Article

Sustainable Transfer of Tomato Landraces to Modern Cropping Systems: The Effects of Environmental Conditions and Management Practices on Long-Shelf-Life Tomatoes

Joan Casals [1,*] , Montserrat Martí [2], Aurora Rull [1] and Clara Pons [3]

1   Department of Agri-Food Engineering and Biotechnology/Miquel Agustí Foundation, UPC-BarcelonaTech, Campus Baix Llobregat, Esteve Terrades, 8, 08860 Castelldefels, Spain; aurora.rull@upc.edu
2   SELMAR, Masía de can Ratés, 08398 Santa Susanna, Spain; selmar@federacioselmar.com
3   Institute for the Conservation and Improvement of Valencian Agrodiversity, Universitat Politècnica de València (COMAV/UPV), Camino de Vera 14, 46022 Valencia, Spain; cpons@upvnet.upv.es
*   Correspondence: joan.casals-missio@upc.edu

Abstract: The individual effects of biotic and abiotic factors on tomatoes have been widely reported. However, under commercial conditions, multiple interactions between factors occur, masking or even changing the direction of their effects in some cases. Here we report a comprehensive analysis of preharvest factors affecting yield, quality (soluble solids content, fruit color, and firmness), and shelf-life of long-shelf-life Mediterranean varieties of tomatoes. We studied five long-shelf-life genotypes under 16 growing environments, including tunnel and open-air systems and suboptimal to excessive fertigation (22–142% crop evapotranspiration). The results enabled us to classify traits into three groups according to the importance of the contributions of different types of factors: mainly genotype (ripening earliness and firmness), genotype plus environment (yield, fruit weight, water-use efficiency (WUE)), or genotype plus environment plus the interaction between genotype and environment (cracking, soluble solids content, and shelf-life). Under similar management practices, open-air conditions optimized yields, and high fertigation doses improved yield and marketability (firmness), but reduced quality (redness and soluble solids content). WUE was maximized under low-input cropping systems (comparable to traditional agrosystems), and the balance between WUE and yield was optimized when fertigation was adjusted to the requirements of the crop. Shelf-life was negatively correlated with high-yielding environments, and day–night amplitude in relative humidity was strongly correlated with the incidence of fruit cracking. The present study sheds light on the contributions of environment and management practices on tomato yield and quality, and provides a basis on which to select better management practices for the novel commercial group of European long-shelf-life tomato landraces.

Keywords: shelf life; water use efficiency; irrigation; ripening mutant; Penjar tomato

1. Introduction

Tomato (*Solanum lycopersicum* L.) is the second most widely grown vegetable in the world, being cultivated with a wide range of techniques in very diverse environments in 177 countries [1], including low-input open-air fields (yielding up to 40 t/ha), low-tech greenhouses (yielding 50–100 t/ha), and high-tech greenhouses (yielding > 400 t/ha) [2,3]. Given the economic importance of the crop and wide variability in growing conditions, large amounts of time and money have been invested in research to understand genetic and environmental factors influencing yield and quality traits [2,4–8]. Studies are usually designed to isolate the effects of particular environmental factors and conducted under controlled conditions; however, when these results are transferred to commercial conditions, the effects can be diluted in the complex matrix of interactions between the myriad factors that simultaneously affect plants in fields. For this reason, to gain a comprehensive

understanding of crop responses to biotic and abiotic factors, it is necessary to assess the combined effects of genotype x environment x management factors (GxExM) [4,9]. Various authors have pointed out the need to consider combinations of factors affecting tomato plant performance in efforts to understand the pathogen–environment complex [2,10], fruit quality [4], or the interactions between irrigation and fertilization doses [11,12].

The impact of preharvest factors on yield and quality in tomato differs among the three main commercial groups (cherry (<20 g) and large fruit varieties (>50 g) for fresh-market, and processing tomatoes) as a result of genetic [13,14] and phenotypic differences [15,16]. For instance, within the group of tomatoes for fresh consumption, both the cherry and large-fruited varieties differ in their sensitivity to salinity [17] or water stress [18], and the widely reported negative correlation between fruit weight and soluble solids content (SSC) [19] seems important in the cherry group, but not in genotypes with larger fruits [15]. Processing tomatoes are grown in highly different cropping systems, and varieties have been bred for their adaptation to nontrellised culture and mechanical harvesting [16], triggering significant changes in plant physiology [20].

Apart from these three commercial types, a fourth, less-studied group of tomatoes comprises Mediterranean long-shelf-life landraces [21], which are characterized by their ability to keep for up to 6 months without refrigeration, small fruit (<80 g) [22–24], and specific culinary usages [21,25]. The alcobaça (*alc*) mutation [25–27] in the *nac.nor* gene [28] has been identified as the genetic factor that confers long shelf-life in some accessions of the Penjar [25] and Ramellet varieties [23], and is also likely responsible for long shelf-life in the da Serbo variety [29]. Penjar and Ramellet show important similarities in fruit and plant traits [23,25,30] and postharvest behavior [22,31,32]; although these varieties share the same market (NE Spain) and culinary uses (mainly for sauces and "*pa amb tomàquet*" (bread with tomato), for which the fruit is halved and rubbed into the surface of sliced bread, and then dressed with olive oil and salt), they seem to have distinct genetic identities [21]. Until 15 years ago, these two landraces were mainly cultivated under traditional low-input agrosystems (unpruned plants, water deficit, open field), and they are highly adapted to this approach [33]. However, recently their market success has led to their cultivation with modern cropping systems (protected cultivation, high irrigation and fertilization doses, development of modern hybrids, grafting) [30,34], drastically changing the landscape of these varieties and resulting in significant genetic erosion [35].

It is important to optimize GxExM factors to attain sustainable productions in crops that consume high inputs, such as tomato, which ranks first among vegetables in environmental impact [36]. To attain maximum yields and quality with the most efficient use of resources (i.e., water-use efficiency (WUE), partial factor productivity of fertilizer (PFP)) [12], it is necessary to understand the complex matrix of GxExM factors that contribute to crop performance and to determine the thresholds of each factor (i.e., maximum levels of inputs inducing efficient responses in the crop). Taking advantage of the abundant information collected for fresh-market, and processing tomatoes [2,3], long-shelf-life landraces can be considered a model group, because they are just starting their trajectory in modern high-input agriculture. To promote the sustainable transfer of long-shelf-life tomatoes to modern production systems, we studied GxExM factors impacting yield, quality (SSC, firmness, and fruit color), and shelf-life, and analyzed if these landraces preserve their singularities under the modern cropping systems as well as if they maintain their high WUE. With this aim, we performed a 16-trial experiment, analyzing the effects of moving five genotypes from low-input to high-input environments (including the effects of cultivation under open-walled tunnels and fertigation dose) on agronomic, quality, and postharvest traits.

2. Materials and Methods

2.1. Plant Materials

Five Spanish long-shelf-life varieties (Penjar and Ramellet) were selected for this study: three open-pollinated landraces from the different historical areas of cultivation of the

varietal type (Penjar: LC649 from Valencia and LC391 from Catalonia; Ramellet: LC732 from the Balearic Islands), and two modern hybrids released by Semillas Fitó in 2013 (cv. 545) and 2016 (cv. 15004). All five genotypes have an indeterminate growth habit. All five genotypes were grown in first-year trials (2017); to validate the results, experiments were repeated in the second year (2018) using only one representative of the landrace group (LC649) and one of the modern hybrids (cv. 545).

2.2. Experimental Conditions and Crop Management Practices

Plants were grown in two consecutive years (2017 and 2018) in two localities (Palafolls (41°40′03.6′′ N 2°44′08.0′′ E) and Santa Susanna (41°37′51.8′′ N 2°41′56.9′′ E)) (Table 1). The experimental factors compared were (i) growing environment: open-air vs. cultivation under open-walled tunnels (open-sided unheated tunnels, 3.4 m tall, 7 m wide, covered with a 200 μ thick polyethylene film with > 91% global and < 45% diffuse light transmission capacities, and thermicity factor > 82%); (ii) crop cycle: early (sowing 01 March, transplanting 5 April), intermediate (sowing 25 March, transplanting 4 May), or late (sowing 11 May, transplanting 15 June). Crops were grown until the end of the production phase (172–223 days after transplanting, depending on the genotype and trial); (iii) fertigation: previous to the opening of the first flower, irrigation was adjusted to the requirements of the crop calculated following the crop evapotranspiration (ET_c) method based on soil–water balance ($ET_c = ET_0 \times K_c$) [37]; subsequently we followed three different irrigation strategies that farmers normally use in the area, which set the irrigation volume to water for 1, 4, or 7 h per week. In our experiment we used a drip tape with five emitters m^{-1} and a discharge of 1.18 L $emitter^{-1}$ h^{-1} (i.e., 8.9 L m^{-2} h^{-1}), thus the different irrigation times were translated to 8.9 (1 h), 35.7 (4 h), and 62.5 L m^{-2} $week^{-1}$ (7 h). This irrigation is commonly used by Penjar growers regardless of weather conditions (except in case of precipitation), hence we wanted to follow these conventional practices, irrespective of whether it represented an excessive watering in some cases. As a result, at the end of the cropping season treatments covered a range from 22% to 140% of crop water requirements (ET_c). Following farmers' practices, fertilization was coupled with the amount of irrigation, adjusting the electrical conductivity to about 2 dS/m, and ranged from 152 to 868 N-NO_3^- kg/ha, and 290 to 1900 K_2O kg/ha. The fertilizer used was potassium nitrate (13.8-0-45.1 NPK); phosphorus was not applied, because soils had a high concentration before transplanting (>100 ppm available phosphorus).

Similar methods were used in all trials: plants were trellised vertically on two stems using the V-shape method, using canes (*Arundo donax* L.) to support the stems and pruning every 10–15 days; plant density was 1.4 pl/m^2; weeds were controlled manually; integrated pest management was used with the support of floral margins to promote the presence of auxiliary fauna (mainly *Macrolophus* sp.) to control fruit worms (*Tuta absoluta* (Meyrick), *Heliothis armigera* Hübner) and whiteflies (*Bemisia tabaci*, *Trialeurodes vaporariorum*). Climatic conditions (rainfall, temperature, relative humidity, reference evapotranspiration (ET_o), and solar radiation) were recorded hourly at a weather station ≤3 km from the experimental fields. Within each trial, a randomized block design was used, with three blocks and nine plants per plot (i.e., 27 plants/genotype). Trial plots were separated by ≥2 m to avoid margin effects.

Table 1. Experimental conditions in the 16 experimental trials (DAS = days after sowing; ET_c = crop evapotranspiration; Pr = precipitation).

