

1 **Title:** Tomato landraces as a source to minimize yield losses and improve fruit quality
2 under water deficit conditions

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1 **Abstract**

2 The predicted climate change conditions are forcing crop improvement researchers to find
3 drought tolerant genotypes. The aim of this experiment was to screen a large tomato
4 (*Solanum lycopersicum* L.) collection cultivated under well-watered and water deficit
5 conditions, in order to identify those genotypes with the best performance under water
6 shortage. Thus, 165 tomato genotypes including different cultivars (landraces and modern
7 genotypes) and fruit types (processing, big size, long-shelf life and cherry) were grown
8 in open field under two different cultivation regimes: well-watered (WW, covering 100%
9 crop evapotranspiration demands) and water deficit (WD, irrigation stopped one month
10 after field transplantation). Several leaf-level traits, yield and fruit quality were measured.
11 Large variability was found under WW, with 20-fold variations in yield among
12 genotypes. No differences in yield or fruit quality traits were found between modern
13 genotypes and landraces, while differences in these parameters were observed based on
14 the fruit type. Water deficit affected the observed variability, with a general decrease of
15 yield and increases of fruit quality. Cluster analysis based on fruit traits placed several
16 landraces in the same cluster that the most productive modern genotypes, irrespective of
17 the water treatment. Variable responses to WD were observed, depending on the fruit or
18 cultivar type. Carbon isotope composition was positively correlated with leaf nitrogen
19 content, and determined the yield limit under both treatments. The results of this study
20 highlight the potential of landraces for minimizing yield reduction under WD and
21 increasing fruit quality, having similar or even better performance as compared to modern
22 improved genotypes.

23

24 **Keywords:**

- 1 Carbon isotope fractionation; Drought stress; Fruit quality; Mediterranean climate;
- 2 Tomato landraces; Water shortage

1 **1. Introduction**

2 Tomato (*S. lycopersicum* L.) is among the most produced and consumed
3 vegetables in the world, with more than 4000 registered varieties only in the European
4 Union (FAO, 2018; Plant variety database). The diverse bottlenecks undergone during its
5 domestication process lead the cultivated tomato to contain less than 5% of the genetic
6 pool found in wild species. After its introduction in Europe from America in the 16th
7 century, its selection was mainly focused on fruit shape and especially fruit size (Blanca
8 et al., 2015; García-Martínez et al., 2006; Lin et al., 2014; Miller and Tanksley, 1990;
9 Sacco et al., 2015; Tanksley, 2009). In this regard, the Mediterranean basin has been
10 considered a secondary center of diversification for the tomato crop (Bai and Lindhout,
11 2007; Lin et al., 2014; Miller and Tanksley, 1990). The diverse cultivation practices and
12 selection criteria in each particular region gave rise to landraces adapted to local
13 conditions and responding to local consumption habits (Bota et al., 2014; Casals et al.,
14 2011; Cebolla-Cornejo et al., 2013; Cortés-Olmos et al., 2015; Flores et al., 2017;
15 Fullana-Pericàs et al., 2017; Mazzucato et al., 2008; J J Ruiz et al., 2005; Terzopoulos
16 and Bebeli, 2010). Thus, in the Western Mediterranean, the long shelf-life phenotype
17 (LSL) was a particularly selected fruit trait. Fruits of LSL phenotypes have great extended
18 shelf-life after harvest (Casals et al., 2012; Conesa et al., 2014; Mercati et al., 2015;
19 Saladié et al., 2007). In past centuries, selection for this trait allowed to have vegetable
20 fruit over-winter, being associated to cultural practices of fruit storage, frequently hung
21 up. Accordingly, many of the LSL landraces in the Mediterranean region have local
22 names related to “storage”, “hanging” or “bunches”, like the Italian “*da serbo*”, “*del*
23 *piennolo*” and “*da appendere*”, or the Eastern Iberian Peninsula and Balearic Islands
24 “*Penjar*” and “*Ramellef*”.

1 Genotypes with LSL phenotype have also been related to drought tolerance,
2 indicating that cultivation conditions have been a key factor in their selection (Conesa et
3 al., 2014; Tranchida-Lombardo et al., 2018). The increased drought tolerance of these
4 landraces has been partially attributed to morphological and physiological adaptations,
5 but also to biochemical traits (Galmés et al., 2013, 2011; Guida et al., 2017; Riccardi et
6 al., 2016).

7 In spite of the large variability of landraces and cultivars, world tomato production
8 concentrates on a few modern genotypes, with increased yield rates but significantly less
9 flavor and quality (Tieman et al., 2017). Beyond the potential risk of genetic erosion of
10 some genotypes, there is a possible loss of aroma, taste or appearance traits only present
11 in landraces (Casals et al., 2011; Causse et al., 2010, 2003). Moreover, modern genotypes
12 have been identified as sensitive to water deficit. In this regard, 70% of world tomato is
13 produced in the three most water consuming countries (China, USA and India) plus the
14 Mediterranean basin (Gilbert, 2012; FAO, 2018). Climate change models predict an
15 increase of drought periods, being the Mediterranean basin one of the most affected
16 regions and thus, water restrictions in agriculture seem to be unavoidable (Gao and
17 Giorgi, 2008; Giorgi and Bi, 2005; Giorgi and Lionello, 2008; Sheffield and Wood,
18 2008). In this sense, a sustainable management of soil-water and land-use resources must
19 start to be considered in agriculture in order to avoid land degradation (Keesstra et al.,
20 2018, 2016).

