines. The cultivar UFU MC TOM 1 is promising and can overcome the wild access *Solanum pennellii* for breeding programs aimed at pest resistance, increasing productivity, and biofortification of fruits to enhance carotenoids.

Index terms: *Solanum lycopersicum* L.; dwarfism in vegetables; hybrids; metabolomics; sustainable production.

RESUMO

A obtenção de linhas de introgressão de tomateiro anão do tipo Saladete pode proporcionar vantagens em programas de melhoramento. Além do aumento de produtividade, a planta anã pode apresentar metabólitos para o estresse biótico. No entanto, não existe linhas de introgressão de tomateiro anão do tipo Saladete. O objetivo do trabalho foi avaliar o potencial agronômico, qualidade de fruto e metabólitos secundários para resistência a pragas visando a obtenção de linhas de introgressão de tomateiro anão do tipo Saladete. Foram avaliados 23 tratamentos, sendo o genitor doador UFU MC TOM 1, genitor recorrente UFU TOM 5, cultivar comercial Pizzadoro (Testemunha), cinco populações provenientes do primeiro e 15 populações do segundo retrocruzanento. Foram avaliadas características agronômicas e nutraceuticas dos frutos, e acilaçúcares nos folíolos. A dissimilaridade genética foi calculada por meio da distância generalizada de Mahalanobis (D^2) e as estimativas de ganhos genéticos a partir dos índices de soma de ranks e da distância genótipo-ideótipo. Foi possível afirmar a importância de se obter o segundo retrocruzamento. As populações UFU_13_1, UFU_17_1, UFU_10_1, UFUi_11_3, UFUi_10_3 e UFU_11_2 possuem potencial para obtenção de linhas de introgressão por apresentarem boas características agronômicas, qualidade de frutos e teores de acilaçúcar similares a UFU MC TOM 1. O germoplasma de tomateiro anão possui variabilidade genética e background do tipo Saladete com potencial para explorar linhas de introgressão. A cultivar UFU MC TOM 1 é promissora e pode superar o acesso silvestre *Solanum pennellii* para programas de melhoramento visando resistência a pragas, produtividade e frutos biofortificados para carotenoides.

Termos para indexação: *Solanum lycopersicum* L.; nanismo em vegetais; híbridos; metabolômica; produção sustentável.

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Introduction

Tomato (*Solanum lycopersicum* L.) is an important vegetable in the agricultural sector worldwide (Ronga et al., 2021), with global production exceeding 186 million tons in an area of more than 5 million hectares (Food and Agriculture Organization of the United Nations – FAOSTAT, 2023). In 2021, tomato cultivation occupied an area of more than 54,000 hectares in Brazil (Instituto Brasileiro de Geografia e Estatística - IBGE, 2022), significantly contributing to direct and indirect employment creation in the country.

The post-COVID-19 pandemic period has sparked the world's interest in eating healthier (Silva et al., 2022). Its culinary versatility and nutritional properties have increased the consumption of this vegetable, which bears fruits rich in minerals, fiber, carotenoids, and vitamin C, in addition to antioxidant properties (Silva et al., 2021).

The preference for Saladette tomatoes has increased considerably in Brazil (Zayat et al., 2022), resulting in a greater demand for research into new technologies used in the production of this plant type. Additionally, research should be directed towards the development of strategies to promote sustainable production with the plans aligned with the Sustainable Development Goals (SDGs) established by the United Nations (United Nations, 2024). In this context, aiming at reducing pesticide application, new cultivars should be resistant to the main types of biotic stress, especially pests (Smith, 2020), have agronomic potential, and be rich in nutrients (Gomes et al., 2023).

In tomato plants, the presence of acylsugars in the leaflets provides resistance against a broad spectrum of tomato pests. So far, the introgression of genes responsible for this characteristic has only occurred from the wild accession *Solanum pennellii* (Maluf et al., 2010; Maciel et al., 2018; Peixoto et al., 2020). There are reports that the dwarf tomato plant UFU MC TOM 1 has acylsugar contents close to those of the *S. pennellii* accession (Oliveira et al., 2022), along with additional advantages, which make it surpassing the wild accession. Despite the potential use of dwarf plants in genetic improvement, there is no advanced saladette-type dwarf tomato germplasm.

To obtain Saladette tomato hybrids from dwarf male parents, it is necessary to initially obtain dwarf introgression lines with the genetic background of the saladette-type. The introgression of dwarfism genes in tomato can be performed using the UFU MC TOM 1 dwarf line (Maciel, Silva, & Fernandes, 2015) through backcrossing (Finzi et al., 2020; Cavasin et al., 2021; Oliveira et al., 2022) focusing on the genetic background for the traits of interest. Backcrossing is a viable and efficient technique, that allows the selection and crossing back of progenies agronomically superior to the donor parent for the characteristics of interest that are introgressed into the genetic background of the recurrent parent (Finzi et al., 2020). Obtaining, selecting, and characterizing the saladette-type dwarf tomato germplasm is important for future breeding programs.

The objective of this study was to evaluate the agronomic potential, fruit quality, and secondary metabolites associated with pest resistance of saladette-type dwarf tomato plants aiming to obtain introgression lines.

Material and Methods

Experiment and treatments

The experiment was conducted between October 2020 and March 2021 in an arched greenhouse (7 × 21 m) with a ceiling height of 4 m, which was covered with 150-micron transparent polyethylene film, with an ultraviolet inhibitor additive and lateral white anti-insect curtains. The greenhouse is located in the Vegetable Experimental Station of the Federal University of Uberlândia (UFU), Monte Carmelo Campus, MG, Brazil (18°42′43,19″ S, 47°29′55,8″ W and altitude of 873 m).

The experiment consisted of 23 treatments, including 5 first backcross populations (BC_1; UFU _17, UFU _4, UFU _13, UFU _10, and UFU _11), 15 s backcross populations (BC_2; UFU_17_1, UFU_10_1, UFU_4_1, UFU_11_1, UFU_10_2, UFU_4_2, UFU_10_3, UFU_17_2, UFU_17_3, UFU _13_1, UFU _13_2, UFU _11_2, UFU _4_3, UFU_10_4, and UFU_11_3), UFU MC TOM 1 donor parent, UFU TOM 5 recurrent parent, and Pizzadoro commercial cultivar (control).

Saladette-type dwarf tomato populations were obtained from the cross between the pre-commercial homozygous line with saladette-type fruits and indeterminate growth (UFU TOM 5) ♀ and the dwarf mini-tomato line UFU MC TOM1) ♂ (Maciel, Silva, & Fernandes, 2015). To obtain the first backcross populations (BC_1), the F generation (UFU TOM 5♀ versus UFU MC TOM1♂) was crossed to UFU TOM 5 (recurrent parent), followed by self-fertilization.

The second backcross (BC_2) generation was derived from the cross between previously selected dwarf plants of the segregating generation BC_1 and UFU TOM 5 (recurrent parent), followed by self-fertilization. Subsequently, only dwarf plants were selected from the segregating generations, and normal plants were discarded. The selection of dwarf plants from the segregating populations, which originated from the natural self-fertilization of BC_1 and BC_2 generations (Figure 1) was possible owing to prior knowledge of the type of genetic inheritance of dwarfism in tomato plants (Maciel, Silva, & Fernandes, 2015; Oliveira et al., 2022).

The seeds were sown in polystyrene trays (200 cells) filled with a coconut fiber substrate. At 40 days after sowing (DAS), the seedlings were transplanted into 5-L plastic pots containing the same substrate used for sowing. The experiment was conducted in a protected environment, which is recommended for tomato cultivation (Alvarenga, 2013). The recurrent parent and the commercial controls were vertically staked with two stems in a staking system using plastic ribbons.

The experiment was laid out in a randomized complete block design (RCBD) with four replications. Each experimental plot consisted of six plants. Agronomic, nutritional, and pest resistance parameters were evaluated.

Agronomic evaluation

Fruit harvest started at 90 DAS. Ripe fruits were harvested, counted, and weighed, and their mean weight (MW, g) was determined. Subsequently, 15 fruits per plot were sampled and evaluated for the following parameters:

Fruit length (FL, cm): measured from the scar in the peduncle inserted at the floral meristem termination of the fruit (Oliveira et al., 2022).

Fruit diameter (FD, cm): measured in the transversal direction of the vertically cut fruit (Oliveira et al., 2022).

Fruit shape index (FS): the ratio of the transversal diameter to the longitudinal diameter of the fruit (Gomes et al., 2021).