Trial	Year	Locality	Environment	Cycle	Cycle Length (DAS)	Water Require-ments (ET_c-Pr) (mm) (*A*)	Irrigation (mm) (*B*)	% Water Require-ment (=*B/A*)	Nitrogen (N-N0$_3$) (kg/ha)	Potassium (K$_2$O) (kg/ha)	Datasets Measured [1]
Exp1	2018	Sta. Susanna	Tunnel	Early	208	833	222	27	168	292	B-G
Exp2	2018	Sta. Susanna	Tunnel	Early	208	833	555	67	408	713	B-G
Exp3	2018	Sta. Susanna	Tunnel	Intermediate	184	729	479	66	339	580	B-G
Exp4	2018	Sta. Susanna	Tunnel	Intermediate	184	729	233	32	152	289	B-G
Exp5	2018	Sta. Susanna	Open air	Intermediate	184	636	233	37	152	289	B-G
Exp6	2018	Sta. Susanna	Open air	Intermediate	184	636	479	75	339	580	B-G
Exp7	2017	Sta. Susanna	Open air	Intermediate	186	648	922	142	868	1913	A-G
Exp8	2017	Sta. Susanna	Open air	Intermediate	186	648	542	84	581	1366	A-G
Exp9	2017	Sta. Susanna	Open air	Intermediate	186	648	173	27	157	342	A-G
Exp10	2017	Sta. Susanna	Tunnel	Intermediate	176	776	922	119	868	1913	A-G
Exp11	2017	Sta. Susanna	Tunnel	Intermediate	176	776	542	70	581	1366	A-G
Exp12	2017	Sta. Susanna	Tunnel	Intermediate	176	776	1727	22	157	342	A-G
Exp13	2017	Palafolls	Tunnel	Early	223	593	5502	93	201	456	A-G
Exp14	2017	Palafolls	Tunnel	Intermediate	208	944	5259	56	329	546	A-G
Exp15	2017	Palafolls	Tunnel	Late	181	528	3346	63	227	420	A-G
Exp16	2017	Palafolls	Open air	Intermediate	172	746	4968	67	258	457	A-G

[1] Traits included in each dataset are described in Section 2.3.

2.3. Measurements

The following five sets of traits (A-E) were evaluated in the field on a single-plant basis (four central plants from each plot; *n* = 12 plants per genotype and trial): Plant architecture (Dataset A, recorded in 2017), including height of the first truss (H1infl, in cm) and distance between inflorescences (DistInfl, in cm), measured from the 2nd to 3rd truss and from the 3rd to 4th truss; Earliness (Dataset B, 2017) (in days), including the components flowering earliness (FlowEarl, from sowing to anthesis of the first flower) and ripening earliness (RipEarl, from sowing to ripening of the first fruit of the 3rd truss); Yield (Dataset C, 2017, 2018), including total yield (kg/m^2), fruit weight (in g), and number of fruits per plant (n), and calculated as the sum of values from sequential harvests in each plant; Physiological disorders (Dataset D, 2017, 2018), including incidence of cracking (in % of fruits affected per plant) and blossom-end rot (BER, in %). We estimated WUE (kg/m^3) (Dataset E, 2017, 2018) by calculating the ratio between harvested yield per unit of water used [38].

The following quality traits (Dataset F, 2017, 2018) were measured individually on nine fruits per genotype and trial harvested at the red-ripe stage from the 2nd to 4th trusses: soluble solids content (SSC, measured with a hand refractometer (Erma, Tokyo, Japan), expressed in °Brix); color (measured with a colorimeter (Konica Minolta CR-410, Minolta, Osaka, Japan) in the equatorial part of the fruit and expressed as Chroma and Hue coordinates from the CIELAB color space); firmness (measured with a durometer (Agrosta Durofel, Compainville, France) in the equatorial part of the fruit, expressed as %).

Postharvest shelf-life (Dataset G, 2017, 2018) was measured in a single harvest of fruits in the red-ripe stage. From each trial, genotype, and block, three replicates of 30 fruits per genotype and trial were stored in a dark room at 18 °C and 95% relative humidity. During storage, fruits were visually inspected every 15 days for signs of desiccation, loss of turgor, or infection by fungal parasites. Fruits with any appreciable defects were discarded, and shelf-life was recorded at 30, 60, and 90 days. The 90-days period was established considering that it is the storage period during which Penjar tomato preserves the organoleptic characteristics most appreciated by consumers [22]. Shelf life was expressed as % of sound fruits (i.e., fruits with a commercial external appearance).

2.4. Data Analysis

Quantitative data from the experimental trials (2017) and validation trials (2018) were analyzed separately. Preliminary assumptions of constancy of variance and normal distribution of the data were confirmed prior to analysis. For each year, differences between genotypes were assessed by two-way factorial ANOVA, considering the factors genotype (G) and trial (E), and their interaction (GxE). Mean separation was conducted by using the Student–Newman–Keuls ($p < 0.05$) procedure. To study the relative contribution of each factor to the phenotypic variation (in %), the total sum of squares was partitioned into the sums of squares of genotype, environment, block, genotype x environment, and residual effects, as proposed in Figàs et al. [34].

To assess the effect of single environmental factors (dose of fertigation or cultivation under tunnel) we selected pairs of trials that differed in only one factor (Exp12/Exp9, Exp14/Exp16, Exp11/Exp8, Exp10/Exp7, Exp4/Exp5, and Exp3/Exp6 differed only in the growing environment; Exp12/Exp11/Exp10, Exp9/Exp8/Exp7, Exp1/Exp2, Exp4/Exp3, and Exp5/Exp6 differed only in the fertigation dose). For each of these pairs of trials, and within each genotype, significant effects were assessed by one-way ANOVA. Heatmaps based on log-2 transformed ratios were used to compare the effects of fertigation dose under open air or tunnel, and the growing environment under different fertigation levels. To assess the correlations between variables, we used Pearson's correlation coefficient. We used SPSS (v.12.0, SPSS Inc., Chicago, IL, USA) for univariate analyses and the "corrplot" package of R (R core team 2019) for bivariate analyses. Graphs were elaborated with the "ggplot2" package of R and GraphPad Prism (San Diego, CA, USA, v. 6.01, 2012).

3. Results

In this study, a panel of five long-shelf-life genotypes were grown in 16 trials representing a wide variability of environments (cultivation under tunnel vs. open air; early, intermediate, and late cycles) and management practices (watering and fertilization doses). Watering ranged from 22% to 142% of plant requirements (based on ET_c calculations), and fertilization ranged from 152 to 868 kg/ha $N\text{-}NO_3$ and from 289 to 1913 kg/ha $K\text{-}K_2O$. In other words, inputs ranged from very low levels to well above plants' needs [37]; this situation is representative of the diversity of conditions that can occur under commercial conditions, where suboptimal inputs or, more generally, excessive fertilization are common [39,40]. The reported levels of fertigation show possible undesirable situations that occur at field-level and highlight the need to improve crop mineral nutrition under commercial conditions, and move to a more sustainable production system to reduce undesirable environmental impacts [41].

During 2017 and 2018 growing cycles, the climatic conditions were highly similar (Figure 1). Rather than to study the effect of individual practices in crop management, the experimental design aimed to create a diversity of growing conditions (from low to high input) to reflect commercial conditions, where environmental and management factors are nested (environment x management) and cannot be dissected. For growing environment (open air, tunnel) and fertigation level (%ET_c) some combination of experiments allowed us to dissect the single effect of these factors, while for crop cycle this was not possible because of the experimental design.
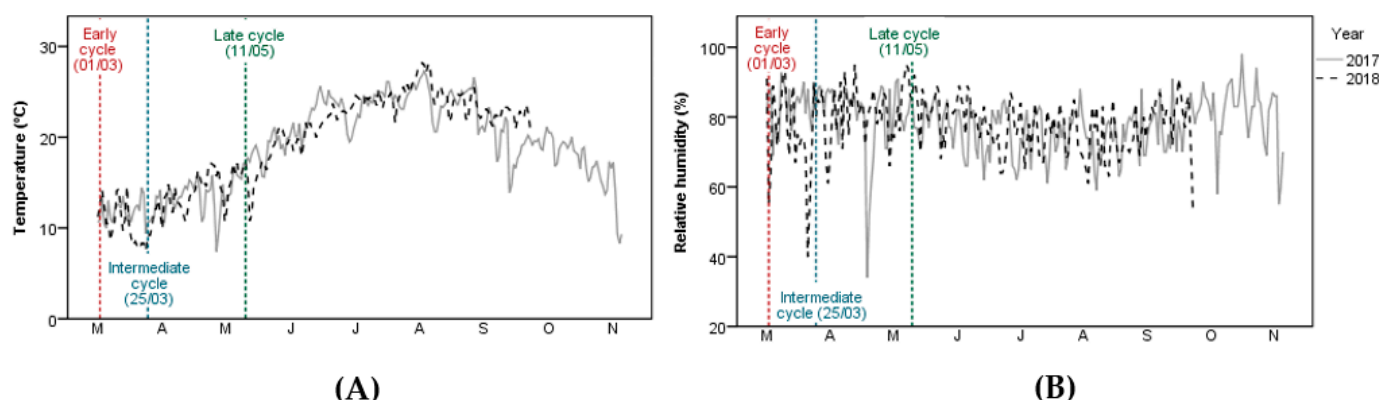
Figure 1. Climatic conditions recorded in the experimental trials: (**A**) temperature, (**B**) relative humidity. Sowing dates for early (in red), intermediate (in blue), and late cycles (in green) are presented inside parentheses. The lengths of the registers for 2017 (continuous line) and 2018 (dashed line) are different because the late cycle was studied only in 2017.

3.1. Earliness and Plant Architecture

The analysis of earliness revealed highly significant differences among genotypes for both flowering earliness and ripening earliness (Figure 2), with genotype accounting for 17% and 56% of the total variance observed for these traits, respectively, and no significant effects of environment or genotype x environment. Modern varieties (545, 15,004) showed a higher precocity, which was more evident for ripening earliness (differences between modern varieties and landraces, 6.7–22.2 days) than for flowering earliness (differences between modern varieties and landraces, 1.3–6.9 days) (Table S1). By contrast, less-significant differences among genotypes were found for plant architecture (height of the first truss and distance between inflorescences), and no clear differences in these traits were found between modern varieties and landraces. Cultivation under tunnel and fertigation dose had little impact on earliness or plant architecture, showing uniquely a tendency of plants grown under tunnel to have a higher height of the first truss and a lower flowering earliness (Figure S1). Pearson correlation coefficients between plant architecture and earliness traits found significant ($p < 0.05$) correlations, but these were r < 0.5, suggesting that these two sets of traits are independently controlled (Figure S2). The highest correlation was between flowering earliness and ripening earliness (r = 0.75, $p < 0.01$), showing that both traits are conjointly regulated. The worst correlation was between height of the first truss and distance between inflorescences (r = 0.47, $p < 0.01$); thus, although related, the height of the first truss does not predict the distance between subsequent trusses.

