



Morpho-agronomic and biochemical diversity of the Tomata Valenciana landrace reveal key traits for its revalorisation and subtype differentiation

Ramón Gabriel Rico Ferrer^{*}, María del Rosario Figàs, Nicolás Arroyo^{id}, Miquel Martínez, Elena Soler, Cristina Casanova, Jaime Prohens^{id}, Salvador Soler

Grup de Conservació i Millora de Varietats Tradicionals Valencianes. Instituto de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV), Universitat Politècnica de València, Camí de vera S/n, 46022, Valencia, Spain

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ABSTRACT

The Tomata Valenciana tomato (*Solanum lycopersicum* L.) landrace, valued for its local importance and unique organoleptic qualities, shows notable intra-varietal diversity. In this study, 46 accessions from three subtypes ('Blanca', 'Masclet', and 'Intermitja') were assessed using 57 morpho-agronomic and 15 biochemical descriptors. High phenotypic variation was observed, particularly in fruit morphology and agronomic traits. Features like fruit weight (FWH), locule number (LCN), and fruit tip formation (FTF) showed high heritability ($H^2 > 0.6$). Principal Component Analysis clearly separated subtypes based on morphology: 'Blanca', which had larger, rounder fruits with lighter immature colour; 'Masclet', with darker green shoulders and pointed tips; and 'Intermitja', which showed intermediate traits and greater plant vigour. In contrast, biochemical traits displayed reduced variation among subtypes and low H^2 . These findings highlight the morphological and agronomic diversity of Tomata Valenciana, especially in fruit traits that are valuable for breeding and varietal authentication. The identification of stable, differentiating traits supports conservation efforts and legal recognition through quality labels. The unique profile of the 'Intermitja' subtype provides new insights into possible hybridization processes within landraces and their contribution to maintaining genetic diversity in traditional farming systems.

1. Introduction

Landraces are dynamic populations of cultivated plants with rich historical lineages, distinctive identities, and no or minimal formal crop improvement [1]. Typically associated with traditional farming systems, landraces have evolved through farmer-driven selection processes within low-input agricultural environments [2–4]. These populations are characterized by local adaptability, tolerance to the prevalent stresses and act like genetic reservoirs as they tend to be genetically diverse [5,6]. Nowadays, beyond their significance for biodiversity, there are also socio-economic implications, primarily at local level, that support the maintenance of landraces [7,8]. The principal strength of local landraces compared to modern cultivars is their reputation for high quality mainly at local level [9,10]. Additionally, their appreciation and integration into local cuisine [11,12] justify consumers' willingness to pay a slightly higher price than for modern cultivars [13,14]. Consequently, the preservation of landraces is crucial for maintaining both biodiversity and the socio-economic stability of local farming

communities [11,15].

The Tomata Valenciana is a tomato (*Solanum lycopersicum* L.) landrace native to the Valencia region on the eastern Mediterranean coast of Spain. This tomato variety is prized for its fresh consumption, offering a mildly sweet taste with soluble solids content ranging between 3.5 and 5.0 Brix degrees and low acidity levels, with citric acid concentrations falling within the range of 0.45–0.75 % as defined in the Tomata Valenciana quality regulation (DOGV, ORDEN 4/2023). Morphologically, it produces medium to large-sized fruits with locules arranged non-uniformly around a circular core. The fruits have a robust, circular-sectioned heart, imparting notable firmness and fleshiness. They also exhibit a distinctive green shoulder with the rest of the fruit having reddish coloration, along with characteristic radial cracking patterns ([16]; Pons et al., 2017 [17]). Within the Tomata Valenciana, two major subtypes are distinguished primarily by their morphology. The 'Masclet' type features a pronounced pointed shape and dark-green shoulders during immature stages, while the 'Blanca' type has fruits ranging from slightly flattened to heart-shaped and have a light green hue during

^{*} Corresponding author.

E-mail addresses: ramonarchivos3397@gmail.com, rarifer1@upv.edu.es (R.G. Rico Ferrer).

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early development [13,18]. In addition, a third subtype referred to as 'Intermitja', displays intermediate features between 'Masclat' and 'Blanca' [17,19,20].

Tomata Valenciana faces several challenges regarding product recognition by consumers, which leads to unfair market competition, and rising production costs. The lack of fruit shape uniformity, which is a typical trait in landraces associated to genetic richness, becomes a problem in this particular landrace because it prevents consumers from identifying a clear recognizable morphology, thus favouring the replacement with other landraces and modern breeds with similar shape and colour, but lacking main fruit quality traits characterising the Tomata Valenciana [18]. Despite the strong local demand for Tomata Valenciana, with an annual marketed production exceeding 1000 t and an estimated value of more than 2×10^6 €, the presence of such imitations, accompanied by potentially misleading labelling, ambiguous varietal denominations, growing tomato imports from third countries into the European Union and increasing production costs further threaten the continued cultivation of Tomata Valenciana [21].

Although these challenges affecting Tomata Valenciana are common to many landraces, increasing efforts are being made to support and revalorise traditional agri-food products. Within the European Union, quality schemes such as Protected Geographical Indication (PGI) and Protected Designation of Origin (PDO) are primarily intended to recognise and promote products linked to a specific geographical origin, production system or traditional know-how (EC Council Regulations 509/2006 [22] and 510/2006 [23]). Furthermore, these frameworks also contribute to the protection of product names and labelling. Well-known examples include the Almagro eggplant (PGI) [24], Pomodorino del Piennolo del Vesuvio (PDO) [25], and Pomodoro San Marzano dell'Agro Sarnese-Nocerino (PDO), whose protection is strictly linked to production within defined geographical areas and compliance with specific production standards [26]. In this context, such quality schemes indirectly reduce the presence of imitations in the market by preventing the misuse of protected names. Similarly, the recent granting of the CV quality seal to Tomata Valenciana, a distinction granted by the Generalitat Valenciana (regional government) to guarantee the unique quality of agri-food products that meet the quality regulations adopted [27], aims to recognise its distinctive quality and production system, while contributing to clearer product identification and reducing potentially misleading marketing practices [28].

Regarding product valorisation at technical level in Tomata Valenciana, previous studies have been carried out with diverse purposes. For example, Cebolla-Cornejo et al. [13] analysed the major factors affecting the genetic erosion of the landrace and Figàs et al. [29, 30] characterized 69 accessions of local tomato from the region of Valencia, including 13 accessions of the Tomata Valenciana, with conventional descriptors and the Tomato Analyzer high-throughput phenotypic tools to find significant differences between accessions as they have implications for the characterisation of local tomato varieties.