Pulp thickness (PT, mm): determined by the greatest distance from the mesocarp of the fruit (Finzi et al., 2020).

Number of loci (NL): the direct count of the number of loci in the fruit (Gomes et al., 2021).

Plant height (PH, cm): the vertical length of the whole plant measured using a tape (Finzi et al., 2020).

Internode length (IL, cm): calculated as the ratio of plant height to internode number determined at the end of the crop cycle (155 DAS)

Assessments of fruit quality properties and acylsugar content in the leaflets

The content of acylsugars (nmol. cm^2 of leaf area), the allelochemicals that provide broad-spectrum suppression of pests (Maluf et al., 2010; Santos et al., 2020), was determined at 75 DAS using a sample which was composed of eight leaf disks (equivalent to 4.2 cm^2) from each plant in the plot. The disks were collected from the leaflets from the upper third of the plants and then placed in test tubes. The extraction and quantification of acylsugars followed the methods described by Maciel and Silva (2014).

The fruit soluble solid content (SSC or ° Brix) was measured in 15 fruit samples per plot using a digital portable refractometer (Atago PAL^{-1} 3810).

β-Carotene and lycopene were extracted and quantified according to the methodology adopted by Nagata and Yamashita (1992), Rodrigues-Amaya (2001), and Rodrigues-Amaya and Kimura (2004). Tomatoes were crushed into a pulp, and 1 g of the pulp was placed in a glass vial containing 3 mL of acetone p.a. The samples were kept in the refrigerator with an absence of light at 8 °C for 48 h. The absorbance of the supernatants of the extracted samples for β-carotene and lycopene was recorded by spectrophotometry at a wavelength of 450 and 470 nm, respectively. The pigments were quantified according to the protocols developed by Rodriguez-Amaya (2001) and Rodriguez-Amaya and Kimura (2004).

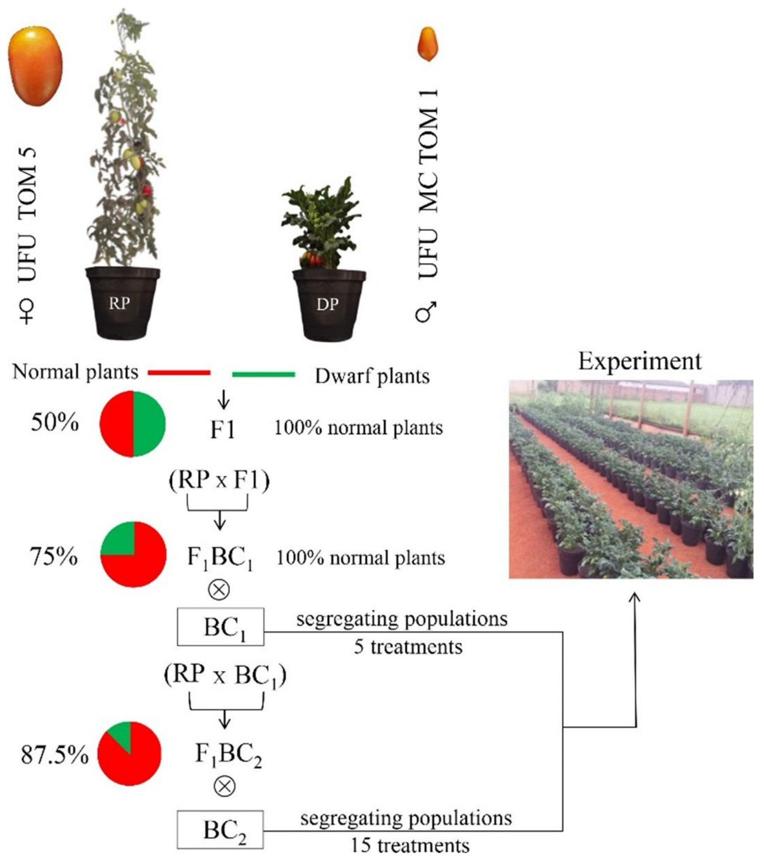

Figure 1: Dwarf tomato populations obtained from the first (BC_1) and second (BC_2) backcross generations used in the experiment; RP = recurrent parent, DP = donor parent, and ⊗= self-fertilization.

Analysis of the metabolic profile using gas chromatography coupled to mass spectrometry (GC-MS)

Six leaflets were collected from the middle portion of the plant and crushed in liquid nitrogen using a mortar and pestle until a fine powder was obtained. Then, 100 mg of the powder was transferred to Eppendorf microtubes containing 2 mL of an extracting solution composed of methanol (MeOH), chloroform ($CHCl_{33}$), and ultrapure water in a 3:1:1 ratio, and 50 µL/mL of Adonitol Purex was added as an internal standard. The samples were then shaken for 5 s using a vortex mixer and allowed to rest for 1 min. Subsequently, 1 mL of the supernatant was transferred to a new microtube containing 300 µL of hexane (p. a.). The samples were left to rest for 3 min, and then, 500 µL of the middle part of the supernatants were collected and transferred to microtubes placed in a concentrator to dry at 40 °C for 24 h. Thereafter, 50 µL methoxyamine hydrochloride dissolved in pyridine (20 mg/mL) was added to dried extracts, and they were incubated at 37 ℃. After 2 h, 50 µL of BSTFA (Bis (trimethylsilyl) trifluoroacetamide) was added, and the samples were again incubated at 37 ℃ for 30 min. The derivatized aliquots were transferred to 2 mL vials containing 200 µL volume-reducing inserts to perform chromatographic analysis.

The analysis was performed by a gas chromatograph-mass spectrometer (GCMS-QP2010, Shimadzu, Kyoto, Japan), with a DB-5MS capillary column (30 m × 250 ***µ***m internal diameter). The temperature of the injection port was 250 °C. Gas chromatographic separation was carried out in a column at an initial column temperature of 80 °C, which was maintained for 2 min and then increased at a rate of 5 °C/min until reaching 250 °C. The final temperature was maintained for 5 min, with a constant flow of helium gas at 1.0 mL/min and an injection volume of 1 ***µ***L with a split ratio of 10:1. Mass spectra were scanned in the range of 40 to 650 m/z in full-scan mode, with 5 scans per second. The solvent cutoff time was set at 3 min, considering the retention time of pyridine used in the derivatization step. The interface and ion source temperatures were 280 °C. The detector voltage was set at 1.2 kV, and the electron-impact (EI) ionization method was selected for metabolite ionization at 70 eV. Standard solutions of n-alkanes (C9-C30) were used for quality control and the calculation of retention indices. Compound identification was performed using the NIST Mass Spectral Library 2017, focusing on compounds with hits that had a similarity score of more than 85% and matched m/z values. The data were processed using MS-DIAL software v. 4.9.221218, MetaboAnalyst v. 5.0, and OriginLab v. 10.0.

Statistical analyses

To perform the presupposition test on data, they were analyzed for the normality of regression residuals (Kolmogorov-Smirnov Test), homogeneity of variances (O'neill and Mathews test), and additivity of blocks (Tukey). Subsequently, the data were subjected to the analysis of variance (ANOVA) using the F test ($\alpha = 0.05$) (Montgomery, 2000). The mean values were compared using the Scott-Knott test ($\alpha = 0.05$) and Dunnett's test ($\alpha = 0.05$), with the dwarf donor parent (UFU MC TOM1) taken as a control to verify the gains obtained by backcrossing (Scott & Knott, 1974; Dunnett,1995).

Contrasts of interest were analyzed by Scheffé's test ($\alpha = 0.01$ and 0.05) for all characteristics to compare dwarf populations obtained from the first backcross (BC_1) versus donor parent (UFU MC TOM1), dwarf populations obtained from the second backcross (BC_2) versus donor parent (UFU MC TOM1), dwarf tomato BC_2 populations versus BC_1 populations, recurrent parent versus BC_1 populations, and recurrent parent versus BC_2 populations. The analyses were performed using the Genes software integrated with R (Cruz, 2016).

Analysis of genetic dissimilarity

The genetic distance between dwarf tomato plant populations derived from the first and second backcross generations (BC_1 and BC_2) and the donor parent (UFU MC TOM1) was calculated by the Mahalanobis generalized distance matrix (D^2) using the Genes software integrated with R (Cruz, 2016). The genetic dissimilarity among genotypes was represented by a heat map of the maximum and minimum distances obtained from the Mahalanobis distance matrix using the R software (R Core Team, 2024) and the ggplot2 package (Wickham, 2016).