3.2. Agronomic Performance

Among all the traits studied, the agronomic traits (yield, physiological disorders, and WUE) were the most influenced by environmental factors (the contribution of environment to the total phenotypic variance was 41% for yield, 18% for cracking, 32% for fruit weight, and 56% for WUE (year 2017); contribution of genotype: 36%, 26%, 21%, 22%, respectively) (Figure 3). The results obtained in 2018 validated the conclusions from the analysis of the 2017 data, with similar patterns regarding the effects of genotype and environment, with small variations due to the different experimental design (e.g., environment maintained a high effect on both fruit weight (43%) and WUE (37%)).
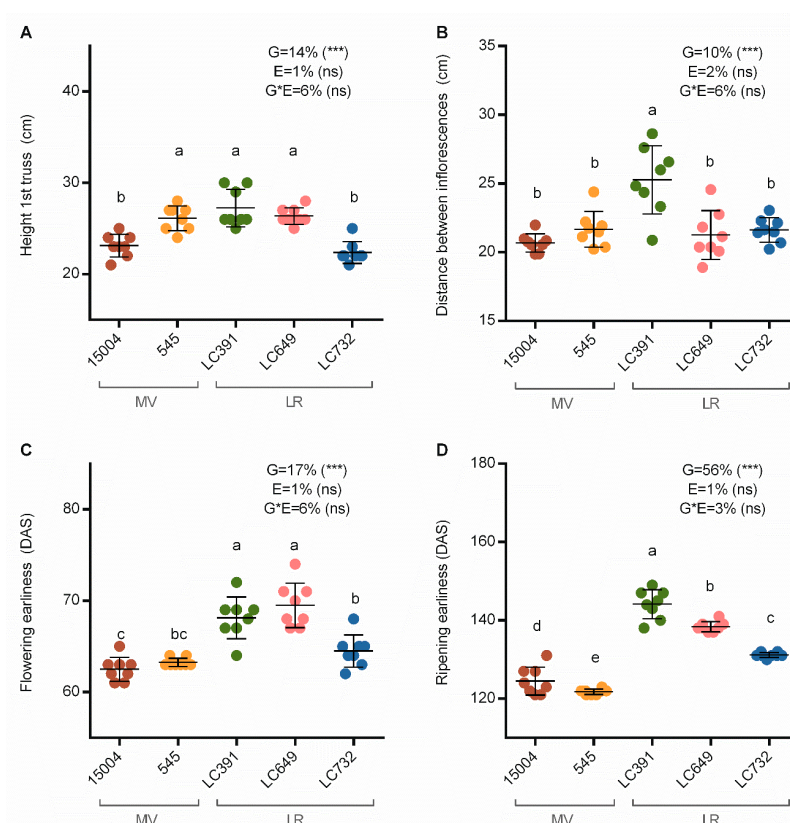
Figure 2. Differences between modern varieties (545, 15004) and landraces (LC391, LC649, LC732) in plant architecture and earliness traits. (**A**) Height of the first truss, (**B**) distance between inflorescences, (**C**) flowering earliness (1st truss), (**D**) ripening earliness (3rd truss). Mean ± SEM calculated from 2017 trials (Exp7–Exp16). Within graphs, different letters indicate significant differences between genotypes (Student–Newman–Keuls, $p < 0.05$). G, E, and G*E percentages indicate the relative contributions of genotype, environment, and genotype-by-environment interaction, respectively, to the total observed phenotypic variation. Level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant ($p > 0.05$).

Yields were significantly higher for modern varieties (averages: 545, 8.4 kg/m^2; 15,004, 8.8 kg/m^2) than for landraces (LC391, 5.3 kg/m^2; LC649, 4.1 kg/m^2; LC732, 4.2 kg/m^2); consequently, WUE was also higher for modern varieties (Table S2). For this trait, the variation overall all the trials and genotypes ranged from 1.8 to 37.8 kg/m^3. The incidence of fruit cracking was low in modern varieties (tolerant genotypes) and high in landraces (sensitive genotypes); this difference between groups was responsible for the significant genotype x environment interaction for this trait (accounting for 15% of phenotypic variance). Landraces were very sensitive to environmental conditions that cause cracking, such as high fertigation regimes used in our experiments [42]; the incidence of cracking ranged from 11% to 51% in LC391, from 4% to 30% in LC649 (2017), from 16 to 36% in LC649 (2018), and from 0% to 25% in LC732.

The growing environment (open air/tunnel) had a profound impact on agronomic behavior: open-air cultivation resulted in significantly higher yields, WUE, and fruit weight. The effect was more pronounced under intermediate and high fertigation levels, while under low fertigation regimes it was not significant (Figure 4). High fertigation doses resulted in significantly higher fruit weight, yield, and lower WUE; for both yield and fruit weight the effect was more pronounced under open-air than in tunnel conditions. WUE was consistently higher under low fertigation doses (significant effects for 18/20 comparisons in 2017 and 5/6 in 2018) (Table S2). Modern varieties achieved optimal values for WUE (>30 kg/m^3) under low fertigation doses (<25% ET$_c$), irrespective of the growing environment (open air or tunnel).
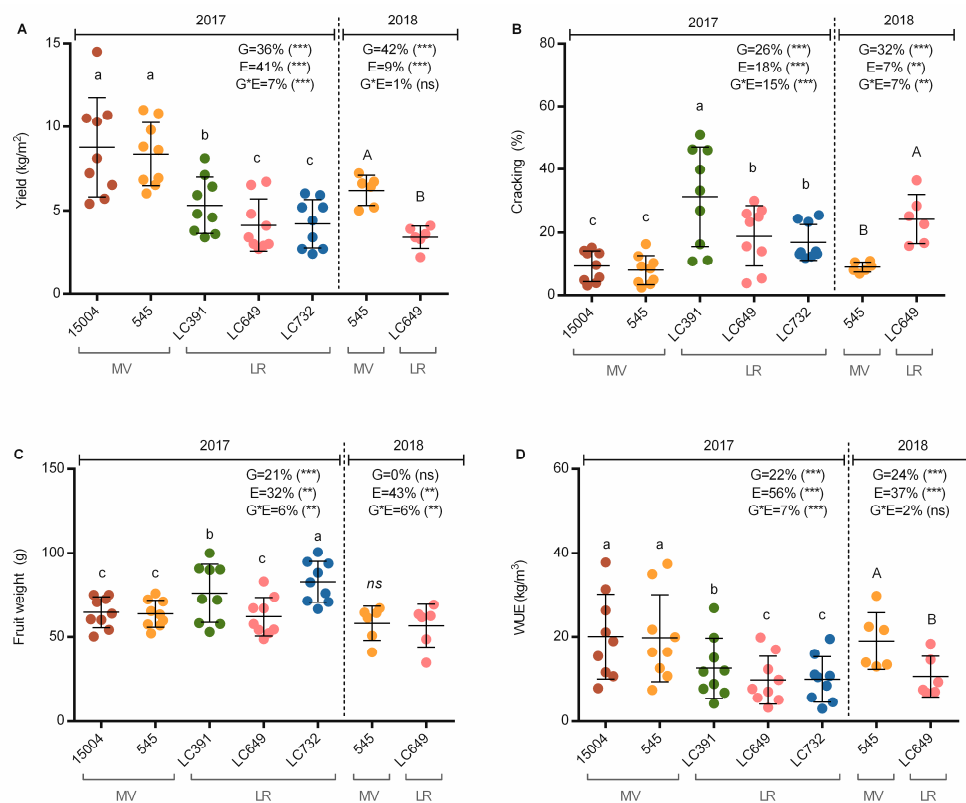
Figure 3. Differences between modern varieties (545, 15004) and landraces (LC391, LC649, LC732) in agronomic traits. (**A**) Yield, (**B**) cracking incidence, (**C**) fruit weight, (**D**) water-use efficiency (WUE). Mean ± SEM calculated from 2017 (Exp7–Exp16) and 2018 trials (Exp1-Exp6). Within graphs, and for each year, different letters (2017, lowercase; 2018, capital letters) indicate significant differences between genotypes (Student–Newman–Keuls, *p* < 0.05). G, E, and G*E percentages indicate the relative contributions of genotype, environment, and genotype-by-environment interaction, respectively, to the total observed phenotypic variation. Level of significance: * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001; ns, not significant (*p* > 0.05).
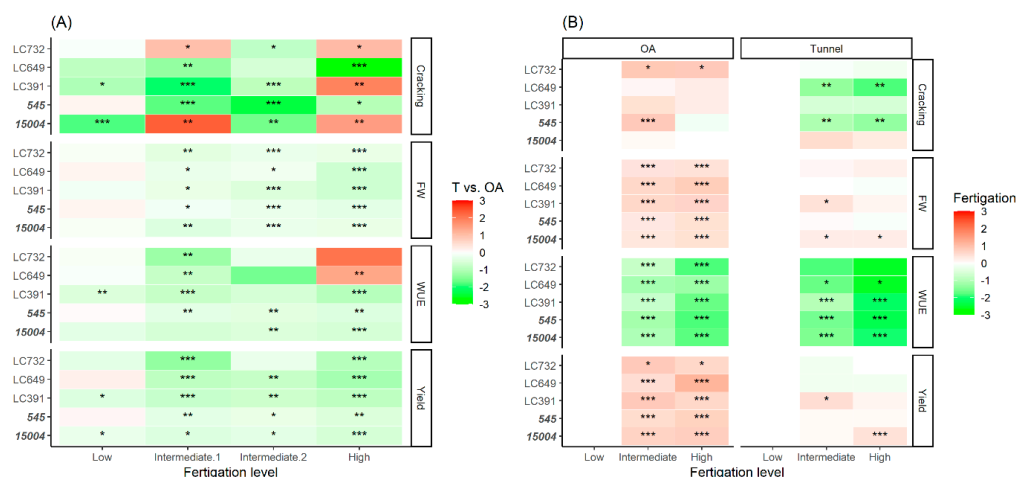

Figure 4. Environmental effects on yield related traits in Penjar tomato landraces (LC732, LC649, LC391) and modern varieties (545, 15004, marked in bold). (**A**) Effect of cultivation under tunnel (T) in comparison with cultivation in open air (OA) conditions, across increasing fertigation regimes. Color scale in heatmap represent the log2-transformed ratio of trait value in T respect to OA. Intermediate.1 and Intermediate.2 refers to two comparisons in the intermediate (75% ETc) range of fertigation. (**B**) Effect of intermediate (75% ETc) and high (120% ETc) fertigation in comparison with low fertigation regimes (25% ETc) under OA and T environments. Color scale in heatmap represent the log2-transformed ratio of trait value at each fertigation respect low fertigation regimes. FW: fruit weight; WUE: water-use efficiency. Level of significance: * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001; empty when not significant (*p* > 0.05).

WUE and yield are interrelated traits, although mathematically they can be considered independent variables. Ideally, both traits should be optimized to achieve the highest yields with the highest WUE. Plotting WUE against yield revealed clearly distinct patterns driven by fertigation doses (Figure 5). Optimal WUE is clearly linked to low fertigation management practices, where small increases in yield are accompanied by dramatic increases in WUE. Thus, in low-input conditions ($ET_c < 50\%$) plants do not show high yields, because there is a deficit in water or fertilizers, but WUE is maximized.
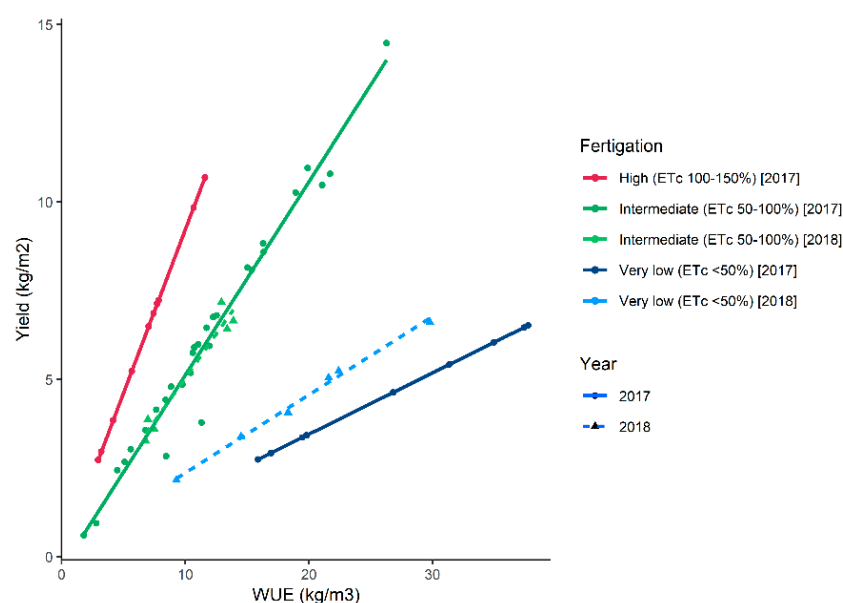
Figure 5. Patterns of water-use efficiency and yield driven by fertigation doses. Points represent the mean values per genotype and trial, and are grouped by fertigation dose (color) and year (2017, continuous line; 2018, dashed line).