Although previous studies have addressed genetic erosion and partial morphological and compositional characterisation of Tomata Valenciana, a comprehensive and integrated evaluation of plant morphology, agronomic performance, fruit morphology, and fruit composition across a broad representation of accessions is still lacking. Moreover, the extent of phenotypic diversity within and among the recognized subtypes ('Masclat', 'Blanca', and 'Intermitja') has not been systematically assessed. This lack of integrated information limits the effective differentiation, protection, and enhancement of the landrace.

Therefore, the objectives of this study were to: (1) comprehensively characterize plant morphology, agronomic performance, fruit morphology, and fruit composition in a representative collection of Tomata Valenciana accessions; (2) assess the extent of phenotypic diversity within the landrace; and (3) identify traits that allow the differentiation of the recognized subtypes. This study not only provides valuable insights into the morphological, agronomic, and compositional diversity of the Tomata Valenciana landrace but also serves as a model

for investigating and preserving other landraces with different typologies. By applying a multidisciplinary approach, the methodologies and findings presented here can be extended to assess and protect traditional varieties facing comparable challenges and threats, ultimately contributing to the conservation of agricultural biodiversity and the promotion of locally adapted landraces.

2. Materials and methods

2.1. Plant material and growing conditions

A collection of 46 local tomato accessions of Tomata Valenciana, originating from different locations of the Comunitat Valenciana region (Spain), were used. Seeds were provided by the germplasm bank of the Instituto Universitario de Conservación y Mejora de la Agrodiversidad Valenciana (COMAV). The municipalities and districts where these accessions were collected, as well as the codes and subtypes assessed for each accession are shown in Table S1, and their geographical distribution within the region is represented in Fig. S1. The accessions were classified into three subtypes of Tomata Valenciana based on the observed fruit morphology phenotypes during fruit characterisation. The classification rendered: thirty accessions grouped under the 'Blanca' subtype (Fig. 1A), four accessions that exhibited intermediate traits forming the 'Intermitja' subtype (Fig. 1B) and twelve accessions were classified under the 'Masclat' subtype (Fig. 1C). The unequal number of accessions per subtype reflects the availability of material in the germplasm bank at the start of the study and was not the result of a predefined experimental design.

The Tomata Valenciana accessions were grown outdoors in the typical growing cycle for this landrace (April–July) in an open field plot located in the municipality of Alcàsser in the Comunitat Valenciana region, Spain (coordinates: 39°23'38"N 0°27'03"W). The accessions were distributed using a randomized block design with 3 blocks and 3 plants per replicate.

Sowing was performed on February 17th, 2022, and transplanting took place on April 2nd, 2022, using a spacing of 0.35 m between plants and 1.25 m between rows. After transplant, plants were grown protected under microtunnels. In the first week of May, the microtunnels and thermal blanket were removed. Subsequently, the plants were trellised as they grew using a typical Valencian *barraca-cane* structure (Fig. S2). This design ensures stability, optimizes growth, improves ventilation, maximizes light exposure, and facilitates harvest. Irrigation was performed by drip irrigation, and nutrition was provided through fertigation. Irrigation was applied at a total rate of 3212 m³/ha over the crop cycle, while fertilization followed a dosage of 249 kg ha⁻¹ of N, 72 kg ha⁻¹ of P₂O₅, and 72 kg ha⁻¹ of K₂O. The experiment ended on July 31st, 2022.

2.2. Characterisation

For plant morpho-agronomic characterisation (including plant traits and agronomic traits) and fruit characterisation (including fruit morphological and fruit biochemical traits), a total of 72 descriptors were evaluated. Most plant and fruit morphological traits were assessed following the standard IPGRI descriptors for tomato [31]. Additional traits not explicitly included in the IPGRI descriptor list—either corresponding to adaptations of existing descriptors or to complementary descriptors previously described in the literature [29,30]—were also recorded. The full list of evaluated traits, together with their abbreviations (three capital letters, four capital letters or three capital letters and a number), units or scoring scales, and indication of their correspondence with IPGRI descriptors, is provided in Table S2. Among the 72 traits evaluated, 13 were related to plant traits, 17 to agronomic traits, 27 to fruit morphology, and 15 to fruit biochemical characterisation. For both steps of characterisation, plants/fruits within each block were treated as subsamples and traits measured on them were averaged prior

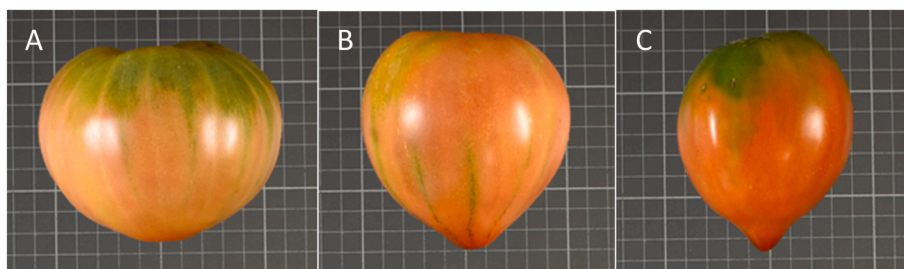


Fig. 1. Representative fruits of each Tomata Valenciana subtype. A. 'Blanca'; B. 'Intermitja'; C. 'Masclat'. Size of the squares in the supporting platform pattern is 1cmx1cm.

to analysis, with blocks considered the experimental units, in order to minimise intra-block variability and avoid pseudoreplication.

2.2.1. Plant morpho-agronomic traits

Plant and agronomic traits were measured in each of the three plants in each block. Individual measurements were averaged within each experimental block, and the resulting block means were subsequently used to compute the overall mean value for each trait across blocks. Leaf traits such as chlorophyll (CHL), epidermal flavonols (FLV) and their ratio, expressed as the nitrogen balance index (NBI), as well as anthocyanins (ANT), were measured *in vivo* and non-destructively using a Dualex sensor (Force-A, Orsay, France). One measurement per plant was taken on a uniform, fully developed, and sun-exposed leaf in each experimental block.

2.2.2. Fruit morphology traits

For the fruit characterisation, harvesting was carried out sequentially on a weekly basis from the onset of fruit set until the end of the crop cycle. To minimise the effect of positional and temporal variability associated with early and late harvests, fruit morphological traits were assessed using fruits collected from the second to forth truss [29], prior to the destructive analyses performed for biochemical characterisation. Within each experimental block, measurements were taken from fruits originary from the trusses of the three plants composing the block and averaged to obtain a block mean; these block means were then used to calculate the overall mean value for each fruit morphology and biochemical trait across blocks.