Estimates of selection genetic gains by different indices

For the estimates of selection gains, only dwarf phenotypes were considered, with a selection intensity of 33.3%. The techniques used were the rank sum index by Mulamba and Mock (1978) (MM) and the genotype-ideotype distance index (GIDI) (Cruz, Regazzi, & Carneiro, 2012). The selection criterion was a decrease in values of IL and PH accompanied by an increase in values of the other characteristics. The economic weight used in the selection indices was equal to the coefficient of the genetic variation (CVg), as recommended by Cruz, Regazzi and Carneiro (2012). As for the GINI, the optimal values and the lower and upper limits were considered the most desirable measures of evaluation.

Analysis of selection gain estimates by the two indices, MM and GIDI, was performed using the Genes software integrated with R (Cruz, 2016).

Results and Discussion

Agronomic evaluation

BC_1 and BC_2 populations of saladette-type dwarf tomato, the UFU MC TOM 1 dwarf donor parent, the UFU TOM 5 recurrent parent, and the Pizzadoro cultivar showed significant differences in all variables, indicating the existence of variability among treatments (F test; $\alpha = 0.05$).

The donor parent exhibited a marked increase in the first (BC_1) and second backcross (BC_2). The fruits produced by BC_1 and BC_2 populations of dwarf tomato had 4.03- and 5.1-fold greater length than those of the UFU MC TOM 1 donor parent, respectively (Scott-Knott and Dunnett; $\alpha = 0.05$) (Table 1).

Table 1: Mean values of agronomic traits evaluated in saladette-type dwarf tomato populations obtained from the first (BC_1) and second backcross (BC_2) generations.

Populations	Backcrosses	WM (g)	FL (cm)	FD (cm)	FS	PT (cm)	NL (locules per fruit)	PH (cm)	IL (cm)
UFU _17_1	BC_2	24.53 c *	5.01 b *	2.84 c *	1.77 a ^{ns}	0.53 b *	2.63 a *	43.56 b *	1.95 c *
UFU _10_1	BC_2	24.38 c *	4.66 b *	2.79 c *	1.70 b ^{ns}	0.51 b *	2.94 a *	34.38 c ^{ns}	1.68 d ^{ns}
UFU_ 4_1	BC_2	24.57 c *	4.57 b *	2.78 c *	1.64 b ^{ns}	0.45 b *	2.64 a *	35.90 c ^{ns}	1.93 c *
UFU _11_1	BC_2	20.40 c *	4.43 b *	2.62 c *	1.70 b ^{ns}	0.48 b *	2.73 a *	36.56 c ^{ns}	1.86 c ^{ns}
UFU _10_2	BC_2	26.58 c *	4.87 b *	2.59 c *	1.88 a ^{ns}	0.40 b *	2.24 b ^{ns}	37.63 c ^{ns}	1.78 d ^{ns}
UFU _4_2	BC_2	23.65 c *	5.04 b *	2.98 c *	1.72 b ^{ns}	0.49 b *	2.54 a *	46.50 b *	2.26 c *
UFU _10_3	BC_2	23.57 c *	4.66 b *	3.02 c *	1.55 b *	0.52 b *	2.80 a *	37.38 c ^{ns}	1.70 d ^{ns}
UFU _17_2	BC_2	23.90 c *	4.49 b *	2.74 c *	1.64 b ^{ns}	0.47 b *	2.46 a *	39.41 c ^{ns}	1.92 c *
UFU _17_3	BC_2	25.61 c *	4.86 b *	2.73 c *	1.79 a ^{ns}	0.51 b *	2.52 a *	46.00 b *	1.86 c ^{ns}
UFU _13_1	BC_2	23.78 c *	4.96 b *	2.78 c *	1.79 a ^{ns}	0.51 b *	2.62 a *	41.56 b *	1.88 c ^{ns}
UFU _13_2	BC_2	20.00 c *	4.72 b *	2.88 c *	1.64 b ^{ns}	0.54 b *	2.65 a *	35.94 c ^{ns}	1.61 d ^{ns}
UFU _11_2	BC_2	20.27 c *	4.36 b *	2.43 c *	1.80 a ^{ns}	0.48 b *	2.63 a *	37.31 c ^{ns}	1.75 d ^{ns}
UFU _4_3	BC_2	26.61 c *	4.86 b *	2.92 c *	1.69 b ^{ns}	0.51 b *	2.73 a *	39.88 c ^{ns}	1.96 c *
UFU _10_4	BC_2	22.12 c *	4.51 b *	2.54 c *	1.78 a ^{ns}	0.48 b *	2.55 a *	49.63 b *	2.17 c *
UFU _11_3	BC_2	24.14 c *	5.15 b *	2.56 c *	2.01 a ^{ns}	0.48 b *	2.86 a *	40.28 c *	1.97 c *
UFU _17	BC_1	22.42 c *	4.83 b *	2.71 c *	1.79 a ^{ns}	0.53 b *	2.55 a *	39.31 c ^{ns}	1.93 c *
UFU _4	BC_1	15.24 d *	3.95 c ^{ns}	2.52 c *	1.58 b *	0.42 b *	2.35 b ^{ns}	32.25 c ^{ns}	1.57 d ^{ns}
UFU _13	BC_1	22.67 c *	4.74 b *	3.20 b *	1.50 b *	0.50 b *	2.79 a *	38.63 c ^{ns}	1.58 d ^{ns}
UFU _10	BC_1	16.60 d *	4.58 b *	2.58 c *	1.78 a ^{ns}	0.42 b *	2.56 a *	43.88 b *	1.69 d ^{ns}
UFU _11	BC_1	16.18 d *	3.57c ^{ns}	2.18d ^{ns}	1.64 b ^{ns}	0.33 c *	2.25 b ^{ns}	42.75 b *	1.60 d ^{ns}
Pizzadoro	Check	56.94 b *	6.93 a *	3.87 a *	1.79 a ^{ns}	0.86 a *	2.75 a *	94.38 a *	7.19 b *
UFU TOM 5	RP	63.41 a *	6.59 a *	3.83 a *	1.72 b ^{ns}	0.85 a *	2.78 a *	95.38 a *	7.86 a *
UFU MC TOM1[a]	DP	4.62 e	3.19 c	1.65 e	1.94 a	0.20 d	2.00 b	30.25 c	1.22 d
DMS Dunnett		6.91	0.91	0.65	0.32	0.13	0.54	10.11	0.66
Mean		24.88	4.76	2.77	1.73	0.50	2.58	44.31	2.29
CV%		13.12	9.01	11.11	8.63	12.40	9.76	10.77	13.64

MW: mean weight; FL: fruit length; FD: fruit diameter; FS: fruit shape index; PT: pulp thickness; NL: number of locules; PH: plant height; IL: internode length; RP: recurrent parent; DP: donor parent; and check (control): commercial cultivar. Mean values followed by different letters in the column differ from each other according to the Scott-Knott test at 0.05. *Mean values in the column differ from the UFU MC TOM 1 dwarf donor line control according to Dunnett's test at the level of 0.05. ^{ns} Mean values in the column do not differ from the UFU MC TOM 1 dwarf donor line control according to Dunnett's test at the level of 0.05. [a] check in the Dunnett's test.

Among the BC_1 dwarf tomato populations, UFU_17 and UFU_13 produced larger fruits with an MW value greater than 22 g, similar to BC_2 populations, for which, a mean MW of 23.6 g was observed (Scott-Knott test; α = 0.05). In addition to the highest fruit weight, UFU_13 from the BC_1 population showed a higher FD value than the other dwarf tomato populations (Scott-Knott test; α = 0.05).

Overall, 90% of the dwarf tomato populations produced fruits with 47.5% and 67.3% higher FL and FD values than the UFU MC TOM 1 donor parent, respectively (Scott-Knott and Dunnett tests; α = 0.05). Furthermore, all BC_1 and BC_2 dwarf tomato populations showed a 2.4-fold higher mean PT value than the donor parent (Scott-Knott and Dunnett tests; α = 0.05).

The superiority of dwarf tomato populations obtained from the first (BC_1) and second backcrosses (BC_2) to the UFU MC TOM 1 donor parent in terms of MW, FL, FD, and PT indicated the efficiency of backcrossing in increasing fruit size. These characteristics are associated with the fruit size (Vazquez et al., 2022). Similar results were obtained by Finzi et al. (2020) and Oliveira et al. (2022), who obtained saladette-type dwarf and salad tomato populations, respectively, from the first-generation backcross (BC_1) with a larger fruit size compared to the dwarf donor parent.