When intermediate fertigation doses (50% to 100% ET_c) were applied, WUE increased linearly with yield. When higher than required fertigation doses (exceeding plant requirements, >100% ET_c) were applied, WUE stagnated and yield did not respond positively to this increase in inputs. The patterns of WUE/yield were similar in the 2017 and 2018 trials. Thus, small increases in yield under low fertigation strategies can have a marked impact on efficiency, and breeding genotypes adapted to low-input environments can lead to high-efficiency agrosystems. By contrast, in modern cropping systems adjusting inputs to crop requirements is the best way to optimize WUE and yield together.

Cracking is a major problem facing producers of tomato landraces. The incidence of cracking was equally affected by genotype (26%), environment (18%), and genotype x environment (15%) (Figure 3). Although significant effects were observed for growing environment or fertigation dose, these were highly dependent on GxExM interactions (Figure 4). For instance, high fertigation doses tended to increase cracking in open-air cultivation, but decrease it in tunnel cultivation; tunnel conditions tended to reduce the incidence of cracking under low and intermediate fertigation doses, but not in all the genotypes, while under high fertigation doses significant increases and decreases occurred depending on the genotype. To dig into environmental factors underlying cracking incidence we analyzed the correlations between the incidence of cracking in single harvests and climatic conditions (temperature, relative humidity, solar radiation, and ET_0; expressed as mean, minimum, maximum values, and the amplitude (max–min, and day–night) for the day before harvesting and for the average among 10 days before harvesting). We found significant correlations between cracking and climatic variables (mostly variables related to relative humidity) (Figure S3). The strongest correlation with the incidence of cracking was the day–night amplitude of relative humidity ($r = 0.52–0.75$, $p < 0.001$) under open-air

conditions, signaling that high amplitudes in relative humidity increase the occurrence of fruit cracking (Figure 6).
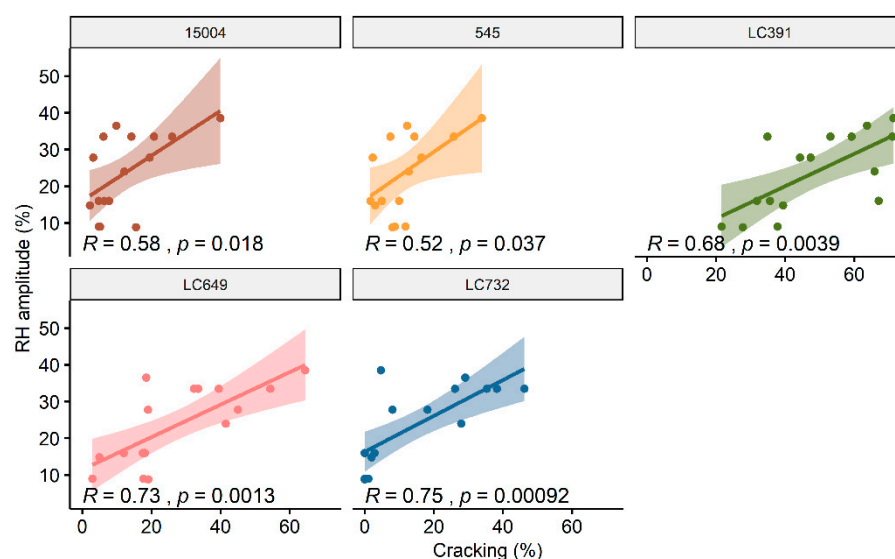

Figure 6. Environmental correlations (Pearson coefficient, *R*; and significance of the correlation, *p*) between cracking incidence and day–night amplitude for relative humidity recorded under open-air conditions. Each value represents the mean incidence in each harvesting day and for each trial (Exp: 7, 8, 9, 16).

3.3. Fruit Quality

Genotype, environment, and genotype x environment were significant for all the quality traits in both years of experimentation (Figure 7). Genotype was the greatest contributor to the phenotypic variance for firmness (59%), and color (Hue (26%), and Chroma (13%)) in 2017. The results for fruit quality traits were highly stable between years (2017, 2018), despite the differences in the experimental design. Values of the trait firmness were significantly higher in modern varieties (545, 15004) than in landraces (LC649, LC391, LC732) (i.e., breeding programs select for increased firmness to reduce postharvest damage due to mechanical injuries). Regarding SSC, genotype (21%), environment (22%), and genotype x environment (20%) contributed equally to the observed variability. The two modern varieties and the landrace LC391 had high levels of SSC, all of which were significantly higher than those of the other two landraces (LC649, LC732). Interestingly, modern varieties' values of SSC were less sensitive to environment; modern varieties' values of SSC were much more constant across environments than those of the two landraces with low SSC, which varied widely across environments. The color coordinates Hue and Chroma differed significantly among all the genotypes; each variety had a distinct color profile. Environment had a much more pronounced effect on Hue than on Chroma.

The effect of cultivation under tunnel on fruit quality traits was not consistent (Figure 8, Table S3). SSC responded positively or negatively to cultivation under tunnel depending on the genotype and the fertigation regime. Firmness did not show any effect regarding cultivation under tunnel. Fruit color seemed to respond to cultivation under tunnel under intermediate and high fertigation regimes, with an increase of Chroma and a decrease of Hue coordinates.
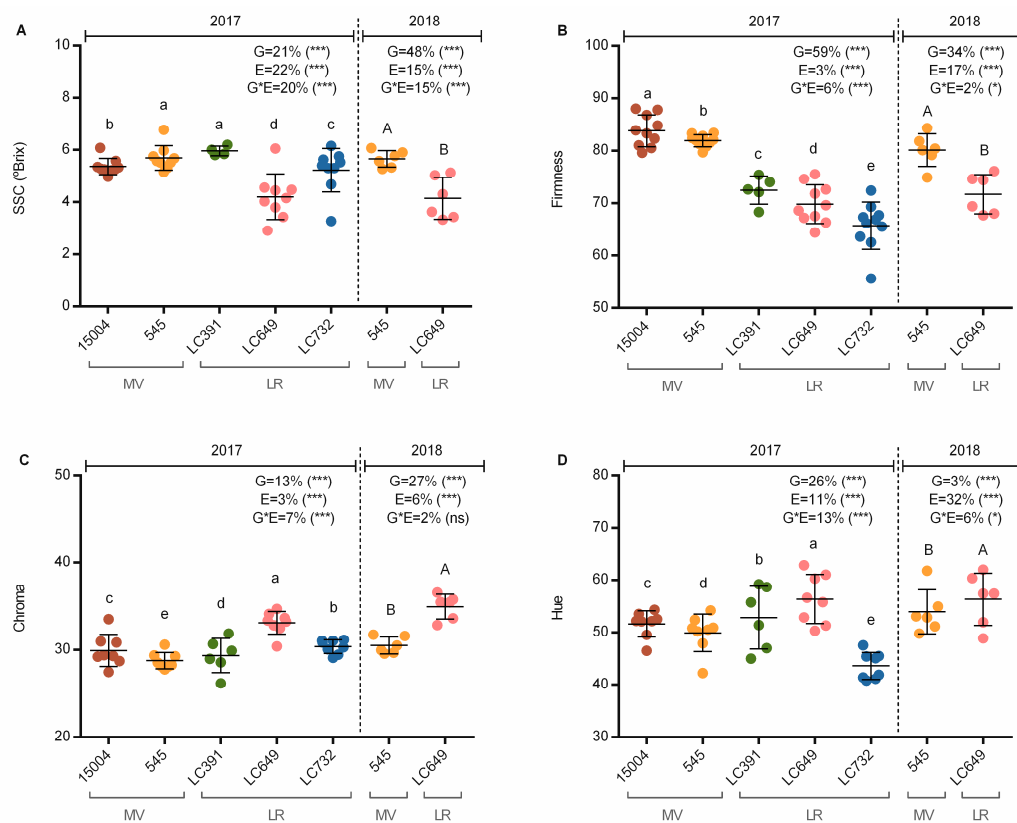
Figure 7. Differences between modern varieties (545, 15004) and landraces (LC391, LC649, LC732) for fruit quality traits. (**A**) Soluble solids content (SSC), (**B**) firmness, (**C**) chroma, (**D**) hue. Mean ± SEM calculated from 2017 (Exp7–Exp16) and 2018 trials (Exp1–Exp6). Within graphs, and for each year, different letters (2017, lowercase; 2018, capital letters) indicate significant differences between genotypes (Student–Newman–Keuls, *p* < 0.05). G, E, and G*E percentages indicate the relative contributions of genotype, environment, and genotype-by-environment interaction, respectively, to the total observed phenotypic variation. Level of significance: * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001; ns, not significant (*p* > 0.05).
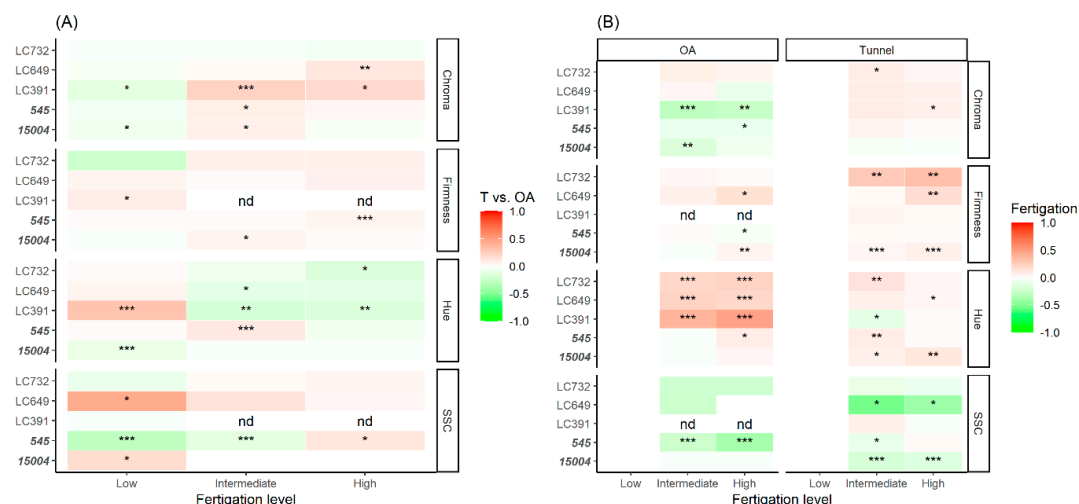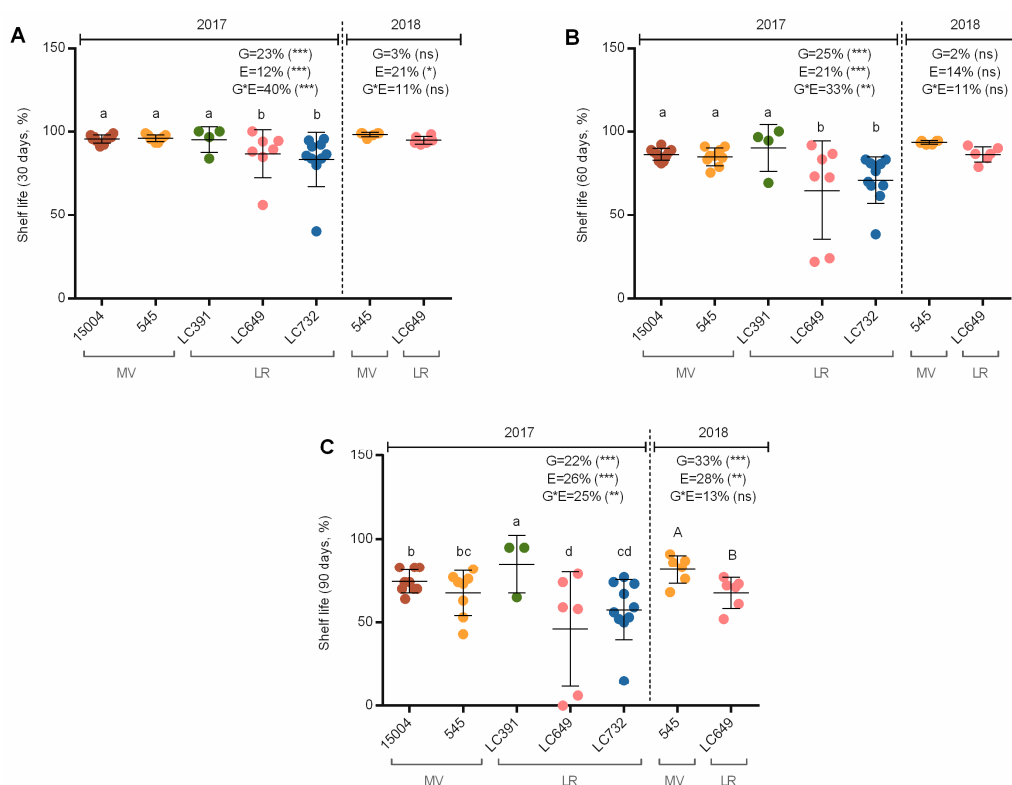