2.2.3. Fruit biochemical traits

For fruit biochemical characterisation, one fruit per plant was collected from each experimental block, resulting in three fruits per accession per block. Fruits were pooled and homogenised, and 750 g of the resulting puree were used to prepare aliquots, which were flash-frozen in liquid nitrogen and immediately stored at -80°C until analysis. Then, using the aliquots, 15 tomato biochemical traits were analysed. The evaluated traits with their corresponding abbreviation and descriptor code are shown in Table S3.

Soluble solids content ($^{\circ}\text{Brix}$) were determined using a digital refractometer (HI 96801, HANNA Instruments, Woonsocket, RI, USA). For pH and titratable acidity (ACD), a volumetric analyzer (Titralab AT1000 Series, HACH, Loveland, CO, USA) was used. Then, the Flavour Index (FVI) was calculated with the equation $\text{FVI} = [\text{ACD} + (^{\circ}\text{Brix}/(20 \times \text{ACD}))]$ that reflects the interaction between acidity and sweetness in the fruit's sensory profile [32].

The antioxidant activity (AOX) was measured using a spectrophotometer (Lambda 365+, PerkinElmer, Waltham, MA, USA) according to the Brand-Williams procedure following the protocol described in Sánchez Moreno et al. [33]. To quantify the AOX, a calibration curve was prepared using a stock solution of 6-Hydroxy-2,5,7,8-tetramethylchromate-2-carboxylic acid (Trolox). An extract was then obtained from one of the tomato juice aliquots using 80 % methanol, following the same protocol. The absorbance of the extract was measured at 515 nm

using the spectrophotometer, and a blank measurement was performed using dissolved 2,2-Diphenyl-1-picrylhydrazyl (DPPH). Finally, the antioxidant concentration was calculated based on the calibration curve. The same spectrophotometer was used for the determination of lycopene (LCP), β -carotene (BCT) and total carotenoids (TCT). An extract of the samples from another aliquot was obtained in ethanol:hexane 4:3 (v/v) and then, using quartz cuvettes, the absorbance was measured at 3 different wavelengths: 452 nm, 485 nm and 510 nm. Finally, LCP, BCT and TCT were calculated following the indications of the Zscheile and Porter [34] protocol.

Total phenolics (TPH) content was determined according to the Folin-Ciocalteu procedure as described in Raigón et al. [35]. Firstly, a calibration curve was prepared using a stock solution of gallic acid, then an extract from an aliquot was obtained in miliQ water and measured in the spectrophotometer at 760 nm. Once absorbance values were obtained, the concentration of phenolics was measured using the calibration curve.

Another aliquot was used to obtain an extract of vitamin C in miliQ water following Cano and Bermejo [36] protocol and, another extract was obtained following Navarro et al. [37] for sugars. Both were analysed in the HPLC (1220 Infinity LC, Agilent Technologies, Santa Clara, CA, USA). The vitamin C content (TVC) was determined considering the two forms in which it is found in the samples: ascorbic acid (ASA) and dehydroascorbic acid (DHA), and their sum represents the total amount of vitamin C in a sample (TVC). For the determination of the sugar content (FRC, GLC, SUG), it was necessary to prepare the fructose and glucose calibration curves.

2.3. Data analysis

Descriptive statistics and univariate analysis of variance (ANOVA) for the traits were performed using the Statgraphics Centurion XVIII software (Statgraphics Technologies, Inc., The Plains, VA, USA). For each trait, the mean, range, coefficient of variation (CV; %) and broad-sense heritability (H^2) were calculated. The H^2 calculations were performed using the mean squares from the ANOVA conducted for each trait, as indicated by Dabholkar [38]. Furthermore, for traits showing statistically significant variation, differences among Tomata Valenciana subtypes were assessed through mean comparisons using the Student–Newman–Keuls multiple range test.

Multivariate Principal Component Analysis (PCA) were performed for plant-related traits and for fruit-related traits. Some of the traits included in the multivariate analyses describe closely related aspects of plant or fruit development and were therefore expected to be correlated (e.g. fruit number across successive trusses, fruit size descriptors or colour parameters). These traits were retained in the PCA to represent the biological structure of the phenotypic variation within the Tomata Valenciana landrace. To verify that multicollinearity did not bias the analyses, alternative PCAs were performed excluding groups of highly correlated variables (Fig. S3). As these reduced models yielded ordination patterns comparable to those obtained with the full datasets, the complete set of traits was finally used, as the inclusion of correlated

descriptors did not alter the interpretation of the results. All multivariate analyses and the generation of PCA graphical outputs (scatter plots and vector/loading plots) were performed using R software (R Foundation for Statistical Computing, Vienna, Austria) [39], through the RStudio integrated development environment (version 2026.01.0 + 392, “Apple Blossom”) [40], with figures rendered using Quarto (version 1.8.25) [41].

3. Results

3.1. Plant morpho-agronomic characterisation

Variation was observed in the collection of materials evaluated for all plant morpho-agronomic descriptors except for the leaf type (LTP), as all the analysed accessions were monomorphic and exhibited standard tomato leaves. Therefore, this trait was excluded from subsequent analyses. None of the other traits resulted monomorphic and the ANOVA analysis revealed that, except for fruits set in truss 2 (NFT-2), plant growth type (PGT), root bulb angle (RBA), stem pubescence density (SPD), style position (STP), inflorescence type (TIF), and yield (YLD), the rest of the traits displayed significant differences among accessions (Table S4).

The analysis of the plant morphological and agronomic traits revealed variation in both the observed ranges and CV (Table S4). Some traits like PGT, leaf attitude (LTT), SPD, SPAD index (SPI), CHL and number of days to maturation (ERL) showed narrow ranges and low variability ($CV < 7\%$). Conversely, traits such as the number of fruits set per truss (NFT) in higher trusses (NFT-4 to NFT-7) displayed relatively wide ranges and extremely high variability ($CV > 50\%$). Other traits such as leaf/bud on inflorescence (LIF), total fruit number (TFN), setting sequence (SSQ), NFT-1 and YLD presented broad ranges and moderate-to-high variability (Table S4).

Regarding the heritability (H^2) of the traits analysed, a wide range of variation was observed, spanning values from 0.06 for STP with the lowest value to 0.89 for the ERL (Table S4). Other traits that exhibited high genetic influence in this population included the TFN and the stem diameter (SDI), both with an $H^2 = 0.64$; plant vigour (PVG) with an $H^2 = 0.62$; LTT with an $H^2 = 0.61$ and LIF with $H^2 = 0.53$. Conversely, some traits displayed low genetic influence: RBA ($H^2 = 0.07$), NFT-2 ($H^2 = 0.14$), PGT ($H^2 = 0.14$), NFT-7 ($H^2 = 0.15$), and the CHL ($H^2 = 0.1$) (Table S4).