21 Wild tomato relatives have been extensively used to breed for biotic and abiotic
22 trait resistances in tomato crops (Bai and Lindhout, 2007; Foolad and Panthee, 2012;
23 Koenig et al., 2013). Particularly, *S. pennellii* has been a target to improve drought
24 tolerance (Eshed et al., 1992; Galdon-Armero et al., 2018). Alternatively, local landraces
25 selected for centuries under the severe conditions of the Mediterranean summer may also

1 be a very suitable genetic pool to improve tomato crop tolerance to drier conditions. Thus,
2 it is necessary to increase the knowledge on the response of those local landraces to water
3 deficit in order determine its possible role to increase drought tolerance under the
4 predicted future conditions.

5 In this study, several leaf-level traits, yield and fruit quality were measured on a
6 large tomato genotype collection, cultivated in open field during Mediterranean summer,
7 under well-watered and water deficit conditions. The studied collection integrated very
8 diverse tomato genotypes, including four different fruit typologies (processing, big-sized
9 genotypes for fresh consumption, LSL genotypes and cherry type) and two cultivar types
10 (landraces and modern genotypes). The hypothesis was that modern big-sized fruit
11 genotypes would be the most affected by water scarcity in terms of yield, also reducing
12 fruit number and weight. On the other hand, LSL landraces were expected to be less
13 affected by water scarcity in terms of yield and fruit quality given their natural severe
14 growing conditions. Moreover, leaf parameters were expected to be correlated to other
15 fruit-related parameters, denoting adaptation to WD in tolerant genotypes.

16 The main objectives of the present study were: (1) to analyze the variability of
17 leaf related traits, yield and fruit quality in a large tomato collection and (2) to assess the
18 impact of WD on the observed variability, identifying outstanding genotypes or genotype
19 groups with high tolerance to water shortage.

1 **2. Material and methods**

2 2.1. Plant material

3 A total of 165 tomato genotypes (*Solanum lycopersicum* L.) constituted the collection
4 used in this study (Table 1, detailed list in Table S1). This collection integrated genotypes
5 mainly from the Mediterranean basin, but also from many diverse locations around the
6 world. Attending to the diversity included in the study, and based on previous work of
7 Lin et al. (2014) and Tieman et al. (2017), genotypes were grouped according to their
8 fruit or cultivar type. For fruit type, four major groups were differentiated, including
9 processing genotypes (PRO), big-sized genotypes for fresh consumption (BIG),
10 genotypes with the long-shelf life fruit phenotype (LSL) and cherry type genotypes
11 (CHE). Regarding to cultivar type, genotypes were classified in landraces (L) and modern
12 genotypes (M), according to Camacho Villa et al. (2005), Casañas et al. (2017) and Zeven
13 (1998). Genotypes were also classified using both group criteria, obtaining eight groups:
14 processing landraces (PRO-L), processing modern (PRO-M), big-sized landraces (BIG-
15 L), big-sized modern (BIG-M), long-shelf life landraces (LSL-L), long-shelf life modern
16 (LSL-M), cherry landraces (CHE-L) and cherry modern (CHE-M) (Table 1). Seeds were
17 obtained from the Hebrew University of Jerusalem, University of Naples, University of
18 the Balearic Islands, Centre de Conservació i Millora de l'Agrodiversitat Valenciana and
19 University of Sassari (Table S1).

20 An antiviral treatment was applied to all seeds before sowing by immersion in a
21 10% sodium triphosphate dissolution for 3 h. After washing with distilled water, seeds
22 were further submerged in a 30% dissolution of commercial bleach for 1 h. Then, they
23 were washed again with distilled water and were placed in a ventilated room for 24 hours.
24 Seeds were placed in a hermetic container with silica gel for at least 24 h and placed in
25 an oven at 74 °C for 24 h.

1

2 2.2. Experimental design and treatments

3 Seedlings were grown in polystyrene trays filled with peat-based substrate in a
4 greenhouse. One month old seedlings were transplanted to a commercial field in Ariany
5 (Mallorca, Balearic Islands, latitude 39°38'N, longitude 3°08'E, altitude 79 m a.s.l.) in
6 late June. The soil was clay, with an electric conductivity as saturated past of 0.55 mS
7 cm⁻¹ and a pH of 8.4. Before transplantation, the field was fumigated (50% metam sodium
8 anhydrous, 50% p/v) at a rate of 300 L ha⁻¹, rototilled and enriched with 250 kg ha⁻¹ of a
9 granulated fertilizer (composition of 12% of total N, 8% of P₂O₅ and 16% of K₂O). Plant
10 beds (0.30 m width) were covered with an opaque plastic film to avoid weeds and to
11 conserve soil humidity. Irrigation was applied via drip tape (AzudPro, 0.33 m emitter
12 spacing, 1 mm thickness, 2.15 L h⁻¹ at 100 kPa). Water applied by irrigation was recorded
13 by volumetric rotatory piston water meters (Genebre SA, Barcelona). Dripping lines were
14 80 m long, separated 2 m from each other.