Figure 8. Environmental effects on quality traits in Penjar tomato landraces (LC732, LC649, LC391) and modern varieties (545, 15004, marked in bold). (**A**) Effect of cultivation under tunnel (T) in comparison with cultivation in open air (OA) conditions, across increasing fertigation regimes. Color scale in heatmap represent the log2-transformed ratio of trait value in T respect to OA. (**B**) Effect of intermediate (75% ETc) and high (120% ETc) fertigation in comparison with low fertigation regimes (25% ETc) under OA and T environments. Color scale in heatmap represent the log2-transformed ratio of trait value at each fertigation respect low fertigation regimes. SSC: soluble solids content. Level of significance: * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001; empty when not significant (*p* > 0.05); nd = data not available.

By contrast, the level of fertigation had much more consistent effects. Higher doses of fertigation decreased SSC and increased Hue both in tunnel and open-air conditions (Figure 8). For some genotypes, also, fruits were firmer when grown under high fertigation regimes. Thus, tomatoes grown under high fertigation tended to have lower sensory quality (lower redness (i.e., higher Hue) and sugar content), but better marketability (higher firmness).

3.4. Shelf-Life

Postharvest shelf-life was evaluated as the percentage of sound fruits at 30, 60 and 90 days after harvest. To avoid possible interactions of fluctuating conditions that occur normally in commercial storage of long-shelf-life varieties [23,25], postharvest experiments were conducted under laboratory conditions (18 °C, 95% relative humidity (RH)), adapting the recommendations from Thole et al. [43]. These conditions were established in order to generate critical storage conditions, in which ripening is not slowed down by low temperatures and infection by fungal parasites is accelerated by high RH.

Not all the trials included shelf-life evaluations, due to the lack of fruits from landraces in some trials. In 2017, genotype (20–25%), environment (12–26%) and genotype x environment (25–40%) had similar contributions to shelf-life in the different storage periods (30, 60, 90d) (Figure 9, Table S4). Results were very similar between years (2017, 2018) in the modern variety (545), while for the landrace (LC649) important differences were found between years, as in 2017 some environment x management combinations drastically reduced shelf life in this genotype (e.g., average shelf-life at 90 days for LC649 was 46% in 2017 and 68% in 2018, but was lower than 10% in two environments). These results signal that shelf life is a trait that largely varies in response to GxExM interactions.

Figure 9. Differences between modern varieties (545, 15004) and landraces (LC391, LC649, LC732) for postharvest shelf-life at (**A**) 30, (**B**) 60, and (**C**) 90 days. Mean ± SEM calculated from 2017 (Exp7–Exp16) and 2018 trials (Exp1–Exp6). For each year, different letters (2017, lowercase; 2018, capital letters) indicate significant differences between genotypes (Student–Newman–Keuls, $p < 0.05$). G, E, and G*E percentages indicate the relative contributions of genotype, environment, and genotype-by-environment interaction, respectively, to the total observed phenotypic variation. Level of significance: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns, not significant ($p > 0.05$).

In 2017, the percentage of sound fruits 90 days after harvesting ranged from 64% to 83% for the modern variety 15004, from 43% to 82% for the modern variety 545, from 65% to 95% for LC391, from 0% to 79% for LC649, and from 15% to 77% for LC732; in 2018 the results were similar (68–91% for 545 and 52–77% for LC649). The influence of growing environment and fertigation regime on postharvest shelf life was clearly dependent on the genotype (Figure S4). For instance, LC732 tended to respond positively to tunnel conditions, while 545 tended to respond negatively; on the other hand, LC649, and LC391 tended to respond positively to higher fertigation regimes in tunnel conditions, but not in open-air conditions. Thus, the effects were divergent and most of them not significant.

3.5. Trait Correlations

Pearson correlation coefficients between traits were calculated on the basis of mean values per trial for each genotype (except LC391, due to the high number of missing values) and year. Some groups of traits were clustered together because of tight correlation in different genetic backgrounds (four genotypes) and years (2017 (Figure 10), 2018 (Figure S5)), whereas other pairs of variables were independent or correlated in only one or two genotypes.
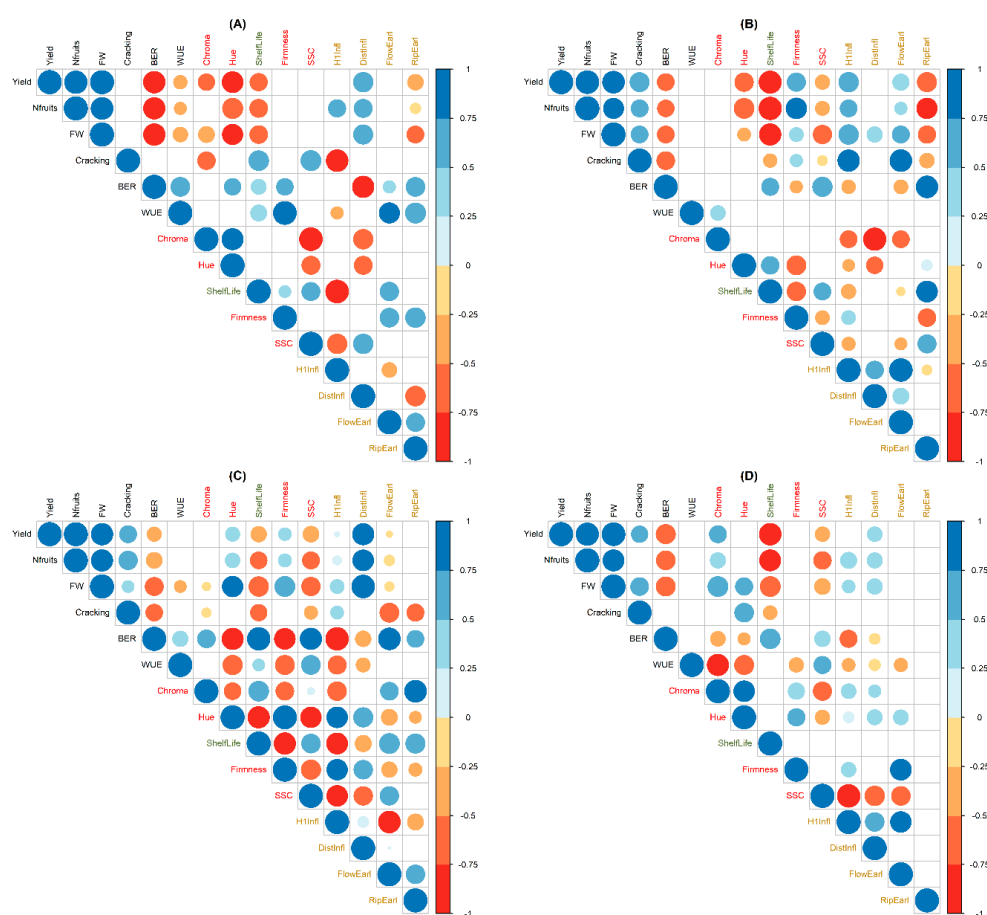

Figure 10. Correlation matrix for earliness, agronomic, fruit quality, and shelf-life traits in modern varieties (**A**) 545, (**B**) 15004, and landraces (**C**) LC649, (**D**) LC732, obtained in 2017 trials (n = 10). Colored boxes denote significant correlations ($p < 0.05$), while uncolored boxes indicate nonsignificant correlations. The size of the circles is proportional to the correlation coefficients. The sign and the magnitude of the correlation are indicated by the colors according to the scale in the right panel. FW: fruit weight; Nfruits: number of fruits per plant; DistInfl: distance between inflorescences; H1infl: height of the first truss; SSC: soluble solids content; BER: blossom-end-rot; WUE: water use efficiency; ShelfLife: shelf life at 90 days. Name of the variables are colored by groups (black = agronomic traits; red = quality traits; green = postharvest shelf life; yellow = plant architecture and earliness traits).

Logically, yield correlated positively with its components (number of fruits per plant, fruit weight) and negatively with the incidence of blossom-end rot. Cracking was positively related to yield in susceptible varieties (landraces LC649, LC732), showing that high-yielding environments and management practices favored the appearance of this physiological disorder, although this could not be explained solely by fertigation level or growing environment (Figure 4). High-yielding environments also had negative effects on SSC (except in 545) and shelf-life after 90 days; these results were validated in both years (except for shelf-life/yield in LC649 in 2018). Several other correlations were detected, although they were less consistent among genotypes. For instance, Hue was negatively correlated with SSC and positively correlated with firmness in most comparisons, signaling a positive relation between redness and SSC and a negative correlation between redness and firmness.