All BC_1 and BC_2 populations of dwarf tomato, the donor parent (UFU MC TOM 1), the recurrent parent (UFU TOM 5), and the Pizzadoro cultivar showed FS values of more than 1.5, indicating fruits with an elongated shape (Andrade et al., 2014), which is ideal for the saladette-type tomatoes. The predominance of this trait (FS) among dwarf tomato parental lines and backcross populations is due to the fact that the elongated shape of the fruits is a recessive trait with monogenic inheritance (Maciel & Silva, 2008).

The increased fruit size of BC_1 and BC_2 tomato populations, which is associated with the elongated fruit shape, similar to that observed for the UFU TOM 5 recurrent parent and the Pizzadoro cultivar, proves that the fruit characteristics of the saladette-type (recurrent parent) were recovered in dwarf tomato populations as a result of backcrossing. Although backcrossing is the most commonly employed method in interspecific hybridization, studies conducted by Finzi et al. (2020), Cavasin et al. (2021), Gomes et al. (2021), and Oliveira et al. (2021) demonstrated the efficiency and effectiveness of this technique in recovering fruit agronomic characteristics of tomatoes from different segments after the introgression of genes that are involved in dwarfism into intraspecific crosses.

NL is a relevant characteristic that determines the shape and size of fruits (Chu et al., 2019). In general, fruits with a smaller NL have more elongated shapes, whereas flattened fruits have multiple locules (Vazquez et al., 2022), which is undesirable for saladette-type tomatoes. The dwarf tomato populations UFU_17 and UFU_11 (BC_1), along with UFU_10_2 (BC_2), showed the lowest NL values among all populations, with no difference from the UFU MC TOM 1 donor parent, which had two locules per fruit (Scott-Knott and Dunnett tests; α = 0.05). However, NL, which is a predominant characteristic in saladette-type fruits, was lower than three in all dwarf tomato populations, the Pizzadoro cultivar, and the recurrent parent (UFU TOM 5) (Alvarenga, 2013).

The UFU MC TOM 1 donor parent exhibited the lowest PH (30.25 cm) and IL (1.22 cm) values. Among the dwarf tomato populations, the BC_1 populations UFU_4 and UFU_13, as well as the BC_2F_2 populations (UFU_10_1, UFU_11_1, UFU_10_2, UFU_10_3, UFU_13_2, and UFU_11_2) did not differ from the donor parent in both of these characteristics (Dunnett test; α = 0.05). In contrast, normal-sized tomato plants (recurrent parent and Pizzadoro cultivar) were superior to saladette-type dwarf tomato populations in terms of PH and IL, with means of 137.2% and 310.6%, respectively (Scott-Knott test; α = 0.05).

IL is a trait that directly influences PH (Sun et al., 2019; Liu et al., 2020). Plants with short internodes are desired in tomato breeding programs, as they have a more compact plant architecture that favors mechanized harvesting and crop treatments, thereby producing higher yields (Rajendran et al., 2022). Thus, the saladette-type dwarf tomato populations evaluated in this study are important genetic resources for obtaining future hybrid crops with more compact architecture and higher productivity, as well as mini-tomatoes (Finzi et al., 2017).

Fruit quality and acylsugar content in the leaflets

BC_1 and BC_2 populations of saladette-type dwarf tomato plants are promising for segments of fresh produce consumers, as they produced fruits with an SSC higher than 4.91 ° Brix (Scott-Knott test; α = 0.05) (Table 2). Tomatoes used for fresh consumption are required to have an SSC ≥ 3 ° Brix, while for industrial purposes, they should have an SSC ≥ 5 ° Brix (Peixoto et al., 2018; Seabra Junior et al., 2022). According to Seabra Junior et al. (2021), the tomatoes from the Saladette segment have good organoleptic quality and a higher SSC content, leading to a more pleasant taste, which makes them suitable for fresh consumption, as observed in this study.

The increase in fruit size promoted by backcrossing may be related to decreased SSC content in the fruits of dwarf tomato populations because, according to Beckles (2012), SSC is inversely proportional to fruit size.

In addition to influencing tomato fruit pigmentation, both lycopene and β-carotene are also important in the human diet owing to their antioxidant and provitamin A properties (Liang et al., 2021; Orchard et al., 2021). Thus, tomato populations rich in these carotenoids are used for the production of functional foods for both fresh and processed consumption (Martínez-Hernández et al., 2016). In this study, 45% of the saladette-type dwarf tomato populations showed a higher lycopene content than both parents and the Pizzadoro cultivar (Scott-Knott test; α = 0.05). Moreover, the donor parent, the Pizzadoro cultivar, and 65% of the dwarf tomato populations had an average 1.7-fold higher β-carotene content than the recurrent parent (1.66 mg/100 g).

Table 2: Mean values of fruit quality characteristics and acylsugar content in the leaflets of saladette-type dwarf tomato populations obtained from the first (BC_1) and second backcross (BC_2) generations.

Populations	Backcrosses	SSC (°Brix)	LC (mg/100 g)	BC (mg/100 g)	AA (nmol/cm² of leaf area)
UFU_SDI_17_1	BC_2	5.36 b*	3.03 b ns	3.01 a ns	22.43 c ns
UFU_SDI_10_1	BC_2	5.54 b*	2.99 b ns	2.50 a ns	27.69 b ns
UFU_SDI_4_1	BC_2	5.64 b*	2.29 c ns	2.31 b ns	27.37 b ns
UFU_SDI_11_1	BC_2	5.25 b*	2.93 b ns	2.72 a ns	30.02 b ns
UFU_SDI_10_2	BC_2	5.77 b*	2.74 c ns	2.44 a ns	27.24 b ns
UFU_SDI_4_2	BC_2	5.69 b *	2.73 c ns	2.09 b ns	23.17 c ns
UFU_SDI_10_3	BC_2	5.54 b*	3.02 b ns	2.56 a ns	27.39 b ns
UFU_SDI_17_2	BC_2	5.55 b*	3.57 a*	3.47 a ns	19.71d *
UFU_SDI_17_3	BC_2	5.43 b*	2.77 c ns	1.64 b*	20.74 c *
UFU_SDI_13_1	BC_2	5.75 b*	2.95 b ns	2.92 a ns	27.59 b ns
UFU_SDI_13_2	BC_2	5.29 b*	2.77 c ns	2.45 a ns	23.84 c ns
UFU_SDI_11_2	BC_2	5.90 b*	3.03 b ns	2.83 a ns	27.99 b ns
UFU_SDI_4_3	BC_2	6.10 b*	2.52 c ns	2.30 b ns	24.61 b ns
UFU_SDI_10_4	BC_2	5.38 b*	2.81 c ns	2.46 a ns	29.42 b ns
UFU_SDI_11_3	BC_2	6.00 b*	3.12 b ns	2.25 b ns	20.97 c *
UFU_SDI_17	BC_1	5.67 b*	2.53 c ns	2.59 a ns	18.24 d *
UFU_SDI_4	BC_1	6.54 b*	2.34 c ns	1.73 b*	23.65 c ns
UFU_SDI_13	BC_1	5.53 b*	2.42 c ns	1.94 b ns	27.29 b ns
UFU_SDI_10	BC_1	5.66 b*	2.56 c ns	2.61 a ns	27.51 b ns
UFU_SDI_11	BC_1	4.91 b *	3.78 a*	3.17 a ns	18.42 d *
Pizzadoro	Check	4.81 b*	2.23 c ns	2.57 a ns	15.48 d *
UFU TOM 5	RP	5.07 b*	2.64 c ns	1.66 b ns	16.57 d *
UFU MC TOM 1[a]	DP	8.71a	2.50 c	2.78 a	29.18 b
Solanum pennellii	Wild access	-	-	-	37.16 a*
DMS Dunnett		1.33	0.67	0.99	6.68
Mean		5.69	2.79	2.47	24.73
CV%		11.02	11.33	18.83	12.76

SSC: soluble solids content; LC: lycopene content; BC: β-carotene content; AA: acylsugar content; RP: recurrent parent; DP: donor parent; and check (control): commercial cultivar; Mean values followed by different letters in the column differ from each other according to the Scott-Knott's test at 0.05. *Mean values in the column differ from the UFU MC TOM 1 dwarf donor line control according to Dunnett's test at the level of 0.05. ns Mean values in the column do not differ from the UFU MC TOM 1 dwarf donor line control according to Dunnett's test at the level of 0.05. a: check (control) in Dunnett's test.