15 Two treatment blocks were designed, the well-watered (WW), and the water
16 deficit (WD), with five plants per genotype and treatment grown in a random distribution
17 within each block. Blocks were separated by a non-cultivated area (6 m wide) to prevent
18 water infiltration among blocks. Both WW and WD were irrigated daily at 100% of the
19 crop evapotranspiration (ET_c) during the first month following transplant. Afterwards,
20 irrigation in the WD treatment was stopped until the end of the experiment, meanwhile
21 the irrigation of the WW treatment was maintained covering the daily ET_c demands (Fig
22 S1, Table S2). Two nearby weather stations were used to calculate weekly reference
23 evapotranspiration (ET_o) according to FAO-56 (Allen et al., 1998). Crop
24 evapotranspiration (ET_c) was obtained as the product of ET_o and the crop coefficient (K_c)
25 at each growth stage (Allen et al., 2006) (Table S2). Over all the cultivation period, WW

1 treatment received 606 l m⁻² and WD treatment 215 l m⁻² (Fig. S1). During the field
2 growth period, the per month averages of the daily average, daily maximum (day) and
3 daily minimum (night) temperatures in the field were (in °C), respectively, 24.1, 31.6 and
4 15.9 in June, 25.8, 33.4 and 17.8 in July, 26.2, 33.8 and 18.9 in August, and 20.6, 27.2
5 and 14.3 in September. The average relative air humidity was 70.45 ± 1.05 % throughout
6 the experiment. Precipitations per month were (in mm), respectively: 0.0 in June, 6.0 in
7 July, 8.3 in August and 19.0 in September.

8 No growth conduction system or pruning was applied for any genotype. Pest
9 control was managed as usually following the typical commercial practices. Weeds were
10 removed manually.

11

12 2.3. Fruit related parameters

13 Yield and total fruit number were measured per plant 79, 92, 96, 107 and 114 days after
14 field transplantation. The average fruit weight was obtained dividing yield and total fruit
15 number for each plant.

16 Fruit quality parameters were measured from 8 healthy fruits per plant. Fruits were
17 squashed and homogenized using an electric mixer (LM310E10, Moulinex, Alençon,
18 France). Total soluble solids (*TSS*) and acidity were determined from the obtained juice.
19 A digital refractometer and electrical conductimeter (PAL-BXACID F5, Atago, Tokyo,
20 Japan) with a 0.2 °Brix and with a 0.10% citric acid precision was used to evaluate *TSS*
21 (results expressed as °Brix) and acidity (results expressed as % of citric acid).

22

23 2.4. Leaf mass per area

1 Leaf mass per area (*LMA*) was measured in a young fully expanded leaf per plant
2 replicate, excluding the leaf rachis, and calculated as the ratio of dry mass to leaf area.
3 Leaf area was determined using a foliar scanner LiDE220 (Canon INC; Tokyo, Japan)
4 and analyzed as in Katabuchi (2015). Dry mass was obtained after oven drying the leaflets
5 at 60 °C until constant weight (*ca.* 72 h).

6

7 2.5. Leaf $\delta^{13}\text{C}$ isotope composition and nitrogen content

8 Leaves used to calculate *LMA* were also used to determine the leaf carbon isotope
9 composition ($\delta^{13}\text{C}$) and nitrogen content (Leaf N). Dry leaf samples were ground to fine
10 powder and were sampled for analysis. Samples were combusted in an elemental analyzer
11 (Thermo Flash EA 1112 Series, Bremen, Germany), and CO_2 and N_2 were directly
12 injected into a continuous-flow isotope ratio mass spectrometer (Thermo-Finnigan Delta
13 XP, Bremen, Germany) for isotope analysis. Leaf nitrogen content (leaf N) was calculated
14 from the area obtained for isotope analysis on mass 28. Peach leaf standards (NIST 1547)
15 were run every six samples. The standard deviation of the analysis was below 0.1‰.
16 Results for $\delta^{13}\text{C}$ are presented as δ vs. PDB, and leaf nitrogen content as mg N g^{-1} leaf
17 dry weight.

18

19 2.6. Statistical analyses

20 Data failed the Shapiro-Wilk test for normality. Thus, the non-parametric Kruskal-Wallis
21 test with Dunn's multiple comparison was used to reveal differences among fruit and
22 cultivar types, and between treatments ($P < 0.05$), using the "FSA" R software package
23 (Ogle, 2018). Interquartile range (IQR) was defined as the difference between the 75th
24 and 25th data percentiles of each parameter. Pearson's correlations (r) were calculated to

1 determine the relationships among the studied parameters. A cluster analysis was
2 performed for all studied genotypes using fruit related parameters (i.e., yield, fruit weight,
3 fruit number, *TSS* and acidity) with “dendextend” R software package (Galili, 2015). All
4 statistical analyses were performed using R software (ver. 3.5.0; R Core Team, Vienna,
5 Austria).

1 3. Results

2 3.1. Analysis of the variability under WW conditions

3 Under WW conditions, a large variability was found among genotypes for leaf carbon
4 isotope composition ($\delta^{13}\text{C}$) and leaf nitrogen content (leaf N), with the lowest values
5 measured in cherry landraces (Fig. 1a). Similar to leaf N, the leaf mass per area (*LMA*)
6 varied ~2-fold across genotypes under WW. In turn, yield ranged between 486.3 ± 234.8
7 g plant^{-1} in LSL-L59 and $9729 \pm 1349.2 \text{ g plant}^{-1}$ in CHE-L34, highlighting the large
8 diversity included in the study (Table 2). A large variability was also observed for the
9 fruit number and weight, with some CHE landraces having a number of fruit more than
10 four times higher than the global mean. Also, nine of the 25 BIG landraces were
11 considered outliers due to extremely high fruit weight (Fig. 1a).