4. Discussion

4.1. Differential Contributions of G, E, and GxE Interactions to Agronomic Performance, Plant Architecture, and Fruit-Quality Traits

Plant responses to environmental factors and agricultural techniques are very complex, and for some traits these responses depend on the genotype. The diversity of growing conditions evaluated in this study enabled us to classify agronomic, quality, and postharvest traits into three groups according to the relative contributions of genotype, environment, and genotype x environment interactions: one group mainly influenced by genotype (ripening earliness and firmness), a second group mainly influenced by genotype and environment (yield, fruit weight, and WUE), and a third group equally influenced by genotype, environment, and genotype x environment interactions (cracking, Hue, SSC, and shelf-life). On the other hand, the factors studied explained < 20% of plant architecture traits (height of the first truss, distance between inflorescences), flowering earliness, and Chroma. Differential contributions of genotype, environment, and genotype x environment interactions have been widely reported for fruit quality [44,45] and agronomic performance in tomato [8,46], and using a similar statistical approach, Figàs et al. [34] reported similar results for different traits (yield, fruit weight, firmness, or color) in long-shelf-life landraces.

4.2. Impact of Modern Breeding

Although some seed companies distributed pure-line selections from the Penjar landrace [34], this variety was largely ignored until Semillas Fitó started breeding it 15 years ago, releasing high-yielding, resistant hybrids such as 545 in 2013 and 15,004 in 2016. In the present study, we compared the behavior of these recently released modern varieties (545, 15,004) to that of traditional accessions of different ecogeographic origins (LC649, Valencia; LC391, Catalonia; LC732, Balearic Islands) selected from among the wide diversity found in each area [23,25,47] for their economic importance (they are still grown on a large-scale) and closeness to consumers' ideotype of the variety. The main differences found between the modern varieties and the landraces were related to earliness, yield, firmness, and resistance to cracking, all of which have been targets for modern tomato breeding, which started a century ago [2]. Compared to the worst-performing landraces, the best modern varieties achieved gains in earliness to ripening (22.2 days), yield (4.4 kg/m^2), and firmness (42%) while maintaining the quality features associated with the landraces (long shelf-life, low fruit weight, and high SSC). These results show the important role that plant breeding can play in revitalizing the cultivation of landraces [48].

Contrary to the widely held view that landraces are highly stable, especially under low-input agrosystems [48,49], in our study the modern varieties were more stable than the landraces across different environments in traits such as fruit weight, firmness, color, and SSC. For instance, SSC was higher and more stable in modern varieties 545 (5.8 °Brix) and 15,004 (5.5 °Brix) and the landrace LC391 (5.9 °Brix) than in the other two landraces (LC732 (5.4 °Brix), LC649 (4.3 °Brix)). Thus, it seems that the stability observed in landraces

within the environmental variations common to the original cropping systems where they evolved is lost when these genotypes are transferred to high-input cropping systems [48].

4.3. Effect of Protected Cultivation and Fertigation Dose on Yield, Quality, and Shelf-Life

Farmers in north-east Spain are adopting low-cost, unheated open-walled tunnels for tomato production to advance crop harvests and protect fruits from inclement weather. Although their effects are less intense than those of closed greenhouses, these structures have a significant impact on climatic conditions [50,51] that can potentially affect yield and quality [6]. We found that cultivation under these tunnels significantly affected the agronomic performance of long-shelf-life varieties (reducing total yield and fruit weight) but did not affect quality or shelf-life. As our experimental design ensured that cycle, watering, fertilization, and crop management were identical in open-air and tunnel cultivation, the observed effects should be related to the impact of polyethylene plastic coverage on transpiration and photosynthesis caused by changes in light intensity, temperature, and/or vapor pressure deficit [5]. Previous studies have shown that polyethylene plastic can reduce light transmittance and photosynthetically active radiation (PAR), thus affecting the growth of tomato plants [52]. These findings contrast with general reports of higher yields of fresh-market tomatoes under greenhouse conditions [3], but corroborate Figàs et al. [34] findings that protected cultivation had a detrimental effect on yield in long-shelf-life tomatoes.

Both irrigation and fertilization affect yield and quality traits [4,5], and low fertilizer doses and high irrigation levels tend to decrease quality [12]. In our study, as is usual in commercial cultivation, we coupled watering and fertilization. We found that high fertigation levels had significant effects on agronomic traits, increasing yield and fruit weight (particularly in open air trials), but reducing WUE, as well as on quality traits, reducing SSC and redness. Nonetheless several GxExM interactions were detected; for instance, the effect of fertigation regime on cracking or Chroma was dependent on the growing environment, or the effect of both growing environment and fertigation regime was dependent on the genotype. These results highlight the importance of developing studies that consider the interaction between environmental (E) and management practices (M), especially in plant breeding programs aiming to select high-yielding and stable genotypes [4,53].

Besides the effects on agronomic and quality traits, it should be considered that increasing the level of irrigation or fertilization also increases cultivation costs. Although it was not an objective of our work, future studies should include an analysis of cultivation costs in order to concomitantly optimize GxExM interactions and economic profitability.

4.4. Relationships between Plant Architecture and Earliness Components

Time to ripening (and thus ripening earliness) comprises distinct concatenated steps (time from sowing to anthesis, time from anthesis to fruit set, time from fruit set to ripening) that can be considered independent heritable traits [54,55]. As previously reported [56], we observed a positive correlation between earliness to flowering and earliness to ripening (r = 0.75, $p < 0.01$). Earliness can be increased by reducing the duration of the vegetative phase before flowering and by reducing the length of sympodial units, mainly by reducing the number of leaves before the first inflorescence or between inflorescences [57], as has been described in the self-pruning mutant [58,59]. We correlated the plant architectural traits height of the first inflorescence and distance between inflorescences with the components of earliness, finding significant but moderate correlations (r < 0.5), showing that although related, distances between reproductive units are not an efficient predictor of earliness [60]. It should be noted, however, that in our study, rather than using the number of leaves to measure plant architectural events, we used distances, and this approach can lead to slightly different results. Finally, we detected no significant, consistent effects of protected cultivation or fertigation dose on earliness or plant architecture traits. Although various cultivation practices have been reported to affect earliness in tomato [61–63], these effects were not observed under our experimental conditions.

4.5. Effects of Cropping Systems on Water Use Efficiency

One key objective in the sustainable intensification of agriculture is to produce more in a more efficient way [64]. Against the background of climate change, where the scarcity of water will place major limits on agricultural productivity, it will be imperative to design management practices and to breed genotypes to ensure high water use efficiency.

In our work, water use efficiency ranged from 1.8 to 37.8 kg/m^3 (average: 13.7 kg/m^3), values that fall in the range of values reported in the literature (e.g., 35–50 [65,66], 9–16 [67], 13–33 [68], or 25–50 kg/m^3 [12]). These results show that farmers can improve the WUE of long shelf life tomato cropping systems. WUE is mainly driven by the potential yield of a genotype per unit of water applied, and the relationship between yield and WUE is mainly a function of the fertigation dose [12]. Low-input management practices maximize WUE, and significant progress towards optimal yield/WUE relationships can be achieved by breeding genotypes adapted to these environments. In these farming systems, various authors have shown that controlled water deficit strategies can substantially improve WUE in exchange for a slight decrease yield, which is however accompanied by an increase in fruit quality parameters [65,69–71]. On the other hand, under "conventional" commercial conditions, it is crucial to adjust irrigation and fertilization doses to the requirements of the crop to attain good WUE.

Above the threshold of crop requirements, plants do not respond positively to increased levels of inputs (water or fertilizers), causing a significant drop in efficiency (e.g., WUE). Moreover, heavy applications of potassium or nitrogen can depress tomato yield [3]. In summary, the results show the need to improve fertilization systems, with the aim of increasing the sustainability of productions.

4.6. Genotype and Day-to-Night Variations in Relative Humidity Play an Important Role in the Incidence of Cracking

Together with blossom-end rot, fruit cracking is the most important physiological disorder that leads to economic losses for growers of tomato landraces. Cracking reduces marketability, facilitates penetration by insects and fungi, and impedes storage in long-shelf-life varieties. The incidence of cracking in some landraces in the current study was >30%, underlining the importance of this disorder for the profitability of long-shelf-life varieties. The incidence of cracking can be either genetically or environmentally controlled [42,72–74], and the main agronomic strategy to prevent cracking is to use resistant cultivars. Several environmental conditions (rainfall, humidity) and management practices (irrigation, fertilization, balance between reproductive and vegetative organs, harvesting at early stages) have been described as affecting cracking incidence in several species, including tomatoes [42,72], cherries (*Prunus avium* L.) [75], or apples (*Malus domestica* L.) [76], among others [77].

In the current study, we found that high-yielding environments tended to result in a higher incidence of cracking (except in modern variety 545), but this effect was not explained by protected cultivation or fertigation dose. Apart from the genotype, the most important factor contributing to the incidence of cracking in our study was day-to-night amplitude of relative humidity (r > 0.5 for modern varieties, $p < 0.05$; r > 0.7 for landraces, $p < 0.01$). This finding is particularly important, as several climatic variables have been related to cracking incidence [42]. Other authors have also pointed out that the amplitude of relative humidity is a key factor driving cracking incidence in tomato [77,78] as well as in other sensitive species, such as pepper (*Capsicum annuum* L.) [79].

4.7. SSC and Shelf-Life Are Negatively Correlated with Yield

In our study, both environment and the genotype x environment interactions had strong significant effects on SSC (accounting for 22% and 20% of the observed phenotypic variance, respectively) and on shelf-life after 90 days of storage (accounting for 26% and 25% of the phenotypic variance, respectively). The environment effect on SSC was mainly due to the negative impact of high fertigation dose on this trait, which was also the main reason

for the negative correlation between SSC and yield. This negative correlation between SSC and yield under varying watering regimes has been extensively reported [12,68,70].

Shelf-life after 90 days was also negatively correlated with yield, and this result was validated in all the genotypes in both 2017 and 2018 trials (except for LC649 in 2018). Thus, modern, high-yielding environments tend to reduce the storability of long-shelf-life tomatoes and consequently hamper the emergence of the specific aromatic profile that fruits acquire during storage [31], which are important quality traits for consumers of these varieties. The negative relation between yield and shelf life can be associated to an increased fruit water content (lower SSC) which potentially can reduce shelf life [27], among other factors [21]. Few reports have been published regarding preharvest factors that affect postharvest shelf-life in tomato [3,6,32,80–82]; our results confirm the difficulty of identifying single factors affecting postharvest storage, a trait affected by complex genotype x environment x management interactions. Studies of long shelf life varieties could play a key role in deciphering these effects.

5. Conclusions

The adoption of modern cultivation techniques for the production of long shelf life tomato landraces can trigger negative impacts in both crop efficiency and the quality characteristics of the fruit. Modern, high-yielding growing conditions can increase yields and profitability of long-shelf life landraces, but with negative effects on fruit quality and postharvest storability, which are key traits for consumer acceptance. Moreover, the failure to adjust inputs to the requirements of the crop can lower efficiency significantly. Optimizing farmers' profits and product quality in the most resource-efficient production systems requires reshaping the genotypes and cultivation systems with contributions from plant breeders, agronomists, farmers, and consumers.