The dwarf tomato populations UFU_17_2 and UFU _11 stood out with lycopene and β-carotene contents of higher than 3.00 mg/100 g. Saladette commercial hybrid tomatoes evaluated by Mian et al. (2021) and Seabra Junior et al. (2022) showed lycopene and β-carotene contents of lower than 2.73 mg/100 g and 1.33 mg/100 g, respectively. The β-carotene and lycopene contents in the fruits of the commercial cultivar Pizzadoro evaluated in these studies were similar to those found by Mian et al. (2021) and Seabra Junior et al. (2022). The populations UFU_17_2 and UFU_11 showed, on average, 1.65 and 1.30 times higher levels of lycopene and β-carotene, respectively, than the Pizzadoro cultivar. The results of this research indicate that saladette-type dwarf tomato plants have the potential to produce high levels of these carotenoids and are also considered biofortified.

Acylsugars are important secondary metabolites synthesized in type-IV glandular trichomes present in tomato leaflets that confer pest resistance (Marinke et al., 2022; Resende et al., 2022). The wild species *Solanum pennellii,* which is used for comparing acylsugar levels among saladette-type dwarf tomato populations, exhibited the highest mean value (37.16 nmol/ cm^2 of leaf area), whereas the recurrent genitor UFU MC TOM 5, the Pizzadoro cultivar, and the tomato populations UFU_SDI_17_2, UFU_SDI_17, and UFU_SDI_11 showed acylsugar levels lower than 20 nmol/ cm^2 of leaf area (Scott-Knott test; $\alpha = 0.05$).

The UFU MC TOM 1 donor parent and 75% of the dwarf tomato populations showed moderate levels of this metabolite, which ranged from 22.43 to 30.02 nmol/ cm^2 of leaf area (Scott-Knott and Dunnet tests; $\alpha = 0.05$). The acylsugar content in these dwarf tomato populations was approximately 65% higher than that in the UFU TOM 5 recurrent parent and the Pizzadoro cultivar. Similar results were reported by Gomes et al. (2021) and Oliveira et al. (2022), who evaluated saladette- (BC_1) and Santa Cruz-type (BC_1) dwarf tomato populations. Furthermore, the classification of dwarf tomato populations based on their acylsugar content into three groups (Table 2) according to Scott-Knott's test ($\alpha = 0.05$) corroborates the findings obtained by Dias et al. (2021), who reported that segregation for acylsugar content is commonly observed in studies on advanced tomato populations.

The BC_2 UFU_SDI_11_1 population showed an acylsugar content of 30.02 nmol per cm^2 of leaf area, indicating the relative superiority of this population (98%) in terms of acylsugar content compared to the commercial check (control) (15.48 nmol/ cm^2 of leaf area). As reported by Maluf et al. (2010), hybrids obtained from crossing between a low-acylsugar-producing line and a high-acylsugar-producing line had moderate acylsugar levels, promoting broad-spectrum pest resistance. Thus, we highlighted the possibility of using UFU_SDI_11_1 dwarf plants that are rich in acylsugars to develop hybrids by intercrossing several existing normal lines with low acylsugar levels.

By analyzing the metabolic profile of the leaves of the dwarf cultivar (UFU MC TOM 1) and the commercial cultivar Santa Clara using GC-MS, significant increases were found in the expression levels of amino acids such as L-alanine, L-aspartate, L-serine, and L-threonine in UFU MC TOM 1 (at the significance level of 5% by T-test) (Figure 2).

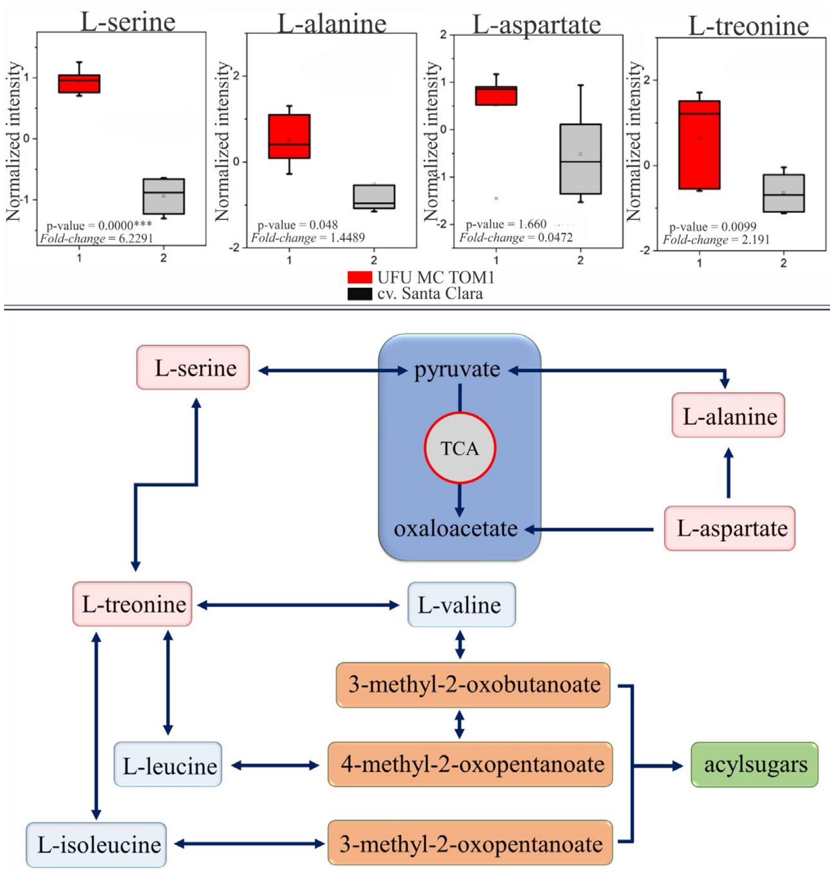

Figure 2: Amino acids identified in the leaves of the UFU MC TOM 1 dwarf tomato plants and the commercial cultivar Santa Clara by metabolomic analysis using GC-MS; precursors in the pathway of fatty acid elongation for the production of acylsugars; TCA cycle: tricarboxylic acid cycle; The statistical T-test was performed at a significance level of 5%. Note: *** indicates p < 0.01.

These compounds play fundamental roles in the tricarboxylic acid (TCA) cycle, one of the most important metabolic pathways involved in cellular defenses against biotic and abiotic stresses (Abdelsalam et al., 2023). This pathway is associated with the production of intermediate metabolites that directly impact the immune response, the modulation of cellular homeostasis, and the cellular antioxidant activity (Choi, Son, & Baek, 2021; MacLean, Legendre, & Appanna, 2023).

The amino acids L-alanine and L-serine act as the precursors for the biosynthesis of pyruvate, while L-aspartate serves as a precursor of oxaloacetate, one of the key substances regenerated in the TCA cycle (Araujo et al., 2012). In addition, L-serine can be used as a precursor of L-threonine, an amino acid essential for the biosynthesis of L-valine, L-leucine, and L-isoleucine, which are of great importance, as they can be metabolized into the precursors for the production of acylsugars in the pathway of fatty acid elongation (3-methyl-2-oxobutanoate, 4-methyl-2-oxopentanoate, and 3-methyl-2-oxopentanoate, respectively) (Figure 2) (Slocombe et al., 2008; Moutiez, Belin, & Gondry, 2017). These processes help in regulating plant homeostasis, conferring resistance to abiotic and biotic stresses, osmotic regulation, and ATP generation (Maeda, 2019; Singh, Dhanapal, & Yadav, 2019; Liu et al., 2023).

Thus, from a biochemical point of view, the UFU MC TOM 1 cultivar has been validated as an accession rich in acylsugars and a potential new alternative for the promotion of breeding programs. Additionally, it can be emphasized that UFU_SDI_11_1 can be considered an important introgressed lineage as it is rich in acylsugars present in the leaflets and already has an advanced genetic background of saladette-type tomato plants.

In view of this, it is suggested by Maluf et al. (2010) to use UFU_SDI_11_1 dwarf plants that are rich in acylsugars to obtain hybrids by intercrossing several existing normal lines with a low acylsugar content.

Contrast estimation

The efficiency of backcrossing in obtaining dwarf tomato populations with fruit characteristics of the Saladette segment is evident from the results of the comparison tests (Scott-Knott and Dunnett), which were confirmed by the estimated contrasts. Estimates of contrasts between BC_2 populations and the UFU MC TOM 1 donor parent and between BC_1 populations and the UFU MC TOM 1 donor parent tested by the Scheffé's test (α = 0.01 and 0.05) indicated the successful improvement of fruit characteristics by backcrossing. The first (BC_1) and second (BC_2) backcrosses increased the MW and PT values of fruits of dwarf tomato populations (Figure 3A and 3C, respectively).