12 Two processing landraces had the lowest values of total soluble solids (*TSS*) and
13 acidity. On the other hand, a cherry landrace (CHE-L7) presented one of the highest
14 acidity values, despite most of the genotypes of this group were located near the first
15 quartile, evidencing a large variability even within fruit and cultivar types (Fig. 1a).

16

17 3.2. Water deficit affected the observed variability

18 A high impact of WD was found in almost all traits. Thus, $\delta^{13}\text{C}$, *LMA*, *TSS* and acidity
19 increased their values under WD conditions while yield and fruit weight decreased (Table
20 2, Fig. S2). The highest reduction of the interquartile range (IQR) was observed in yield
21 while $\delta^{13}\text{C}$ and *TSS* increased their values. There was a highly significant relationship
22 between $\delta^{13}\text{C}$ values under WW and WD (Fig. S2; $r = 0.72$, $P\text{-value} < 0.001$) and low
23 data dispersion, indicative that the WD did not alter the relative position of the genotypes
24 with respect to the leaf CO_2 diffusion and the water use efficiency. For instance, LSL-
25 L38 scored the highest $\delta^{13}\text{C}$ value both under WW and WD conditions (Table 2, Fig. S2).
26 Contrarily, the relationship between values under WW and WD for leaf N and *LMA*

1 presented a much larger data dispersion, denoting a stronger interaction effect between
2 genotype and irrigation (Fig. S2).

3 Under WD, yield ranged between 255 ± 175.9 g plant⁻¹ in LSL-L29 and $6694.6 \pm$
4 1571 g plant⁻¹ in LSL-M2, having also this genotype one of the highest yields in WW
5 (Table 2). When comparing data dispersion, yield was the parameter most affected by
6 WD, with a reduction of ~40% of its IQR compared to that of WW. The reason being that
7 those genotypes with high yield under WW suffered a higher yield reduction under WD
8 (Fig. S2). In spite of this, most of the outstanding genotypes identified in WW for their
9 high fruit weight and number had similar values under WD (Fig. 1b).

10 The range of *TSS* varied between 3.70 ± 0.55 °Brix (PRO-M8) and 10.05 ± 0.95
11 °Brix (CHE-L37). With a few exceptions, all genotypes increased *TSS* under WD
12 treatment (Fig. S2). The effect of WD was less evident for acidity, with a larger number
13 of genotypes increasing acidity under WD as compared to WW (Fig. S2).

14

15 3.3. Response to water deficit of the different fruit and cultivar type

16 When classifying the genotypes based on fruit-related parameters, four major clusters
17 were differentiated under WW conditions (Fig. 2a). Cluster number 4 was completely
18 composed by landraces, mainly LSL genotypes. Genotypes contained in this cluster had
19 the lowest yield and fruit number. Almost all modern genotypes were included in cluster
20 3, also containing most of the BIG and PRO genotypes. Cluster 2 was mainly composed
21 by CHE, while no clear fruit or cultivar aggrupation was observed for cluster 1, which
22 grouped the 12 genotypes with the highest yield.

23 Under WD conditions, only three clusters were differentiated (Fig. 2b). Cluster 3
24 was almost completely composed by LSL landraces, containing the genotypes with the
25 lowest yield under WD conditions, and including genotypes that under WW were grouped

1 in clusters 2 and 3. However, some LSL landraces, with low yield under WW, were
2 included in clusters containing the most productive genotypes under WD. Most BIG and
3 PRO genotypes were integrated in cluster 2. Finally, cluster 1 included the 12 genotypes
4 with highest yield under WD. Only LSL-M2, PRO-M1 and BIG-M1 were classified in
5 the most productive clusters under both treatments, indicating a low impact of WD on
6 these genotypes.

7 The cluster analysis was consistent with the results obtained when comparing
8 among fruit and cultivar types. Thus, differences were found for fruit-related parameters,
9 but also for leaf traits (Table 3). Landraces and LSL displayed the highest $\delta^{13}\text{C}$ and leaf
10 N content values while CHE the lowest. Under WD, the differences in $\delta^{13}\text{C}$ among groups
11 were similar to those under WW conditions with higher values, while landraces presented
12 the highest leaf N content. Differences in *LMA* were found depending on both fruit and
13 cultivar type, with LSL showing the lowest values, and PRO and CHE the highest. Under
14 WD, CHE had the lowest values, with no differences between cultivar types. Landraces,
15 LSL and BIG were the only groups that increased *LMA* under WD as compared to WW
16 plants.

17 Regarding to yield, CHE presented the highest values and LSL the lowest under
18 WW (4538.8 ± 230.7 g plant⁻¹ and 2733.5 ± 142.2 g plant⁻¹ respectively). Under WD
19 conditions, lower yield was observed for all groups, having CHE the highest values and
20 LSL and BIG the lowest. Modern genotypes had higher yield than landraces only under
21 WD (Table 3). As expected, BIG and CHE presented the lowest and the highest values
22 for fruit number, respectively. On the other hand, CHE had the lowest fruit weight and
23 BIG the highest. Nevertheless, WD did not reduce fruit number in BIG, as did not reduce
24 fruit weight in PRO. Neither landraces nor modern genotypes decreased fruit weight
25 under WD conditions.