The multivariate PCA analysis of plant morpho-agronomic traits

(Fig. 2) revealed that the first principal component (PC1) accounts for 21.78 % of the total variance and the second principal component (PC2) for 13.48 %. Together, the first four principal components explain 52.86 % of the total variance, indicating that a limited number of components captures a substantial proportion of the variation (Fig. 2A). The vectors plot shows that traits with the highest absolute weights for PC1 are agronomic and associated with yield-related aspects, particularly fruit production during plant development (SSQ, TFN, NFT-3, NFT-4, NFT-5, and NFT-6) all of which are positively correlated with PC1. Some plant traits also show high positive correlation with PC1 like LTT and the main root diameter (MRD) (Fig. 2A). Regarding the PC2, this component mostly captures patterns related to the physiological health, with traits such as CHL and NBI, together with PVG and SDI positively correlated with PC2. Few traits are negatively correlated with the PC2, being the one with highest absolute value for the correlation the ANT (Fig. 2A).

The PCA scatter plot reveals a relatively clear, though not clean, separation of the two main varietal types, ‘Mascler’ and ‘Blanca’ (Fig. 2B). However, PAT-1 (‘Blanca’) and CAT-3 (‘Mascler’) plot away from the other accessions of their varietal subtype. Considering the influence of the traits related to fruit yield over the PC1, the disposition of PAT-1 responds to the fact that this accession presents a TFN count of 22.67 on average, more than twice the average TFN of the ‘Blanca’ type (11.29); something similar happens regarding CAT-3, which presents a relatively low YLD (2555.14 g of fruit/plant) in comparison to the average ‘Mascler’ YLD (4052.59 g of fruit/plant), thus positioning this accession near the ‘Blanca’ ones. Furthermore, ‘Intermitja’ accessions are intermingled with both subtypes, showing an upper-central distribution in the space of components (Fig. 2B). ‘Blanca’ accessions generally show lower PC1 values because their yield-associated traits show lower mean values than the other subtypes (i.e. SSQ = 4.30; TFN = 11.29; NFT-3 = 2.58; NFT-4 = 1.63; NFT-5 = 0.73; and NFT-6 = 0.39) while ‘Mascler’ accessions display higher PC1 values as they have higher mean values regarding these type of traits (i.e. SSQ = 4.78; TFN = ; NFT-3 = 3.52; NFT-4 = 3.04; NFT-5 = 2.00; and NFT-6 = 1.14). Same pattern is observed with LTT (‘Blanca’ = 6.46 vs. ‘Mascler’ = 6.92) and MRD (‘Blanca’ = 1.65 vs. ‘Mascler’ = 1.95), which are also related with positive PC1 values. Regarding the PC2, the distribution of both main subtypes is similar. ‘Intermitja’ accessions are distributed amongst both main subtypes in terms of the PC1, however, it is remarkable that all the ‘Intermitja’ samples have high PC2 values due to the accessions presenting high values for physiological health traits influencing the second component (i.e. NBI and CHL) and for traits related with plant

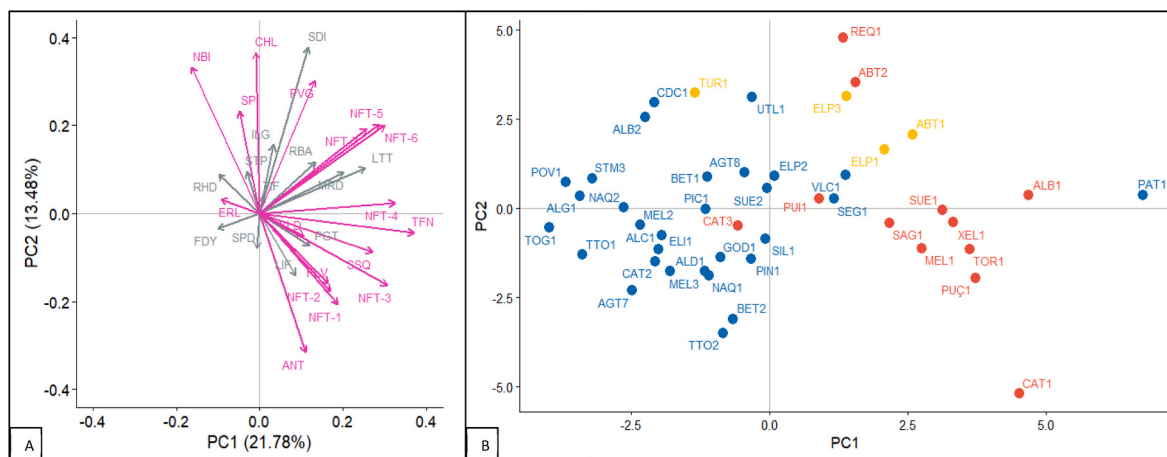


Fig. 2. Principal component analysis (PCA) based on 29 plant morpho-agronomic traits evaluated in 46 Tomata Valenciana accessions. (A) Vector plot showing the direction and relative contribution of each trait to the first two principal components. Arrow length indicates the weight of each trait in the multivariate space, while arrow orientation reflects correlations with PC1 and PC2. Grey arrows indicate traits related with plant morphology and pink arrows traits related with plant agronomy. Percentages in axis labels indicate the proportion of total variance explained by each principal component. (B) PCA scatter plot of the 46 accessions projected onto the first two principal components. Points represent individual accessions and are coloured according to varietal subtype: ‘Blanca’ (blue), ‘Intermitja’ (yellow), and ‘Mascler’ (red).

robustness (i.e. PVG and SDI) (Fig. 2B).

3.2. Fruit characterisation

In total, 42 morphology and biochemistry-related traits were evaluated (Table S5). Regarding traits related with fruit morphology, significant differences among accessions were found for almost every trait except fruit fasciation (FFS), pericarp thickness (PTK) and radial cracking of the fruits (RDK). On the other hand, regarding the traits related with fruit biochemistry, the ANOVA analysis revealed no significant differences among the 46 accessions, indicating that the main differences amongst the accessions arise from their fruit morphology (Table S5).