References

1. FAO. Food and Agriculture Organisation of the United Nations. Available online: http://faostat.fao.org (accessed on 6 December 2020).
2. Causse, M.; Zhao, J.; Diouf, I.; Wang, J.; Lefebvre, V.; Caromel, B.; Génard, M.; Bertin, N. Genomic Designing for Climate-Smart Tomato. In *Genomic Designing of Climate-Smart Vegetable Crops*; Springer: Vienna, Austria, 2020; pp. 47–159.
3. Heuvelink, E. (Ed.) *Tomatoes*; CABI: Wallingford, UK, 2018; ISBN 9781780641935.
4. Bertin, N.; Génard, M. Tomato quality as influenced by preharvest factors. *Sci. Hortic.* **2018**, *233*, 264–276. [CrossRef]
5. Beckles, D.M. Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. *Postharvest Biol. Technol.* **2012**, *63*, 129–140. [CrossRef]
6. Dorais, M.; Papadopoulos, A.P.; Gosselin, A. Greenhouse Tomato Fruit Quality. *Hortic. Rev.* **2010**, *26*, 239–319. [CrossRef]
7. Davies, J.N.; Hobson, G.E.; McGlasson, W.B. The constituents of tomato fruit—The influence of environment, nutrition, and genotype. *Crit. Rev. Food Sci. Nutr.* **1981**, *15*, 205–280. [CrossRef] [PubMed]
8. Cuartero, J.; Cubero, J.I. Genotype-environment interaction in tomato. *Theor. Appl. Genet.* **1982**, *61*, 273–277. [CrossRef]
9. Bertin, N.; Martre, P.; Génard, M.; Quilot, B.; Salon, C.; Quilot-Turion, B. Under what circumstances can process-based simulation models link genotype to phenotype for complex traits? Case-study of fruit and grain quality traits. *J. Exp. Bot.* **2009**, *61*, 955–967. [CrossRef] [PubMed]
10. Suzuki, N.; Rivero, R.M.; Shulaev, V.; Blumwald, E.; Mittler, R. Abiotic and biotic stress combinations. *N. Phytol.* **2014**, *203*, 32–43. [CrossRef] [PubMed]
11. Zotarelli, L.; Dukes, M.; Scholberg, J.; Muñoz-Carpena, R.; Icerman, J. Tomato nitrogen accumulation and fertilizer use efficiency on a sandy soil, as affected by nitrogen rate and irrigation scheduling. *Agric. Water Manag.* **2009**, *96*, 1247–1258. [CrossRef]
12. Wang, X.; Xing, Y. Evaluation of the effects of irrigation and fertilization on tomato fruit yield and quality: A principal component analysis. *Sci. Rep.* **2017**, *7*, 1–13. [CrossRef]
13. Van Berloo, R.; Zhu, A.; Ursem, R.; Verbakel, H.; Gort, G.; Van Eeuwijk, F.A. Diversity and linkage disequilibrium analysis within a selected set of cultivated tomatoes. *Theor. Appl. Genet.* **2008**, *117*, 89–101. [CrossRef]
14. Sim, S.-C.; Robbins, M.D.; Van Deynze, A.; Michel, A.P.; Francis, D.M. Population structure and genetic differentiation associated with breeding history and selection in tomato (*Solanum lycopersicum* L.). *Heredity* **2010**, *106*, 927–935. [CrossRef]
15. Casals, J.; Rivera, A.; Sabaté, J.; Del Castillo, R.R.; Simó, J. Cherry and Fresh Market Tomatoes: Differences in Chemical, Morphological, and Sensory Traits and Their Implications for Consumer Acceptance. *Agronomy* **2018**, *9*, 9. [CrossRef]
16. Grandillo, S.; Zamir, D.; Tanksley, S.D. Genetic improvement of processing tomatoes: A 20 years perspective. *Euphytica* **1999**, *110*, 85–97. [CrossRef]
17. Caro, M.; Cruz, V.; Cuartero, J.; Estan, M.T.; Bolarin, M.C. Salinity tolerance of normal-fruited and cherry tomato cultivars. *Plant Soil* **1991**, *136*, 249–255. [CrossRef]
18. Albert, E.; Segura, V.; Gricourt, J.; Bonnefoi, J.; Derivot, L.; Causse, M. Association mapping reveals the genetic architecture of tomato response to water deficit: Focus on major fruit quality traits. *J. Exp. Bot.* **2016**, *67*, 6413–6430. [CrossRef] [PubMed]
19. Ho, L. The mechanism of assimilate partitioning and carbohydrate compartmentation in fruit in relation to the quality and yield of tomato. *J. Exp. Bot.* **1996**, *47*, 1239–1243. [CrossRef] [PubMed]
20. Soyk, S.; Müller, N.A.; Park, S.J.; Schmalenbach, I.; Jiang, K.; Hayama, R.; Zhang, L.; Van Eck, J.; Jiménez-Gómez, J.M.; Lippman, Z.B. Variation in the flowering gene SELF PRUNING 5G promotes day-neutrality and early yield in tomato. *Nat. Genet.* **2016**, *49*, 162–168. [CrossRef]
21. Conesa, M.À.; Fullana-Pericàs, M.; Granell, A.; Galmés, J. Mediterranean Long Shelf-Life Landraces: An Untapped Genetic Resource for Tomato Improvement. *Front. Plant Sci.* **2020**, *10*, 1651. [CrossRef]
22. Casals, J.; Cebolla-Cornejo, J.; Roselló, S.; Beltran, J.; Casañas, F.; Nuez, F. Long-term postharvest aroma evolution of tomatoes with the alcobaça (alc) mutation. *Eur. Food Res. Technol.* **2011**, *233*, 331–342. [CrossRef]
23. Bota, J.; Conesa, M.À.; Ochogavia, J.M.; Medrano, H.; Francis, D.M.; Cifre, J. Characterization of a landrace collection for Tomàtiga de Ramellet (*Solanum lycopersicum* L.) from the Balearic Islands. *Genet. Resour. Crop. Evol.* **2014**, *61*, 1131–1146. [CrossRef]
24. Tranchida-Lombardo, V.; Cigliano, R.A.; Anzar, I.; Landi, S.; Palombieri, S.; Colantuono, C.; Bostan, H.; Termolino, P.; Aversano, R.; Batelli, G.; et al. Whole-genome re-sequencing of two Italian tomato landraces reveals sequence variations in genes associated with stress tolerance, fruit quality and long shelf-life traits. *DNA Res.* **2018**, *25*, 149–160. [CrossRef] [PubMed]
25. Casals, J.; Pascual, L.; Cañizares, J.; Cebolla-Cornejo, J.; Casañas, F.; Nuez, F. Genetic basis of long shelf life and variability into Penjar tomato. *Genet. Resour. Crop. Evol.* **2012**, *59*, 219–229. [CrossRef]
26. Kopeliovitch, E.; Rabinowitch, H.D.; Mizrahi, Y.; Kedar, N. Mode of inheritance of Alcobaca, a tomato fruit-ripening mutant. *Euphytica* **1981**, *30*, 223–225. [CrossRef]
27. Kumar, R.; Tamboli, V.; Sharma, R.; Sreelakshmi, Y. NAC-NOR mutations in tomato Penjar accessions attenuate multiple metabolic processes and prolong the fruit shelf life. *Food Chem.* **2018**, *259*, 234–244. [CrossRef] [PubMed]
28. Gao, Y.; Wei, W.; Fan, Z.; Zhao, X.; Zhang, Y.; Jing, Y.; Zhu, B.; Zhu, H.; Shan, W.; Chen, J.; et al. Reevaluation of the nor mutation and the role of the NAC-NOR transcription factor in tomato fruit ripening. *J. Exp. Bot.* **2020**, *71*, 3560–3574. [CrossRef]
29. Mercati, F.; Longo, C.; Poma, D.; Araniti, F.; Lupini, A.; Mammano, M.M.; Fiore, M.C.; Abenavoli, M.R.; Sunseri, F. Genetic variation of an Italian long shelf-life tomato (*Solanum lycopersicon* L.) collection by using SSR and morphological fruit traits. *Genet. Resour. Crop. Evol.* **2014**, *62*, 721–732. [CrossRef]

30. Fullana-Pericàs, M.; Ponce, J.; Conesa, M.À.; Juan, A.; Ribas-Carbó, M.; Galmés, J. Changes in yield, growth and photosynthesis in a drought-adapted Mediterranean tomato landrace (*Solanum lycopersicum* 'Ramellet') when grafted onto commercial rootstocks and Solanum pimpinellifolium. *Sci. Hortic.* **2018**, *233*, 70–77. [CrossRef]

31. Missio, J.C.; Renau, R.M.; Artigas, F.C.; Cornejo, J.C. Sugar and acid profile of Penjar tomatoes and its evolution during storage. *Sci. Agric.* **2015**, *72*, 314–321. [CrossRef]

32. Conesa, M.À.; Galmés, J.; Ochogavía, J.M.; March, J.; Jaume, J.; Martorell, A.; Francis, D.M.; Medrano, H.; Rose, J.K.; Cifre, J. The postharvest tomato fruit quality of long shelf-life Mediterranean landraces is substantially influenced by irrigation regimes. *Postharvest Biol. Technol.* **2014**, *93*, 114–121. [CrossRef]

33. Galmés, J.; Conesa, M.A.; Ochogavía, J.M.; Perdomo, J.A.; Francis, D.M.; Ribas-Carbó, M.; Savé, R.; Flexas, J.; Medrano, H.; Cifre, J. Physiological and morphological adaptations in relation to water use efficiency in Mediterranean accessions of *Solanum lycopersicum*. *Plant Cell Environ.* **2010**, *34*, 245–260. [CrossRef]

34. Figàs, M.R.; Prohens, J.; Raigón, M.D.; Pereira-Dias, L.; Casanova, C.; García-Martínez, M.D.; Rosa, E.; Soler, E.; Plazas, M.; Soler, S. Insights into the Adaptation to Greenhouse Cultivation of the Traditional Mediterranean Long Shelf-Life Tomato Carrying the alc Mutation: A Multi-Trait Comparison of Landraces, Selections, and Hybrids in Open Field and Greenhouse. *Front. Plant Sci.* **2018**, *9*, 1774. [CrossRef]

35. Casals, J.; Casañas, F.; Simó, J. Is it Still Necessary to Continue to Collect Crop Genetic Resources in the Mediterranean Area? A Case Study in Catalonia. *Econ. Bot.* **2017**, *71*, 330–341. [CrossRef]

36. Poore, J.; Nemecek, T. Reducing food's environmental impacts through producers and consumers. *Science* **2018**, *360*, 987–992. [CrossRef]

37. Peet, M.M. Irrigation and fertilization. In *Tomatoes*; Heuvelink, E., Ed.; CABI: Wallingford, UK, 2005; pp. 171–198.