1 Under WW, CHE had the highest *TSS* and the lowest acidity. No differences were
2 found for *TSS* between cultivar types under both treatments, whereas landraces had higher
3 acidity (Table 3). Under WD, all groups increased their *TSS*, having CHE the highest
4 values. Only BIG and CHE increased their acidity, with BIG and LSL presenting the
5 highest values. Landraces also increased their acidity, leading to a larger difference
6 between both cultivar types.

7 3.4. Fruit parameters were related to leaf traits

8 Yield was negatively correlated with $\delta^{13}\text{C}$ ($r = -0.36$; $P\text{-value} < 0.001$; Fig. 3a) and leaf
9 N ($r = -0.26$; $P\text{-value} < 0.001$) under both treatments (Table 4). Also, a positive correlation
10 was observed between $\delta^{13}\text{C}$ and leaf N ($r = 0.31$; $P\text{-value} < 0.001$; Fig. 3b). The
11 relationship between *LMA* and yield was only significant under WD (Table 4).

12 When considering data from WW and WD treatments together, there was a
13 negative correlation between fruit number and fruit weight ($r = -0.46$; $P\text{-value} < 0.001$,
14 Table S3). However, yield was only correlated with fruit number ($r = 0.53$; $P\text{-value} <$
15 0.001 ; Fig. 4a). Total soluble solids increased when fruit number increased and fruit
16 weight decreased, regardless of the treatment ($r = 0.33$; $P\text{-value} < 0.001$ and $r = -0.19$; $P\text{-}$
17 $\text{value} < 0.05$ respectively in WW, and $r = 0.29$; $P\text{-value} < 0.001$ and $r = -0.35$; $P\text{-value} <$
18 0.001 respectively in WD, Table S4). On the other hand, acidity was negatively correlated
19 with fruit number under both treatments ($r = -0.26$; $P\text{-value} < 0.001$ in WW and $r = -0.16$;
20 $P\text{-value} < 0.05$ in WD, Table S4), as with yield ($r = -0.28$; $P\text{-value} < 0.001$; Fig. 4b).

1 4. Discussion

2 The aim of this study was to identify genotypes that could prove to be useful to increase
3 tolerance to water shortage. In order to do so, a wide selection up to 165 different
4 genotypes were studied. Consequently, there were several advantages and disadvantages
5 that had to be considered. First of all, the complexity of the experimental design was vast
6 and did not allow for more than a single year of field evaluation, reason why we refused
7 to deeply analyze the treatment \times fruit or cultivar type interactions, and they must be taken
8 carefully. On the other hand, the large number of genotypes included and their variability
9 (Fig. 1), and the homogeneity of the applied treatment makes the obtained information
10 very useful to detect general trends or clear treatment effects.

11

12 4.1. A large diversity among tomato genotypes was found under WW

13 In this study we describe the large variability found among the 165 genotypes cultivated
14 under WW and in their response to WD. Under WW, remarkable differences were found
15 among genotypes, with a \sim 20-fold variation in yield (Table 2).

16 Previous studies reported a lower stomatal conductance (g_s) of LSL landraces as
17 compared to other tomato genotypes under WW, pointing to a lower water consumption
18 and higher water-use efficiency (WUE) (Fullana-Pericàs et al., 2017; Galmés et al., 2011).
19 The lower g_s , result from a stomatal closure, lead to a limitation of CO₂ diffusion and a
20 lower ¹³CO₂ discrimination (Farquhar et al., 1982). As a consequence, plants with higher
21 $\delta^{13}\text{C}$ had higher WUE, being finally reflected in yield (Table 3, Fig. 3a). Taken into
22 consideration the trade-off between WUE or $\delta^{13}\text{C}$ and yield, the high $\delta^{13}\text{C}$ and lower g_s
23 of LSL landraces may reflect an adaptation to severe water stress (Tardieu, 2011). Most
24 LSL landraces studied are original from the Mediterranean basin, traditionally selected

1 under rain-fed conditions leading to severe stress during the Mediterranean summer (Bota
2 et al., 2014; Guida et al., 2017). On the contrary, modern LSL were included in the most
3 productive cluster when grouping genotypes based on their fruit related parameters,
4 having intermediate $\delta^{13}\text{C}$ (Fig. 2a). These results highlight the potential of landraces, and
5 specifically LSL, to be included in breeding programs to optimize yield and fruit quality
6 under severe water deficit.

7 The yield recorded for the different fruit and cultivar types is in accordance with
8 previous studies (Bota et al., 2014; Di Gioia et al., 2010; Eshed and Zamir, 1994; Guida
9 et al., 2017; Makkouk et al., 1979). However, due to the large diversity surveyed, some
10 genotypes were poorly adapted to the specific growing conditions of the present study
11 (open-field, high temperature, lack of pruning schedules) even under WW conditions
12 (Fig. 1). This was the case of some PRO and BIG genotypes, which presented lower yield
13 in this study compared to previous reports (Fig. 1a) (Davis and Estes, 1993; Fanasca et
14 al., 2007; Favati et al., 2009; Patanè and Cosentino, 2010; Zotarelli et al., 2009).