Large variation among accessions was found regarding fruit morphology traits, although some of them showed narrow ranges and low variability ($CV < 10\%$): PTK, fruit length (FLT), L^* parameter of immature fruit (UFC-L), L^* parameter of green shoulder (GSH-L), a^* parameter of green shoulder (GSH-A), b^* parameter of green shoulder (GSH-B), L^* parameter of mature fruit (EFC-L), a^* parameter of mature fruit (EFC-A) and b^* parameter of mature fruit (EFC-B). Broad ranges and high variability ($CV > 40\%$) were exclusively found in traits related with fruit shape (e.g., fruit tip formation (FTF), blossom end rot (BER), puffiness appearance (PFA), concentric cracking (CCK) and predominant fruit shape (PFS)). Other traits showing broad ranges but moderate variation in the population were the number of locules (LCN) and the fruit weight (FWH). Main traits describing fruit colour of unripe fruits (UFC) and green shoulders (GSH) also showed moderate-to-high variability amongst the accessions ($CV > 15\%$), however the external fruit colour (EFC) of ripe fruits did not show it (Table S5).

High H^2 values in general were observed regarding fruit morphology traits (Table S5), even with FTF rendering a $H^2 = 1$ indicating that its control in Tomata Valenciana is exclusively genetic. Other fruit morphology traits with high H^2 were FWH ($H^2 = 0.65$), width/length ratio (WLR, $H^2 = 0.62$), predominant fruit shape (PFS, $H^2 = 0.60$) and fruit width (FWD, $H^2 = 0.58$). Fruit colour traits displayed moderate-to-high H^2 which is present in all the 12 measurements done, from GSH-B = 0.19 to the EFC showing a $H^2 = 1$ indicating that the fruit colour once it is definitively ripened is fully controlled by genetics.

In contrast, biochemical traits generally displayed low-to-mid variation except for vitamin C related measurements (ASA, DHA and TVC) which were relatively high in comparison with the others. Moderate variation was shown by traits related with carotenoids content (LCP,

BTC and TCT), and results indicated that there is low variation regarding fruit's soluble solids content and acidity in Tomata Valenciana (Table S5).

Regarding heritability, biochemical traits generally showed low H^2 values ($H^2 < 0.13$ for all the traits), indicating that the phenotypic variations observed are almost entirely attributable to environmental factors (Table S5).

The multivariate PCA analysis of fruit morphological and biochemical traits (Fig. 3) revealed that the PC1 accounted for 24.32 % of the total variance and the PC2 for 11.44 %. The first four principal components together explained 51.69 % of the total variance indicating that a limited number of components captures a substantial proportion of the variation (Fig. 3A). The vector plot shows that PC1 appears to capture general physical attributes such as size, shape, and fruit colour. Traits like FWH, FWD, WLR, and LCN are correlated positively with the PC1. Regarding fruit colour, the primary contributors to the first component are traits associated with unripe fruit colour and green shoulders with UFC-A, UFC-L, GSH-A and GSH-L being positively correlated with the PC1 and UFC-B, UFC and GSH having high negative correlations with the first component (Fig. 3A). PC2 seems to be associated with internal quality attributes of the fruit, particularly those related to flavour (sugars and acidity) and nutritional profile (vitamins and antioxidants). In this sense, traits related with sugar content (GLC, FRC, SUG and °Brix) display a positive correlation with PC2. Additionally, traits related to quality attributes, such as FVI, TPH, and ASA, are positively correlated with this component (Fig. 3A).

The PCA scatter plot reveals a clear separation of accessions according to the varietal subtypes based on fruit phenotypes (Fig. 3B). 'Blanca' accessions cluster on the right side of the plot, associated with bigger and wider fruits (higher FWH, FWD, WLR and LCN) than the 'Masclat' accessions, thus with higher PC1 values (Fig. 3B). Conversely, 'Masclat' accessions are grouped on the left side of the plot. Fruits of the 'Masclat' accessions are associated to darker colour when the fruit is developing (higher UFC values) and marked green shoulders (higher GSH values), both traits that negatively influence the second component. Most 'Masclat' samples form a marked cluster, except for ABT2, REQ1, and PUI1, which overlap with some 'Blanca' accessions (Fig. 3B). Notably, 'Intermitja' accessions are positioned in the central region of the components space, between the two main clusters. This positioning confirms that overall, this subtype presents fruit traits are intermediate between those of the 'Blanca' and 'Masclat' accessions. No clear pattern of sample or subtype separation is observed along PC2, since the traits

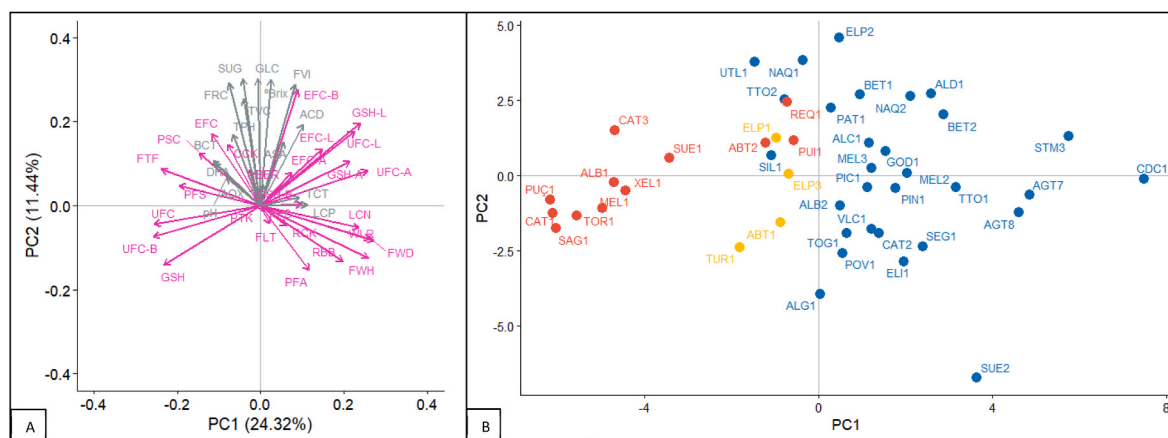


Fig. 3. Principal component analysis (PCA) based on 42 fruit traits evaluated in 46 Tomata Valenciana accessions. (A) Vector plot showing the direction and relative contribution of each trait to the first two principal components. Arrow length indicates the weight of each trait in the multivariate space, while arrow orientation reflects correlations with PC1 and PC2. Grey arrows indicate traits related with fruit biochemistry and pink arrows traits related with fruit morphology. Percentages in axis labels indicate the proportion of total variance explained by each principal component. (B) PCA scatter plot of the 46 accessions projected onto the first two principal components. Points represent individual accessions and are coloured according to varietal subtype: 'Blanca' (blue), 'Intermitja' (yellow), and 'Masclat' (red).

contributing most strongly to this component are associated with fruit biochemical characteristics, for which subtype mean values show little or no significant differentiation (Fig. 3B).