38. De Pascale, S.; Rouphael, Y.; Gallardo, M.; Thompson, R. Water and fertilization management of vegetables: State of art and future challenges. *Eur. J. Hortic. Sci.* **2018**, *83*, 306–318. [CrossRef]

39. Albornoz, F. Crop responses to nitrogen overfertilization: A review. *Sci. Hortic.* **2016**, *205*, 79–83. [CrossRef]

40. Good, A.G.; Beatty, P.H. Fertilizing Nature: A Tragedy of Excess in the Commons. *PLoS Biol.* **2011**, *9*, e1001124. [CrossRef] [PubMed]

41. Lemaire, G.; Tang, L.; Bélanger, G.; Zhu, Y.; Jeuffroy, M.-H. Forward new paradigms for crop mineral nutrition and fertilization towards sustainable agriculture. *Eur. J. Agron.* **2021**, *125*, 126248. [CrossRef]

42. Peet, M. Fruit Cracking in Tomato. *HortTechnology* **1992**, *2*, 216–223. [CrossRef]

43. Thole, V.; Vain, P.; Yang, R.; Da Silva, J.A.B.; Enfissi, E.M.A.; Nogueira, M.; Price, E.J.; Alseekh, S.; Fernie, A.R.; Fraser, P.D.; et al. Analysis of Tomato Post-Harvest Properties: Fruit Color, Shelf Life, and Fungal Susceptibility. *Curr. Protoc. Plant Biol.* **2020**, *5*, e20108. [CrossRef]

44. Panthee, D.R.; Cao, C.; Debenport, S.J.; Rodríguez, G.R.; Labate, J.A.; Robertson, L.D.; Breksa, A.P.; Van Der Knaap, E.; Gardener, B.B.M. Magnitude of Genotype × Environment Interactions Affecting Tomato Fruit Quality. *HortScience* **2012**, *47*, 721–726. [CrossRef]

45. Causse, M.; Damidaux, R.; Rousselle, P. Traditional and Enhanced Breeding for Quality Traits in Tomato. In *Genetic Improvement of Solanaceous Crops*; CRC Press: Boca Raton, FL, USA, 2006; Volume 2, pp. 153–192.

46. Ortiz, R.; Crossa, J.; Vargas, M.; Izquierdo, J. Studying the effect of environmental variables on the genotype × environment interaction of tomato. *Euphytica* **2006**, *153*, 119–134. [CrossRef]

47. Figàs, M.R.; Prohens, J.; Raigón, M.D.; Fita, A.; García-Martínez, M.D.; Casanova, C.; Borràs, D.; Plazas, M.; Andújar, I.; Soler, S. Characterization of composition traits related to organoleptic and functional quality for the differentiation, selection and enhancement of local varieties of tomato from different cultivar groups. *Food Chem.* **2015**, *187*, 517–524. [CrossRef]

48. Casañas, F.; Simó, J.; Casals, J.; Prohens, J. Toward an Evolved Concept of Landrace. *Front. Plant Sci.* **2017**, *8*, 145. [CrossRef] [PubMed]

49. Zeven, A. Landraces: A review of definitions and classifications. *Euphytica* **1998**, *104*, 127–139. [CrossRef]

50. De Gelder, A.; Dieleman, J.A.; Bot, G.; Marcelis, L.F.M. An overview of climate and crop yield in closed greenhouses. *J. Hortic. Sci. Biotechnol.* **2012**, *87*, 193–202. [CrossRef]

51. O'Connell, S.; Rivard, C.; Peet, M.M.; Harlow, C.; Louws, F. High Tunnel and Field Production of Organic Heirloom Tomatoes: Yield, Fruit Quality, Disease, and Microclimate. *HortScience* **2012**, *47*, 1283–1290. [CrossRef]

52. Erhioui, B.M.; Gosselin, A.; Hao, X.; Papadopoulos, A.P.; Dorais, M. Greenhouse Covering Materials and Supplemental Lighting Affect Growth, Yield, Photosynthesis, and Leaf Carbohydrate Synthesis of Tomato Plants. *J. Am. Soc. Hortic. Sci.* **2002**, *127*, 819–824. [CrossRef]

53. Van Eeuwijk, F.A.; Bustos-Korts, D.; Millet, E.J.; Boer, M.P.; Kruijer, W.; Thompson, A.; Malosetti, M.; Iwata, H.; Quiroz, R.; Kuppe, C.; et al. Modelling strategies for assessing and increasing the effectiveness of new phenotyping techniques in plant breeding. *Plant Sci.* **2019**, *282*, 23–39. [CrossRef]

54. Doganlar, S.; Tanksley, S.D.; Mutschler, M.A. Identification and molecular mapping of loci controlling fruit ripening time in tomato. *Theor. Appl. Genet.* **2000**, *100*, 249–255. [CrossRef]

55. Powers, L.; Lyon, C.B. Inheritance studies on duration of developmental stages in crosses within the genus Lycopersicon. *Agric. Res.* **1941**, *63*, 129–148.

56. Monforte, A.J.; Asíns, M.J.; Carbonell, E.A. Salt tolerance in Lycopersicon spp. VII. Pleiotropic action of genes controlling earliness on fruit yield. *Theor. Appl. Genet.* **1999**, *98*, 593–601. [CrossRef]

57. Atherton, J.G.; Harris, G.P. Flowering. In *The Tomato Crop: A Scientific Basis for Improvement*; Atherton, J.G., Rudich, J., Eds.; Springer: Dordrecht, The Netherlands, 1986; pp. 167–200. ISBN 978-94-009-3137-4.

58. Pnueli, L.; Carmel-Goren, L.; Hareven, D.; Gutfinger, T.; Alvarez, J.; Ganal, M.; Zamir, D.; Lifschitz, E. The SELF-PRUNING gene of tomato regulates vegetative to reproductive switching of sympodial meristems and is the ortholog of CEN and TFL1. *Development* **1998**, *125*, 1979–1989.

59. Jones, C.M.; Rick, C.M.; Adams, D.; Jernstedt, J.; Chetelat, R.T. Genealogy and fine mapping of obscuravenosa, a gene affecting the distribution of chloroplasts in leaf veins, and evidence of selection during breeding of tomatoes (*Lycopersicon esculentum*; Solanaceae). *Am. J. Bot.* **2007**, *94*, 935–947. [CrossRef] [PubMed]

60. Samach, A.; Lotan, H. The transition to flowering in tomato. *Plant Biotechnol.* **2007**, *24*, 71–82. [CrossRef]

61. Heuvelink, E. Growth, development and yield of a tomato crop: Periodic destructive measurements in a greenhouse. *Sci. Hortic.* **1995**, *61*, 77–99. [CrossRef]

62. Uzun, S. The quantitative effects of temperature and light on the number of leaves preceding the first fruiting inflorescence on the stem of tomato (*Lycopersicon esculentum*, Mill.) and aubergine (*Solanum melongena* L.). *Sci. Hortic.* **2006**, *109*, 142–146. [CrossRef]

63. Dieleman, J.A.; Heuvelink, E. Factors affecting the number of leaves preceding the first inflorescence in the tomato. *J. Hortic. Sci.* **1992**, *67*, 1–10. [CrossRef]

64. Pretty, J. Intensification for redesigned and sustainable agricultural systems. *Science* **2018**, *362*. [CrossRef]

65. Cui, J.; Shao, G.; Lu, J.; Keabetswe, L.; Hoogenboom, G. Yield, quality and drought sensitivity of tomato to water deficit during different growth stages. *Sci. Agric.* **2020**, *77*. [CrossRef]

66. Cantero-Navarro, E.; Romero-Aranda, R.; Fernández-Muñoz, R.; Martínez-Andújar, C.; Pérez-Alfocea, F.; Albacete, A. Improving agronomic water use efficiency in tomato by rootstock-mediated hormonal regulation of leaf biomass. *Plant Sci.* **2016**, *251*, 90–100. [CrossRef]

67. Hooshmand, M.; Albaji, M.; Nasab, S.B.; Ansari, N.A.Z. The effect of deficit irrigation on yield and yield components of greenhouse tomato (*Solanum lycopersicum*) in hydroponic culture in Ahvaz region, Iran. *Sci. Hortic.* **2019**, *254*, 84–90. [CrossRef]

68. Patanè, C.; Tringali, S.; Sortino, O. Effects of deficit irrigation on biomass, yield, water productivity and fruit quality of processing tomato under semi-arid Mediterranean climate conditions. *Sci. Hortic.* **2011**, *129*, 590–596. [CrossRef]

69. Valcárcel, M.; Lahoz, I.; Campillo, C.; Martí, R.; Leiva-Brondo, M.; Roselló, S.; Cebolla-Cornejo, J. Controlled deficit irrigation as a water-saving strategy for processing tomato. *Sci. Hortic.* **2020**, *261*. [CrossRef]

70. Chen, J.; Kang, S.; Du, T.; Qiu, R.; Guo, P.; Chen, R. Quantitative response of greenhouse tomato yield and quality to water deficit at different growth stages. *Agric. Water Manag.* **2013**, *129*, 152–162. [CrossRef]

71. Fereres, E.; Soriano, M.A. Deficit irrigation for reducing agricultural water use. *J. Exp. Bot.* **2007**, *58*, 147–159. [CrossRef]

72. Abbott, J.; Peet, M.; Willits, D.; Sanders, D.; Gough, R. Effects of irrigation frequency and scheduling on fruit production and radial fruit cracking in greenhouse tomatoes in soil beds and in a soil-less medium in bags. *Sci. Hortic.* **1986**, *28*, 209–217. [CrossRef]

73. Lichter, A.; Dvir, O.; Fallik, E.; Cohen, S.; Golan, R.; Shemer, Z.; Sagi, M. Cracking of cherry tomatoes in solution. *Postharvest Biol. Technol.* **2002**, *26*, 305–312. [CrossRef]

74. Matas, A.J.; López-Casado, G.; Cuartero, J.; Heredia, A. Relative humidity and temperature modify the mechanical properties of isolated tomato fruit cuticles. *Am. J. Bot.* **2005**, *92*, 462–468. [CrossRef]

75. Correia, S.; Schouten, R.; Silva, A.P.; Gonçalves, B. Sweet cherry fruit cracking mechanisms and prevention strategies: A review. *Sci. Hortic.* **2018**, *240*, 369–377. [CrossRef]

76. Opara, L.U.; Hodson, A.D.; Studman, S.P. Stem end splitting and internal ring-cracking of 'Gala' apples as influenced by orchard management practices. *J. Hortic. Sci. Biotechnol.* **2000**, *75*, 465–469. [CrossRef]

77. Khadivi-Khub, A. Physiological and genetic factors influencing fruit cracking. *Acta Physiol. Plant.* **2015**, *37*, 1–14. [CrossRef]

78. Domínguez, E.; Fernández, M.D.; Hernández, J.C.L.; Parra, J.P.; España, L.; Heredia, A.; Cuartero, J. Tomato fruit continues growing while ripening, affecting cuticle properties and cracking. *Physiol. Plant.* **2012**, *146*, 473–486. [CrossRef] [PubMed]

79. Aloni, B.; Karni, L.; Rylski, I.; Cohen, Y.; Lee, Y.; Fuchs, M.; Moreshet, S.; Yao, C. Cuticular cracking in pepper fruit. I. Effects of night temperature and humidity. *J. Hortic. Sci. Biotechnol.* **1998**, *73*, 743–749. [CrossRef]

80. Costan, A.; Stamatakis, A.; Chrysargyris, A.; Petropoulos, S.A.; Tzortzakis, N. Interactive effects of salinity and silicon application on *Solanum lycopersicum* growth, physiology and shelf-life of fruit produced hydroponically. *J. Sci. Food Agric.* **2020**, *100*, 732–743. [CrossRef]

81. Arah, I.K.; Amaglo, H.; Kumah, E.K.; Ofori, H. Preharvest and Postharvest Factors Affecting the Quality and Shelf Life of Harvested Tomatoes: A Mini Review. *Int. J. Agron.* **2015**, *2015*, 1–6. [CrossRef]

82. Janse, J. Quality research of tomatoes. *Anual Rep. Glas. Crop. Res. Stn. Naaldwijk* **1988**, 24–26.