15 No differences were found between landraces and modern genotypes for *TSS*.
16 Diverse authors described lower flavor in modern genotypes, defined by the combination
17 of sugars, acids and volatile compounds (Baldwin et al., 2000; Juan J. Ruiz et al., 2005;
18 Tieman et al., 2017, 2012). Although volatile compounds were not quantified in this
19 study, we found differences in acidity when comparing cultivar types (Table 3). The
20 consumer perception of poor taste and flavor in modern genotypes might be a
21 combination of their lower quality, mainly due to the lack of genetic fruit quality
22 improvement by breeders, but also an influence of harvest and postharvest practices (Klee
23 and Tieman, 2013; Roberts et al., 2002; Slimestad and Verheul, 2005).

24

1 4.2. Different responses to WD were found among genotypes

2 All groups increased $\delta^{13}\text{C}$ under WD, indicative of an effect of the treatment on stomatal
3 conductance and WUE (Condon, 2004; Martin et al., 1999; Rytter, 2005). Under stress
4 conditions, $\delta^{13}\text{C}$ has been widely used as a WUE indicator in several crops (Adiredjo et
5 al., 2014; Galmés et al., 2011; Martin and Thorstenson, 1988; Sánchez-Díaz et al., 2002),
6 and correlated with other indicators as the intrinsic water-use efficiency (WUE_i , defined
7 as the ratio of carbon assimilated to water lost) (Galdon-Armero et al., 2018). However,
8 plants with increased WUE are usually related with lower yields (Blum, 2009, 2005;
9 Tardieu, 2011). In fact, CHE and PRO had lower $\delta^{13}\text{C}$ but higher yield than the other fruit
10 types (Table 3).

11 Yield was strongly affected by WD (Table 3). _____Despite reductions in yield in tomato
12 under WD have been previously reported, no consistent results are found in literature
13 when assessing the impact of water deficit on yield, with reductions from 15 up to 80%
14 depending on the specific growing conditions and the used genotypes (Baselga et al.,
15 1993; Cantore et al., 2016; Favati et al., 2009; Patanè and Cosentino, 2010). In this study,
16 a general reduction of 30% was found for the different fruit and cultivar types (Table 3).
17 Surprisingly, modern genotypes did not reduce yield under WD, leading to higher values
18 as when compared to landraces.

19 The cluster analysis revealed a low impact of WD on BIG-M1, PRO-M1 and LSL-
20 M2 as compared to the other genotypes (Fig. 2b). When comparing treatments, yield in
21 LSL-M1 decreased ~52% while only about 24% in LSL-M2. It is notorious that LSL-M1
22 and LSL-M2 are the same genotype although the latter is grafted onto a commercial
23 rootstock (Table S1), meaning that grafting must be considered a useful tool to improve
24 yield under water deficit (Sánchez-Rodríguez et al., 2012; Schwarz et al., 2010; Yang et
25 al., 2015). On the other hand, no remarkable differences were found in the cluster

1 containing the genotypes with the lowest yield under both treatments. Previous studies
2 revealed the high heterogeneity of landraces in yield or fruit quality, even with the same
3 fruit type (Casals et al., 2012; Cebolla-Cornejo et al., 2013; Sacco et al., 2015). Hence,
4 different responses to WD were found, being remarkable PRO-L2, LSL-L47 and LSL-
5 L51 genotypes, which maintained or even increased yield under WD conditions and also
6 increased their fruit quality parameters values (Fig 2).

7

8 4.3. Maximum yield was related to plant WUE

9 As mentioned above, this study has been performed in a large number of genotypes. Thus,
10 correlations between parameters should be taken carefully given that relationships with
11 low correlation coefficient become statistically significant. Far from being a negative
12 aspect, the large scattering observed for some of the relationships denotes disparity in the
13 response to the WD among different genotypes, offering a diversity of alternatives for the
14 future improvement of tomato tolerance to water deficit and adapt tomato crop to climate
15 change conditions (Mohammed et al., 2018; Muluneh et al., 2015).:-

16 A negative correlation was found between $\delta^{13}\text{C}$ and yield (Table 4). Remarkably,
17 when considering all genotypes under both watering conditions, $\delta^{13}\text{C}$ determined the
18 maximum yield, but not its actual value (Fig. 3a). No differences in leaf N content
19 between treatments were found (Table 2). This may be explained by the lower growth
20 and therefore lower nutrient demand under WD. The mechanism by which leaf N content
21 is affected by water deficit is not clear, with studies revealing a positive (van den
22 Boogaard et al., 1995), negative (Morgan, 1984; Shangguan et al., 2000) or no effect
23 (Damour et al., 2008). However, in the present study a trend was found with increased N
24 content in those genotypes with higher $\delta^{13}\text{C}$ (Fig. 4b) and thus lower stomatal
25 conductance. This trend might be related with the accumulation of proline or other

1 osmoprotectants, which have been associated to prevent protein and enzyme denaturation
2 under WD conditions (Chaves et al., 2003 and references therein).

3 The different fruit types largely differed in their fruit load (Fig. 1), being changes
4 in yield within treatments more dependent on fruit number than on fruit weight (Fig. 4a,
5 Table 4). The impact of WD on yield was also translated to fruit quality. Despite
6 controversial effects of water shortage on acidity have been reported (Bertin et al., 2000;
7 Ripoll et al., 2014; Veit-Köhler et al., 1999), a general increase of both *TSS* and acidity
8 under WD was observed. However, yield correlated with acidity but not with *TSS*,
9 regardless of the treatment (Table 4, Fig. 4b). The inclusion of such diverse fruit types
10 can partially explain this lack of general correlation, since variations in *TSS* are very
11 dependent on the genotype (Ripoll et al., 2014). Similar to $\delta^{13}\text{C}$, the relationship between
12 acidity and yield draw a scenario where, for a particular yield, different acidity values
13 could be found, depending on the fruit and cultivar type (Fig. 4b).