3.3. Comparison of the Tomata Valenciana varietal subtypes

Means' comparisons of the three subtypes for the 72 traits evaluated revealed significant differences for 26 of them (Table 1). The largest number of differences is found amongst 'Blanca' and 'Masclat', with a total of 21 significantly different traits, affecting fruit colour (UFC, UFC-L, UFC-A, UFC-B, GSH, GSH-L, GSH-A, EFC-L), fruit shape (FWH, FWD,

Table 1

Mean values $\pm$ SE of the descriptors for Tomata Valenciana for which significant ($P < 0.05$) differences have been found among subtypes ('Blanca', 'Intermitja', and 'Masclat') means. Different letters within a row indicate statistically significant differences according to the Student–Newman–Keuls test multiple range test.

Trait	Subtype		
	Blanca	Intermitja	Masclat
PLANT TRAITS			
Leaf Attitude (LTT)	6.46 $\pm$ 0.08 a	6.92 $\pm$ 0.08 b	6.92 $\pm$ 0.06 b
Stem Diameter (SDI)	13.57 $\pm$ 0.37 a	16.10 $\pm$ 0.44 b	14.57 $\pm$ 0.60 ab
Main Root Diameter (MRD)	1.65 $\pm$ 0.04 a	1.66 $\pm$ 0.09 a	1.95 $\pm$ 0.05 b
AGRONOMIC TRAITS			
Plant Vigour (PVG)	5.46 $\pm$ 0.14 a	6.50 $\pm$ 0.22 b	5.53 $\pm$ 0.17 a
Nitrogen balance Index (NBI)	26.44 $\pm$ 0.55 a	30.15 $\pm$ 1.07 b	23.17 $\pm$ 1.36 a
Chlorophyll (CHL)	42.59 $\pm$ 0.42 a	46.03 $\pm$ 0.81 b	42.50 $\pm$ 0.65 a
Flavonols (FLV)	1.66 $\pm$ 0.03 ab	1.56 $\pm$ 0.05 a	1.83 $\pm$ 0.05 b
Fruits Set in Truss 4 (NFT-4)	1.63 $\pm$ 0.18 a	2.17 $\pm$ 0.48 ab	3.04 $\pm$ 0.27 b
Fruits Set in Truss 5 (NFT-5)	0.73 $\pm$ 0.09 a	1.50 $\pm$ 0.41 b	2.00 $\pm$ 0.24 b
Fruits Set in Truss 6 (NFT-6)	0.39 $\pm$ 0.06 a	1.2 $\pm$ 0.25 5b	1.14 $\pm$ 0.11 b
Fruits Set in Truss 7 (NFT-7)	0.22 $\pm$ 0.05 a	0.53 $\pm$ 0.12 ab	0.63 $\pm$ 0.14 b
Total Fruit Number (TFN)	11.29 $\pm$ 0.61 a	15.00 $\pm$ 1.61 b	17.39 $\pm$ 0.71 b
FRUIT MORPHOLOGY TRAITS			
Exterior Fruit Colour of Immature Fruit (UFC)	2.36 $\pm$ 0.10 a	2.83 $\pm$ 0.17 a	3.67 $\pm$ 0.26 b
L* parameter of immature fruit (UFC-L)	66.96 $\pm$ 0.32 b	65.65 $\pm$ 0.49 ab	64.08 $\pm$ 0.64 a
a* parameter of immature fruit (UFC-A)	−9.15 $\pm$ 0.18 b	−9.90 $\pm$ 0.54 b	−11.57 $\pm$ 0.46 a
b* parameter of immature fruit (UFC-B)	22.43 $\pm$ 0.35 a	23.42 $\pm$ 1.00 a	26.82 $\pm$ 0.84 b
Green shoulder (GSH)	1.17 $\pm$ 0.05 a	1.17 $\pm$ 0.10 a	1.92 $\pm$ 0.17 b
L* parameter of green shoulder (GSH-L)	54.48 $\pm$ 0.50 b	53.77 $\pm$ 0.57 b	49.21 $\pm$ 0.83 a
a* parameter of green shoulder GSH-A	−12.28 $\pm$ 0.12 b	−13.07 $\pm$ 0.27 a	−13.58 $\pm$ 0.19 a
L* parameter of mature fruit (EFC-L)	43.42 $\pm$ 0.29 b	41.56 $\pm$ 1.03 a	41.93 $\pm$ 0.27 a
Fruit Tip formation (FTF)	0.70 $\pm$ 0.11 a (0.00–2.00)	1.50 $\pm$ 0.29 b (1.00–2.00)	2.42 $\pm$ 0.15 c (2.00–3.00)
Ribbing at calyx end (RBB)	2.73 $\pm$ 0.07 a	2.67 $\pm$ 0.14 a	2.22 $\pm$ 0.10 b
Locule Number (LCN)	11.79 $\pm$ 0.44 b	10.81 $\pm$ 0.76 b	8.23 $\pm$ 0.28 a
Fruit Width (FWD)	9.30 $\pm$ 0.19 b	8.17 $\pm$ 0.39 a	7.32 $\pm$ 0.12 a
Width/Length ratio (WLR)	1.19 $\pm$ 0.02 b	1.12 $\pm$ 0.03 b	0.93 $\pm$ 0.02 a
Fruit Weight (FWH)	402.66 $\pm$ 20.77 b	305.49 $\pm$ 27.52 a	239.00 $\pm$ 9.92 a

WLR, LCN), and fruit production (TFN, NFT-4, NFT-5, NFT-6, NFT-7). When comparing 'Blanca' and 'Intermitja', 14 traits are significantly distinct amongst varieties. These differences are primarily associated with fruit production throughout plant development (TFN, NFT-4, NFT-5, NFT-6, NFT-7) and fruit size and shape (FWH, FWD). Similarly, in the comparison between 'Masclat' and 'Intermitja', 14 significant differences can be detected mainly related with fruit colour (UFC, UFC-A, UFC-B, GSH, GSH-L) as well as fruit shape (WLR, LCN and RBB).

Overall, 'Blanca' and 'Masclat' accessions show the most differences when comparing subtype means of traits with significant differences amongst subtypes. In contrast, the 'Intermitja' subtype exhibits intermediate characteristics, displaying variation in its association with either 'Blanca' or 'Masclat' depending on the specific trait analysed (Table 1). Nonetheless, there are 3 traits (NBI, CHL and PVG) in which the two extreme classical subtypes of Tomata Valenciana do not display significant differences with each other, but they differ from the 'Intermitja' subtype, whose mean surpasses those from the 'Blanca' and 'Masclat' accessions. Finally, the FTF exhibits significant differences among all three subtypes (Table 1).