The differences in MW and PT between BC_1 populations of dwarf tomato and the donor parent were 14.01 g and 0.24 cm, respectively. Comparisons between BC_2 populations and the UFU MC TOM 1 donor parent showed that the second backcrossing further improved MW, PT, FL, and FD (Scheffé's test; α = 0.01 and 0.05) (Figures 3A, 3B, 3C, and 3D, respectively). The difference in MW between BC_2 populations of dwarf tomato and the donor parent was approximately 19 g. Furthermore, fruits of BC_2 populations showed differences of 0.29, 1.55, and 1.10 cm in PT, FL, and FD, respectively, compared to UFU MC TOM1 fruits.

The contrasts between BC_1 and BC_2 populations and the UFU MC TOM 1 donor parent and between backcross populations BC_1 and BC_2 of dwarf tomato showed no significant differences in PH and IL (Figures 3E and 3F, respectively). On the contrary, the normal-sized recurrent parent showed improved PH and IL. The recurrent parent was 55.63 cm higher, on average, than the dwarf tomato populations BC_1 and BC_2 and also exhibited more elongated internodes, with a mean difference of 6.08 cm from the dwarf tomato populations.

In contrast, there were no differences between the dwarf salad tomato populations BC_2 and BC_1 in the evaluated variables. This suggests that backcrossing contributes to significant enhancement of genetic gains relative to the donor parents; however, although there were differences between BC_1 and BC_2 populations of saladette-type dwarf tomato, they were small and not significant.

This improvement in several agronomic traits in tomato plants after the first backcrossing was also reported by Gomes et al. (2023). In the F1 generation, the plants have already recovered 50% of the recurrent parent genome, and the first backcrossing increased the value to 75%. After the second backcrossing, further smaller increases were observed (Borém, Miranda, & Fritsche-Neto, 2021); however, this was not evident in dwarf plants. The smaller increase observed in BC_2 may be due to the smaller size of the plant. Hybrids from different dwarf tomato backcrosses should be used to evaluate the breeding potential of introgression lines.

Genetic dissimilarities between saladette-type dwarf tomato populations

The measure of dissimilarity using the Mahalanobis distance D^2 showed genetic variability in the analyzed germplasm of dwarf tomato plants. The distances ranged from 2.05 to 153.48, and the greatest distances were observed between all BC_1 and BC_2 populations of saladette-type dwarf tomato plants and the UFU MC TOM1 donor parent (Figure 4).

The maximum distance between saladette-type dwarf populations was found between the UFU_4 and UFU_11 populations (79.04). Genetic variability is fundamental to genetic improvement in plant breeding programs (Borém, Miranda, & Fritsche-Neto, 2021). Despite the potential use of dwarf tomato plants in breeding, there is great difficulty in creating genetic variability in these plants because only plants that are not commercially standard (dwarf plants) are evaluated, with the use of normal plant morphological traits only for obtaining hybrids (Maciel, Silva, & Fernandes, 2015; Finzi et al., 2017). The results obtained showed the great potential of the evaluated germplasm to be used in fostering future genetic improvement programs.

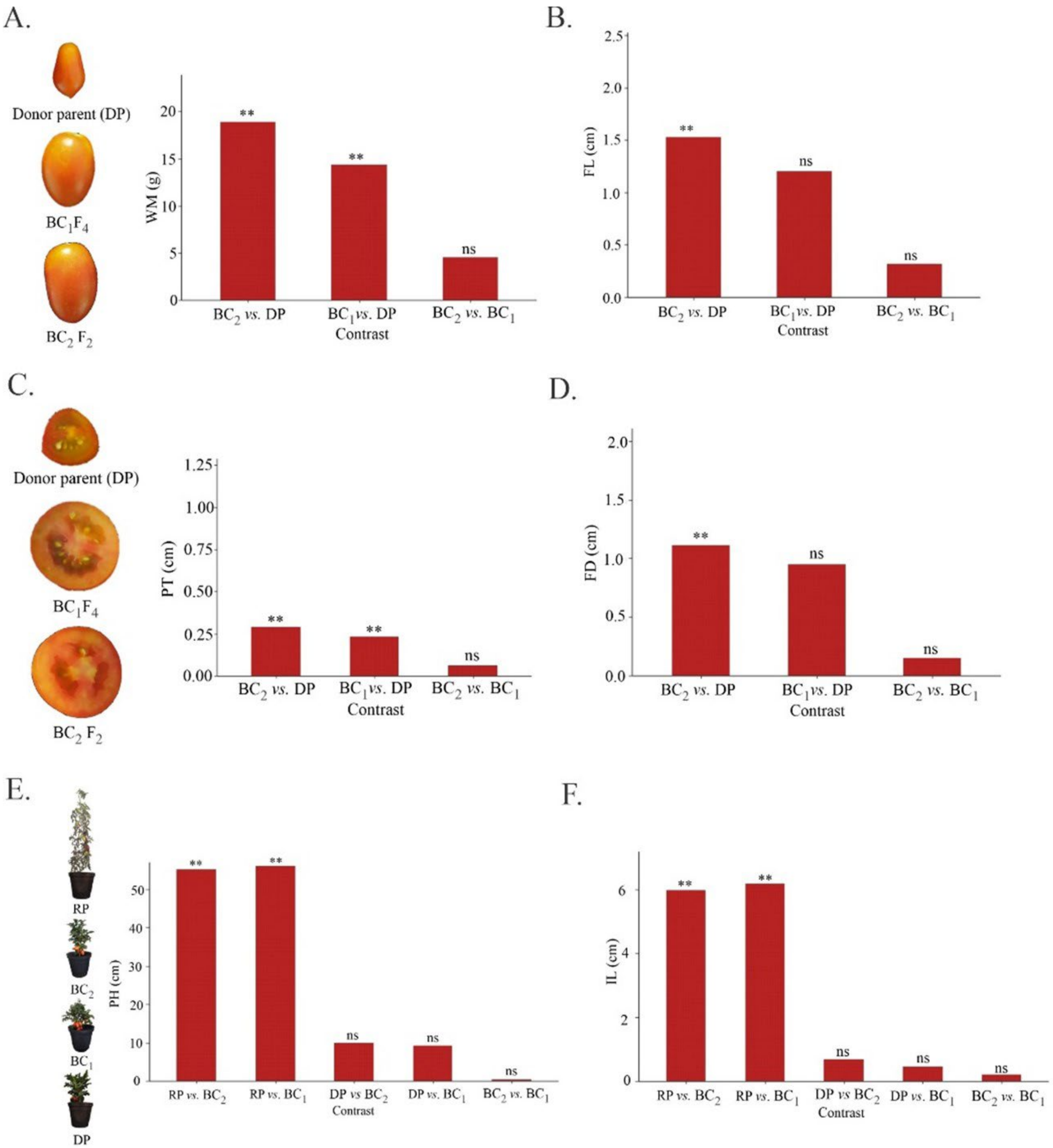

Figure 3: Comparison between BC_1 and BC_2 populations and the donor parent (UFU MC TOM 1) and the recurrent parent (UFU TOM 5) based on the contrasts of interest; ** and * indicate significant differences at α= 0.01 and α= 0.05, respectively, according to the Scheffé's test. ^{ns} = not significant according to the Scheffé's test; *vs.*: versus; BC_1: BC_1 populations; BC_2: BC_2 populations; DP: donor parent (UFU MC TOM 1); RP: recurrent parent (UFU TOM 5); MW = mean weight, FL = fruit length, PT = pulp thickness, FD = fruit diameter, PH = plant height, and IL = internode length.