14

15 4.4. Concluding remarks

16 The screening of a large tomato collection, including different fruit and cultivar types,
17 revealed the existence of a high variability in leaf parameters, yield and fruit quality. Such
18 large variability was also observed when analyzing the effects of WD on the performance
19 of the tomatoes. This variability was partially explained by the fruit and cultivar types.
20 An overall decrease in yield and an increase in fruit quality traits was observed under
21 WD, with significant relationships between leaf and fruit traits. In this regard, $\delta^{13}\text{C}$
22 determined the maximum yield of a genotype, but not its actual value. Several landraces
23 with promising behavior under WD as compared to WW have been identified,

- 1 highlighting the potential use of these genotypes to increase water stress tolerance and
- 2 maintain fruit quality.

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14

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4

Highlights:

- Large trait diversity among tomato genotypes under both water treatments
- Cluster analysis grouped genotypes according to their cultivar and fruit type
- Carbon isotope composition determines yield limit
- Different response of landraces to WD among genotypes
- Landraces constitute a genetic source to improve tomato under drought

Table 1. Number of genotypes used in this experiment. From left to right, columns indicate the fruit type group and the cultivar type group of the genotypes. Letters in brackets refers to the abbreviations used to refer to a particular genotype. See Table S1 for detailed genotype label.

Fruit type	Cultivar type	
	Landrace (L)	Modern (M)
Processing (PRO)	19	10
Big-sized (BIG)	25	4
Long-shelf life (LSL)	63	2
Cherry (CHE)	41	1

Table 2 Minimum value (Min), mean (Mean), maximum value (Max) and interquartile range (IQR) for leaf, yield and fruit quality parameters under well-watered (WW) and water deficit (WD) conditions. $\delta^{13}\text{C}$ refers to leaf carbon isotope composition, leaf N to leaf nitrogen content, LMA to leaf mass per area and TSS to total soluble solids. For Min and Max, values are means \pm S.E of a particular genotype. Label between brackets indicate the genotype where the value was obtained. See Table 1 for *n* specifications and genotype abbreviations. For Mean, values are means \pm S.E for each parameter and treatment. Asterisks denotes significant differences between treatments for means of each parameter by Kruskal-Wallis test.

	WW				WD			
	Min	Mean	Max	IQR	Min	Mean	Max	IQR
$\delta^{13}\text{C}$ (‰)	-29.62 \pm 0.43 (CHE-L40)	-27.83 \pm 0.04 *	-26.32 \pm 0.60 (LSL-L38)	0.75	-29.32 \pm 0.54 (PRO-M6)	-26.66 \pm 0.04	-24.73 \pm 0.4 (LSL-L38)	0.88
Leaf N (mg N mg⁻¹ DW)	30.32 \pm 9.22 (CHE-L3)	47.9 \pm 0.3	57.51 \pm 3.21 (LSL-L39)	5.3	31.22 \pm 5.1 (CHE-L12)	47.43 \pm 0.38	63.5 (LSL-L17)	7.72
LMA (g m⁻²)	42.9 \pm 1.9 (BIG-L25)	56.4 \pm 0.5 *	72.6 \pm 1.9 (LSL-L7)	9.3	39.8 \pm 1.6 (CHE-L31)	58.5 \pm 0.4	83.9 \pm 8.4 (LSL-L7)	7.8
Yield (g plant⁻¹)	486.3 \pm 234.8 (LSL-L59)	3521.6 \pm 103.3 *	9729 \pm 1349.2 (CHE-L34)	2550.6	255 \pm 175.9 (LSL-L29)	2516.0 \pm 69.2	6694.6 \pm 1571 (LSL-M2)	1622.3
Fruit number (fruit plant⁻¹)	19.4 \pm 2.9 (BIG-L4)	201.5 \pm 9.9 *	1051.3 \pm 179.8 (CHE-L4)	184	11.6 \pm 9.2 (LSL-L29)	163.1 \pm 7.6	1224 \pm 159.8 (CHE-L19)	150.7
Fruit weight (g fruit⁻¹)	2.42 \pm 0.11 (CHE-L1)	31.48 \pm 1.21 *	173.08 \pm 25.93 (PRO-L7)	19.7	1.75 \pm 0.15 (CHE-L1)	27.01 \pm 0.99	129.63 \pm 25.45 (PRO-L7)	18.3
TSS (°Brix)	2.7 (PRO-L3)	5.01 \pm 0.05 *	7.63 \pm 0.15 (CHE-L37)	1.11	3.7 \pm 0.55 (PRO-M8)	6.23 \pm 0.06	10.05 \pm 0.95 (CHE-L37)	1.4
Acidity (% citric acid)	0.37 \pm 0.13 (PRO-L2)	0.96 \pm 0.02 *	1.76 \pm 0.06 (LSL-L48)	0.37	0.41 \pm 0.13 (CHE-L34)	1.08 \pm 0.02	2.03 \pm 0.38 (BIG-L16)	0.35

Table 3 Leaf, yield and fruit quality traits in the different fruit and cultivar types under well-watered (WW) and water deficit (WD) conditions. Values are means \pm S.E. See Table 1 for *n* specifications and group abbreviations. Letters denote significant differences among fruit types within each treatment, ¥ between cultivar types within each treatment and asterisks between treatments for each group by Kruskal-Wallis test and Dunn's multiple comparison ($P < 0.05$).