4. Discussion

The characterisation of plant, agronomic, fruit, and biochemical traits is essential for understanding the diversity and agronomic potential of landraces, whose variability is going to be crucial in plant breeding for developing a more resilient agriculture [42–45]. Establishing the guidelines for conducting in-depth characterizations of landraces is key for the protection and exploitation of these varieties that act as biodiversity reservoirs in a changing world [46]. In this regard, this study aims to provide the most comprehensive and accurate characterisation of the Tomata Valenciana landrace to date. The analysis of traits related to plant structure, agronomic performance, fruit morphology, and biochemical composition, along with the clear definition of the three varietal subtypes, the assessment of variability in the crop, and the determination of key traits characterising the Tomata Valenciana, offers a holistic perspective on this landrace.

The morpho-agronomic characterisation of the plant, together with the morphological and biochemical characterisation of the fruit, allowed not only to confirm the well-established role of fruit traits in defining Tomata Valenciana subtypes, but also to identify which traits show limited variability across accessions and which are more variable, thereby acting as relevant sources of diversity within this traditional variety. Plants of Tomata Valenciana generally show indeterminate growth, with standard tomato leaves close to a dropping position, mid foliar density and intermediate-to-high stem pubescence density. Inflorescences are predominantly uniparous, and generally present leaves on them and the style position is close to the stamen level (Table S4). The inclination of the leaf (LTT) is significantly lower in the 'Blanca' accessions when compared to 'Intermitja' and 'Masclat' ones (Table 1). In tomato, downward leaf bending is a morphological adaptation towards waterlogging, which has been shown to induce a range of metabolic and hormonal changes. These hormonal changes have been proved to be under genetic control by Geldhof et al. [47], identifying two genes involved in the response to water stress including *SIBTB12* (*Solyc05g052960*) and a hydroxycinnamoyl transferase (*HCT*) (*Solyc05g052680*). This suggests that the 'Intermitja' and 'Masclat' subtypes may exhibit a comparatively better tolerance to conditions associated with excess soil moisture and reduced oxygen availability in the root zone than 'Blanca'. This finding is consistent with the fact that 'Masclat' accessions show significantly higher main root diameter (MRD) than the other subtypes, and as it has been demonstrated in maize (*Zea mays* subsp. *mays*), rice (*Oryza sativa*) and wheat (*Triticum aestivum*), that the areas of whole root and cortex of the three species increased under stagnant water conditions [48].

Among the plant and agronomic traits evaluated, the nitrogen balance index (NBI), chlorophyll content (CHL), and plant vigour (PVG)

exhibited significant differences among subtypes, with consistently higher mean values observed in 'Intermitja' accessions compared with both the 'Blanca' and 'Masclat' subtypes (Table 1). NBI, defined as the ratio between chlorophyll and epidermal flavonoids (CHL/FLV), is widely used as an integrative indicator of plant nitrogen status [49,50]. In the present study, higher NBI values were associated with increased PVG across subtypes, suggesting a close relationship between nitrogen nutritional status and overall vegetative performance in Tomata Valenciana. Although the physiological basis of this relationship has not been previously described in tomato, the concurrent increase in NBI, CHL, and PVG observed in 'Intermitja' accessions points to a coordinated expression of physiological and architectural traits. This combination of traits is consistent with phenotypic patterns commonly associated with increased vegetative performance and has been described in the context of heterosis-related architectural traits in other crops [51–54].

Beyond these observations, the differentiation of the 'Intermitja' subtype has traditionally been discussed in relation to its intermediate phenotypic expression within the Tomata Valenciana landrace. In the present study, some plant and agronomic traits showed higher mean values in 'Intermitja' accessions (Table 1); nevertheless, these differences were accompanied by substantial overlap in variation ranges among subtypes, and the limited number of 'Intermitja' accessions must be taken into account when interpreting these results. Therefore, while the observed trait combinations may be compatible with patterns often associated with increased vegetative performance, they cannot be considered conclusive evidence of heterosis and thus, hybridization as the origin of the 'Intermitja' subtype. However, in this context, preliminary genetic data based on Single Primer Enrichment Technology (SPET) genotyping [20] indicated that some accessions classified phenotypically as 'Intermitja' occupied intermediate positions between 'Blanca' and 'Masclat' groups in a PCA. Although these genetic results are not sufficient to establish the origin of the 'Intermitja' subtype, they are consistent with the hypothesis that its differentiation may be influenced by historical hybridization events. This hypothesis should be addressed in future studies including larger and more balanced accession sets and targeted genetic analyses.

High variability in the landrace is found in agronomic traits related to fruit production in higher trusses when compared to the lower ones (Table 1). The setting sequence is homogeneous in lower trusses but heterogeneity in the number of fruits produced in each truss grows upwards. This information, together with the moderate broad-sense heritability of SSQ compared to other agronomic traits (Table S4), suggests that there is genetic variability underlying the determination of this trait that could be exploited through selection. Similar patterns of variability and moderate heritability for yield components such as fruit number per truss and fruit weight have been reported in tomato, reflecting the strong influence of plant developmental stage on fruit set and yield-related traits, highlighting potential for selection [55].

Another trait, the TFN in the plant, which is closely related to the SSQ, displays high variability in the population. In this case, the heritability is higher, indicating that selection could be even more efficient to modulate the TFN in Tomata Valenciana, as also observed for yield component traits in tomato [55]. However, it must be considered that this would not necessarily result in increased yield, which is typically a low-heritability trait. In tomato, final yield is determined by a balance between fruit set efficiency and fruit growth processes, which depend on coordinated cell division and expansion during early fruit development and are tightly regulated by genetic and hormonal factors [56]. Therefore, selection for a higher number of fruits could result in smaller fruit size. Consistently with this, Figàs et al. [57] reported a decrease in fruit weight and setting percentage in higher trusses of Tomata Valenciana accessions. In that study, three populations of *Valenciana d'El Perelló* tomato derived from a mass selection program were compared with the commercial variety *Eufrates*. Although the Tomata Valenciana populations exhibited superior fruit setting and greater fruit weight in the

first trusses, a marked decline was observed from the fourth truss onwards compared to the commercial hybrid, resulting in significantly lower final production. This experiment may provide guidelines on how to approach improvement in this aspect of the crop, as it suggests that the key to increasing production in Tomata Valenciana relies on achieving a more uniform fruit-setting sequence throughout the plant's development rather than increasing the total number of fruits produced by the plant.