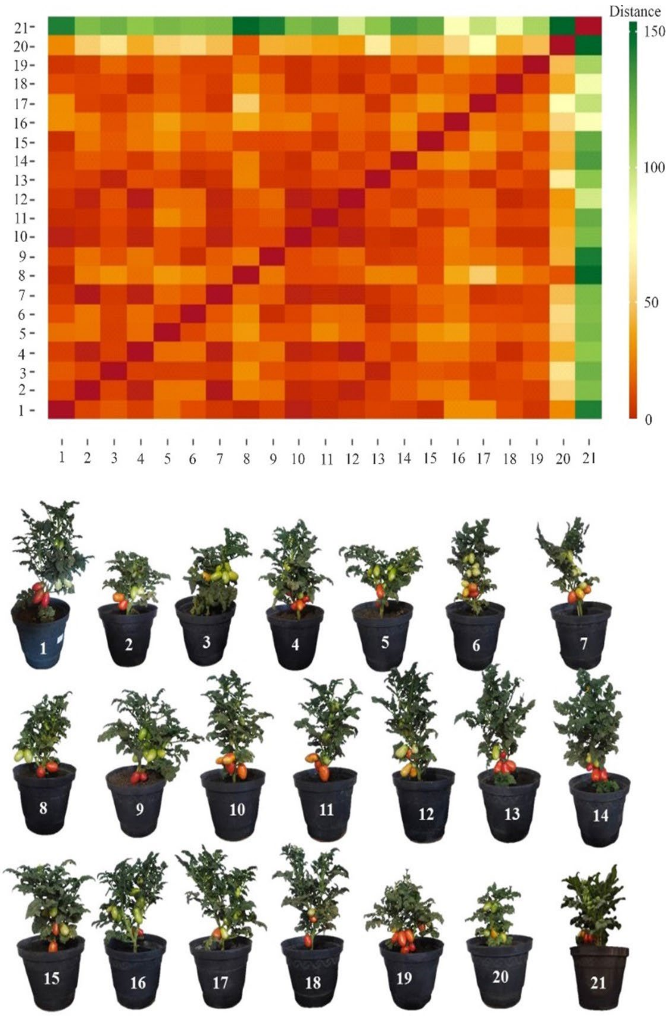

Figure 4: Genetic dissimilarity in the germplasm of dwarf tomato plants based on the Mahalanobis distance D² (1- UFU_SDi_17_1, 2- UFU_SDi_10_1, 3- UFU_SDi_4_1, 4-UFU_SDi_11_1, 5- UFU_10_2, 6- UFU_SDi_4_2, 7- UFU_SDi_10_3, 8- UFU_SDi_17_2, 9- UFU_SDi_17_3, 10- UFU_SDi_13_1, 11-UFU_SDi_13_2, 12-UFU_SDi_11_2, 13- UFU_SDi_4_3, 14- UFU_SDi_10_4, 15- UFU_SDi_11_3, 16- UFU_SDI_17, 17- UFU_SDI_4, 18- UFU_SDi_13, 19- UFU_SDi_10, 20- UFU_SDi_11, and 21- UFU MC TOM 1).

Genetic gain estimates by different selection indices

The total selection genetic gains estimated by MM and GIDI were similar (both greater than 38%) (Table 3).

Selection based on the MM index generated the greatest genetic gains in all characteristics related to fruit size (MW, FL, FD, FS, PT, and NL). Additionally, selection by this index provided the greatest gain in acylsugar content. In contrast, selection using the GIDI resulted in gains of approximately 8% in lycopene and β-carotene, as well as lower gains in PH and IL.

Table 3: Estimates of genetic gains from selection in saladette-type dwarf tomato populations using different selection indices.

Variables	%SG	
	MM	GIDI
WM	9.95	8.33
FL	4.27	3.31
FD	2.78	2.05
FS	1.07	0.79
PT	7.21	6.21
NL	4.69	3.62
PH	-0.55	-0.67
IL	1.24	1.06
SS	-0.41	-1.53
LC	3.57	7.87
BC	3.19	7.98
AA	1.79	-0.49
Total	38.8	38.5
Selected populations	UFU_13_1	UFU _13_1
	UFU_17_1	UFU _17_1
	UFUi_11_3	UFU _11_2
	UFU_4_3	UFU _11_3
	UFU_10_1	UFU _10_3
	UFUi_10_3	UFU _10_1
	UFU_11_2	UFU _17_2

MW: mean weight; FL: fruit length; FD: fruit diameter; FS: fruit shape index; PT: pulp thickness; NL: number of locules; PH: plant height; IL: internode length; SS: soluble solids content; LC: lycopene content; BC: β-carotene content; AA: acylsugar content; MM: rank sum index of Mulamba and Mock; and GIDI: genotype-ideotype distance index.

Both indices selected mostly the dwarf tomato populations obtained from the second backcrossing (BC_2). This result suggests that dwarf tomato populations selected by both indices are promising for the development of introgression lines and subsequently hybrids with additional advantages (Finzi et al., 2017) compared to those by the traditional methodologies (Maciel et al., 2010; Tamta & Singh, 2017). It is suggested that the selection of the best populations can be advanced by successive self-fertilization and obtaining tomato introgression lines and hybrids through exploring the advantages of using dwarf parents in the production of saladette-type tomato plants.

Conclusions

The populations UFU_13_1, UFU_17_1, UFU_10_1, UFU_11_3, UFU_10_3, and UFU_11_2 have the potential to obtain introgression lines as they presented improved agronomic characteristics, fruit quality and acylsugar levels similar to UFU MC TOM 1. The dwarf tomato germplasm showed genetic variability and a genetic background of the saladette-type with the potential for exploring. The cultivar UFU MC TOM 1 can surpass the wild access *S. pennellii* in breeding programs aimed at pest resistance, productivity, and biofortification of fruits (β-carotene and lycopene).

Author Contribution

Conceptual idea: Maciel, G.M.; Methodology design: Oliveira, C.S.; Maciel, G.M.; Data collection: Oliveira, C.S.; Siquieroli, A.C.S.; Ikehara, B.R.M.; Pereira, L.M.; Data analysis and interpretation: Oliveira, C.S.; Maciel, G.M.; Siquieroli, A.C.S.; Pinto, F.G.; Ikehara, B.R.M.; and Writing and editing: Oliveira, C.S.; Maciel, G.M.; Siquieroli, A.C.S; Pinto, F.G.

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References

Abdelsalam, A. et al. (2023). Effect of stress hormones on the metabolome of a suspension culture of the aromatic medicinal plant *Cymbopogon schoenanthus* subsp. proximus. *Plant Cell, Tissue and Organ Culture, 155*:137-163.

Alvarenga, M. A. R. (2013). *Tomate: Produção em campo, em casa-de-vegetação e em hidroponia*. Lavras, Minas Gerais, Brasil: Editora UFLA, 455p.

Andrade, M. C. et al. (2014). Combining ability of tomato lines in saladette-type hybrids. *Bragantia, 73*(3):237-245.

Araujo, W. L. et al. (2012). Metabolic control and regulation of the tricarboxylic acid cycle in photosynthetic and heterotrophic plant tissues. *Plant, cell & environment, 35*(1):1-21.

Beckles, D. M. (2012). Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biology and Technology, 63*(1):129-140.

Borém, A., Miranda, G. V., & Fritsche-Neto, R. (2021). *Melhoramento de plantas*. Sao Paulo, Brazil: Oficina de textos, 384p.

Cavasin, P. Y. et al. (2021). Evaluation of families derived from backcrosses of processed tomato with dwarfism gene. *Crop Breeding and Applied Biotechnology*, *21*(1):e362221113.

Choi, I., Son, H., & Baek, J. H. (2021). Tricarboxylic acid (TCA) cycle intermediates: Regulators of immune responses. *Life, 11*(1):69.

Chu, Y. H. et al. (2019). Tomato locule number and fruit size controlled by natural alleles of lc and fas. *Plant Direct,* 3(7):e00142.

Cruz, C. D. (2016). Genes Software- extended and integrated with the R, matlab and selegen. *Acta Scientiarum. Agronomy, 38*(4):547-552.

Cruz, C. D., Regazzi, A. J., & Carneiro, P. C. S. (2012). *Modelos biométricos aplicados ao melhoramento genético*. Viçosa, Minas Gerais, Brazil: Editora UFV, 514p.

Dias, D. M. et al. (2021). Acylsugars in tomato varieties confer resistance to the whitefly and reduce the spread of fumagine. *Bragantia, 80*:e4421.

Dunnett, C. W. (1955). A multiple comparison procedure for comparing several treatments with control. *Journal American State Association*, *50*(272):1096-1121.

Food and Agriculture Organization of the United Nations - FAOSTAT. 2023. *Agricultural production statistics 2000-2022*. Available in: <https://openknowledge.fao.org/items/43fde039-dc0f-484a-97ef-e2e335c0bf1a >.

Finzi, R. R. et al. (2017). Agronomic performance of mini-tomato hybrids from dwarf lines. *Ciência e Agrotecnologia*, *41*(1):15-21.

Finzi, R. R. et al. (2020). Agronomic potential of BC1F2 dwarf round tomato populations. *Ciência e Agrotecnologia*, *44*:e028819.

Gomes, D. A. et al. (2021). Selection of BC1F3 populations of Santa Cruz type dwarf tomato plant by computational intelligence techniques. *Bragantia*, *80*:e4821.

Gomes, D. A. et al. (2023). Agronomic potential of BC_1F_2 populations of Santa Cruz dwarf tomato plants. *Acta Scientiarum. Agronomy*, *45*:e56482.

Instituto Brasileiro de Geografia e Estatística - IBGE. *Produção de tomate*. 2022. Available in: <https://www.ibge.gov.br/explica/producao-agropecuaria/tomate/br>.

Liang, J. X. et al. (2021). Enhancing lycopene stability and bioaccessibility in homogenized tomato pulp using emulsion design principles. *Innovative Food Science & Emerging Technologies, 67*(12):102525.

Liu, H. J. et al. (2023). Exogenous leucine alleviates heat stress and improves saponin synthesis in Panax notoginseng by improving antioxidant capacity and maintaining metabolic homeostasis. *Frontiers in Plant Science, 14*:1175878.

Liu, X. et al. (2020). SlGID1a is a putative candidate gene for qtph1.1, a major-effect quantitative trait locus controlling tomato plant height. *Frontiers in Genetics,* 11:881.

Maciel, G. M., & Silva, E. C. da. (2008). Inheritance of fruit shape in cherry tomato group. *Horticultura Brasileira*, *26*:495-498.

Maciel, G. M. et al. (2010). Heterosis and combining ability of acylsugar-rich tomato lines. *Ciência e Agrotecnologia*, *34*(5):1161-1167.

Maciel, G. M., & Silva, E. C. (2014). Methodological proposal to quantify acylsugars in tomato leaflets. *Horticultura Brasileira, 32*(2):174-177.

Maciel, G. M., Silva, E. C., & Fernandes, M. A. R. (2015). Dwarfism occurrence in tomato plant type grape. *Revista Caatinga*, *28*(4):259-264.

Maciel, G. M. et al. (2018). Tomato genotypes with determinate growth and high acylsugar content presenting resistance to spider mite. *Crop Breeding and Applied Biotechnology*, *18*:1-8.

Maclean, A., Legendre, F., & Appanna, V. D. (2023). The tricarboxylic acid (TCA) cycle: A malleable metabolic network to counter cellular stress. *Critical Reviews in Biochemistry and Molecular Biology, 58*(1):81-97.

Maeda, H. A. (2019). Harnessing evolutionary diversification of primary metabolism for plant synthetic biology. *Journal of Biological Chemistry, 294*(45):16549-16566.

Maluf, W. R. et al. (2010). Broad-spectrum arthropod resistance in hybrids between high- and low-acylsugar tomato lines. *Crop Science*, *50*(2):439-450.

Marinke, L. S. et al. (2022). Selection of tomato genotypes with high resistance to *Tetranychus evansi* mediated by glandular trichomes. *Phytoparasitica, 50*:629-643.

Martínez-Hernández, G. B. et al. (2016). Processing, packaging, and storage of tomato products: Influence on the lycopene content. *Food Engineering Reviews, 8*:52-75.

Mian, S. et al. (2021). Post-harvest quality and sensory acceptance of Italian tomatoes grown under organic, integrated and conventional management. *Horticultura Brasileira, 39*(4):417-424.

Montgomery, D. C. (2000). *Design and analysis the experiments*. New York: John Wiley, 684p.

Moutiez, M., Belin, P., & Gondry, M. (2017). Aminoacyl-tRNA-utilizing enzymes in natural product biosynthesis. *Chemical reviews, 117*(8):5578-5618.

Mulamba, N. N., & Mock, J. J. (1978). Improvement of potential of the eto blanco maize (*Zea mays* L.) population by breeding for plant traits. *Egyptian Journal Genetics and Cytology, 7*:40-51.

Nagata, M., & Yamashita, I. (1992). Simple method for simultaneous determination of chlorophyll and carotenoids in tomatoes fruit. *Nippon Shokuhin Kogyo Gakkaishi, 39*(10): 925-928.

Oliveira, C. S. et al. (2021). Artificial neural networks and genetic dissimilarity among saladette type dwarf tomato plant populations. *Food Chemistry: Molecular Sciences*, *3*:100056.

Oliveira, C. S. et al. (2022). Selection of F_2RC_1 saladette-type dwarf tomato plant populations for fruit quality and whitefly resistance. *Revista Brasileira de Engenharia Agrícola e Ambiental*, *26*(1):28-35.

Orchard, C. J. et al. (2021). Identification and assessment of alleles in the promoter of the Cyc-B gene that modulate levels of β-carotene in ripe tomato fruit. *Plant Genome, 14*:e20085.

Peixoto, J. V. M. et al. (2018). Post-harvest evaluation of tomato genotypes with dual purpose. *Food Science and Technology, 38*(2):255-262.

Peixoto, J. V. M. et al. (2020). Productivity, acylsugar concentrations and resistance to the two-spotted spider mite in genotypes of salad tomatoes. *Revista Brasileira de Engenharia Agricola e Ambiental*, *24*:596-602.

Rajendran, S. et al. (2022).Tomato yield effects of reciprocal hybridization of *Solanum lycopersicum* cultivars M82 and micro-tom. *Plant Breeding and Biotechnology, 10*:37-48.

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available in: <https://www.R-project.org/>.

Resende, J. T. V. et al. (2022). The introgression of resistance to *Tuta absoluta* in tomato based on glandular trichomes. *Arthropod-Plant Interactions, 16*:87-99.

Rodriguez-Amaya, D. B. (2001). *A guide to carotenoid analysis in foods*. Washington, United States: Internacional Life Sciences Institute Press, 64p.

Rodriguez-Amaya, D. B., & Kimura, M. (2004). *Handbook for carotenoid analysis*. Washington, United States: HarvestPlus, 58p.

Ronga, D. et al. (2021). Agronomic comparisons of heirloom and modern processing tomato genotypes cultivated in organic and conventional farming systems. *Agronomy*, *11*:349.

Santos, N. C. et al. (2020). Resistance of round tomato genotypes with determinate growth habit to two-spotted spider mites and silverleaf whitefly. *Bioagro*, *32*:15-22.

Scott, A., & Knott, M. (1974). Cluster-analysis method for grouping means in analysis of variance. *Biometrics, 30*(3):507-512.

Seabra Junior, S. et al. (2022). Selection of thermotolerant Italian tomato cultivars with high fruit yield and nutritional quality for the consumer taste grown under protected cultivation. *Scientia Horticulturae, 291*:110559.

Silva, P. T. P. et al. (2021). Yield prediction of experimental plots based on the harvest of specific fruit clusters for selection of fresh market tomato hybrids. *Horticultura Brasileira*, *39*:58-64.

Silva, T. A. et al. (2022).Entre orientações e normatizações: Cartilhas brasileiras sobre alimentação e nutrição no contexto da pandemia de covid-19. *Saúde e Sociedade*, *31*(3):e210745.

Singh, A. K., Dhanapal, S., & Yadav, B. S. (2019). The dynamic responses of plant physiology and metabolism during environmental stress progression. *Molecular Biology Reports, 47*(2):1459-1470.

Slocombe, S. P. et al. (2008). Transcriptomic and reverse genetic analysesof branched-chain fatty acid and acylsugar production in *Solanum pennellii* and *Nicotiana benthamiana*. *Plant physiology, 148*(4):1830-1846.

Smith, C. M. (2020). Conventional breeding of insect-resistant crop plants: Still the best way to feed the world population. *Current Opinion in Insect Science*, *45*:7-13.

Sun, X. R. et al. (2019). Genetic analysis of tomato internode length via mixed major gene plus polygene inheritance model. *Scientia Horticuturae, 46*:759-764.

Tamta, S., & Singh J. P. (2017). Heterosis in tomato for growth and yield traits. *International Journal of Vegetable Science, 24*(2):169-179.

United Nations. (2024). Department of Economic and Social Affairs. Sustainable Development.*The 17 Goals*. Available in: <https://sdgs.un.org/goals>.

Vazquez, D. V. et al. (2022). Genetic basis of the lobedness degree in tomato fruit morphology. *Plant Science,* 319:111258.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. New York: Springer-Verlag. Available in: <https://link.springer.com/book/10.1007/978-3-319-24277-4>.

Zayat, J. Z. M. et al. (2022). Viabilidade econômica da produção de tomate do tipo saladete no sul do estado de goiás. *Revista Ibero-Americana de Humanidades, Ciências e Educação*, *8*(6):1455-1486.