Diversity is also preeminent in Tomata Valenciana's fruit morphology, as it could be expected, because fruit morphological traits have remained the main classical way of differentiating among subtypes in this landrace during the past two decades [13,58,18,57,17,20]. Diversity at fruit level could be classified within two different categories: colour and fruit architecture. Regarding the fruit colour, variability has been found in the three types of measurements performed, which are unripe fruit, green shoulder and ripe fruit and are ligated to different subtypes (Table 1), what explains the high heritability values generally observed for these traits (Table S5).

Fruit shape and size also display variation associated with the subtypes. 'Blanca' fruits are bigger than 'Masclat' ones ([13]; Pons et al., 2017; [17,20]). In this study, this is confirmed by the large and significant differences in fruit width and width/length ratio among 'Blanca' and 'Masclat' subtypes. However, 'Intermitja' accessions only show significant differences with 'Blanca' accessions regarding the width. As indicated by Chu et al., in 2019, fruit size is strongly correlated with locule number, because the alleles controlling the locule number, *lc* and *fas* [59], are encoded by the tomato orthologs of *WUSCHEL* (*SIWUS*) and *CLAVATA3* (*SLCLV3*) respectively, involved in meristematic cell differentiation. Single and double mutant alleles of *lc* and *fas* maintain higher *SIWUS* expression during the development of the carpel primordia in the floral bud. This augmentation and altered spatial expression of *SIWUS* provided a mechanistic basis for the formation of multilocular and large fruits. In this sense, significant differences are also found in Tomata Valenciana regarding locule number (LCN), with the 'Masclat' subtype (smaller fruits) displaying a significantly lower LCN than the 'Blanca' and 'Intermitja'. Furthermore, *lc* and *fas* alleles are also responsible of fasciated inflorescences and enlarged meristems [60], thus they are directly correlated with RBB, a trait that also demonstrates differential behaviour in 'Masclat' fruits when compared with the bigger 'Blanca' and 'Intermitja' ones, which display significantly more RBB and higher locule count (Table 1). It remains to be studied if differences in the expression of these genes are responsible of the differences in fruit shape and size observed among the three Tomata Valenciana subtypes.

Protuberance of tomato fruit tips (FTF) arises as the only differential trait amongst all the Tomata Valenciana defined subtypes. The gradation goes from 'Masclat' subtype, with the sharpest tip to 'Blanca' subtype whose accessions show no tip and the 'Intermitja' accessions displaying some protuberance. The use of germplasms with pointed-tip fruit is a common strategy in breeding programs to reduce rough blossom-end scarring in large, fresh-market tomatoes [61] and Tomata Valenciana is not an exception as the fruit tip is, together with the green shoulder, probably the most recognizable trait of this variety. Fruit tip formation in tomato has been associated with allelic variation at the *POINTED TIP* (*PT*) locus, which regulates fruit shape through the control of auxin-related developmental processes [62]. Although differences in fruit tip morphology were observed among Tomata Valenciana subtypes in the present study, no genetic data is available to confirm the involvement of this locus, and therefore any inference on its genetic basis remains hypothetical. If confirmed by further molecular analyses, variation at this locus could be considered in future Tomata Valenciana breeding programmes; however, genetic validation is required.

Finally, the biochemical characterisation revealed a high degree of homogeneity among the analysed accessions. None of the biochemical traits showed significant differences in the ANOVA, either among the 46 accessions or among the three Tomata Valenciana subtypes. This limited within-landrace variability is consistent with previous reports

describing a stable biochemical profile for Tomata Valenciana [29]. Taken together, these results support the existence of a relatively standard and consistent biochemical composition within the landrace, which contributes to uniform product quality and reinforces its varietal identity, a relevant aspect for the revalorisation and commercial recognition of landraces [63].

5. Conclusions

The results reveal a high degree of phenotypic diversity within the landrace and enable the differentiation of three varietal subtypes ('Blanca', 'Intermitja', and 'Masclat') primarily through plant architectural, agronomic, and fruit morphological traits. Significant differences among subtypes were observed for several traits related to plant structure, nitrogen balance, vigour, fruit set sequence, fruit size, locule number, ribbing, and fruit tip protuberance, which remains as the only trait showing a clear and consistent gradient across all three subtypes. In contrast, the biochemical traits analysed did not show significant variation among accessions or subtypes. These findings document the extent of variability present in Tomata Valenciana and provide a detailed phenotypic framework for its characterisation.

Some limitations of the study should be acknowledged. The first one is the unequal representation of the three Tomata Valenciana subtypes within the analysed population (30 'Blanca', 4 'Intermitja' and 12 'Masclat' accessions), that reflects the availability of material in the germplasm bank at the time seed samples were collected, which may affect the robustness of some statistical comparisons, particularly for 'Intermitja', where the lower number of accessions is associated with larger standard errors and therefore requires cautious interpretation of the results. Another limitation is that trait evaluation was conducted under single experimental context, restricting the assessment of the interactions between the genotypes and the environment thus limiting the extrapolation of heritability estimates. Furthermore, the genetic basis of the observed phenotypic variation was not directly examined because it was not part of the main purpose of this study. Although well documented, explanations to the observed results were inferred from analysis' results and scientific literature on each specific topic, meaning that the hypothesis put forward must be corroborated through molecular analysis.

Future studies should prioritise the evaluation of Tomata Valenciana under multiple environments and growing seasons with a better-balanced representation of the varietal subtypes. The integration of molecular and genomic approaches will be necessary to validate the genetic control of key agronomic and fruit morphological traits and to clarify the relationships among varietal subtypes. Such approaches will strengthen the understanding of Tomata Valenciana diversity and facilitate its effective utilisation in breeding programmes aimed at this landrace's revalorisation.

CRedit authorship contribution statement

Ramón Gabriel Rico Ferrer: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **María del Rosario Figàs:** Supervision, Methodology, Formal analysis. **Nicolás Arroyo:** Methodology, Investigation, Formal analysis, Data curation. **Miquel Martínez:** Formal analysis, Data curation. **Elena Soler:** Formal analysis, Data curation. **Cristina Casanova:** Formal analysis, Data curation. **Jaime Prohens:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Salvador Soler:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Ramon Gabriel Rico Ferrer reports financial support was provided by Polytechnic University of Valencia. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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During the preparation of this work the author(s) used ChatGPT in order to assist with language editing, including spelling correction, grammatical refinement, and improvement of text clarity. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the published article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jafr.2026.102717>.

Data availability

Data will be made available on request.

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