		$\delta^{13}\text{C}$	Leaf N	LMA	Yield	Fruit number	Fruit weight	TSS	Acidity
		‰	mg N g ⁻¹ DW	g m ⁻²	g plant ⁻¹	fruit plant ⁻¹	g fruit ⁻¹	°Brix	% citric acid
WW	PRO	-28.02 \pm 0.09 ^{bc*}	47.95 \pm 0.78 ^b	60.11 \pm 1.30 ^a	3905.5 \pm 233.1 ^{ab*}	167.5 \pm 16.5 ^{b*}	39.74 \pm 3.44 ^b	4.81 \pm 0.11 ^{b*}	0.90 \pm 0.04 ^{bc}
	BIG	-27.83 \pm 0.08 ^{b*}	47.66 \pm 0.71 ^b	56.90 \pm 1.28 ^{ab*}	3412.7 \pm 226.3 ^{b*}	92.8 \pm 9.5 ^c	59.91 \pm 2.56 ^{a*}	4.95 \pm 0.10 ^{b*}	0.97 \pm 0.04 ^{ab*}
	LSL	-27.57 \pm 0.05 ^{a*}	49.70 \pm 0.41 ^a	54.11 \pm 0.63 ^{b*}	2733.5 \pm 142.2 ^{c*}	106.5 \pm 6.3 ^{c*}	28.69 \pm 1.03 ^{b*}	4.89 \pm 0.07 ^{b*}	1.07 \pm 0.03 ^a
	CHE	-28.10 \pm 0.07 ^{c*}	45.00 \pm 0.66 ^c	57.01 \pm 0.90 ^a	4538.8 \pm 230.7 ^{a*}	439.4 \pm 27.8 ^{a*}	13.21 \pm 0.64 ^{c*}	5.39 \pm 0.10 ^{a*}	0.82 \pm 0.03 ^{c*}
	Landraces	-27.80 \pm 0.04 [*]	47.89 \pm 0.32	56.02 \pm 0.47 [*]	3448.5 \pm 107.0 [*]	194.6 \pm 9.8 [*]	32.25 \pm 1.33	5.04 \pm 0.05 [*]	0.97 \pm 0.02 [*]
	Modern	-28.05 \pm 0.09 ^{¥*}	48.03 \pm 0.95	59.26 \pm 2.01	4162.3 \pm 363.5	261.8 \pm 43.8 [¥]	24.67 \pm 1.78	4.82 \pm 0.16 [*]	0.83 \pm 0.05 [¥]
WD	PRO	-27.10 \pm 0.10 ^c	45.63 \pm 0.86 ^b	60.25 \pm 0.84 ^a	2780.3 \pm 151.8 ^b	124.2 \pm 12.1 ^b	37.94 \pm 3.03 ^b	5.98 \pm 0.16 ^b	1.00 \pm 0.04 ^b
	BIG	-26.55 \pm 0.09 ^b	47.46 \pm 0.91 ^b	59.27 \pm 0.94 ^a	2262.3 \pm 137.0 ^c	81.3 \pm 8.0 ^c	44.69 \pm 3.68 ^a	6.58 \pm 0.17 ^a	1.18 \pm 0.05 ^a
	LSL	-26.27 \pm 0.06 ^a	50.07 \pm 0.55 ^a	59.10 \pm 0.67 ^a	2078.8 \pm 113.0 ^c	85.3 \pm 4.7 ^c	25.90 \pm 0.83 ^b	5.76 \pm 0.09 ^b	1.12 \pm 0.03 ^a
	CHE	-26.99 \pm 0.08 ^c	44.86 \pm 0.78 ^b	56.15 \pm 0.96 ^b	3085.7 \pm 135.4 ^a	342.4 \pm 19.2 ^a	11.21 \pm 0.54 ^c	6.73 \pm 0.11 ^a	1.02 \pm 0.04 ^b
	Landraces	-26.62 \pm 0.04	47.64 \pm 0.40	58.34 \pm 0.45	2443.0 \pm 70.3	161.4 \pm 8.2	27.12 \pm 1.07	6.26 \pm 0.07	1.10 \pm 0.02
	Modern	-27.04 \pm 0.15 [¥]	45.60 \pm 1.22 [¥]	60.27 \pm 1.38	3145.5 \pm 264.5 [¥]	178.1 \pm 18.5 [¥]	26.07 \pm 2.37	5.92 \pm 0.17	0.92 \pm 0.05 [¥]

Table 4. Pearson bivariate correlations between yield and other parameters included in the study, for well-water (WW) and water deficit (WD) conditions. Asterisks mean significance level at: * $P \leq 0.05$, ** $P \leq 0.01$ or *** $P \leq 0.001$; ns refers to non-significant.

Parameter	Yield
	WW
LMA	0.04
$\delta^{13}\text{C}$	-0.21 **
Leaf N	-0.35 ***
Fruit number	0.54 ***
Fruit weight	ns
TSS	ns
Acidity	-0.26 ***
	WD
LMA	-0.18 *
$\delta^{13}\text{C}$	-0.27 ***
Leaf N	-0.22 **
Fruit number	0.49 ***
Fruit weight	ns
TSS	ns
Acidity	-0.19 *

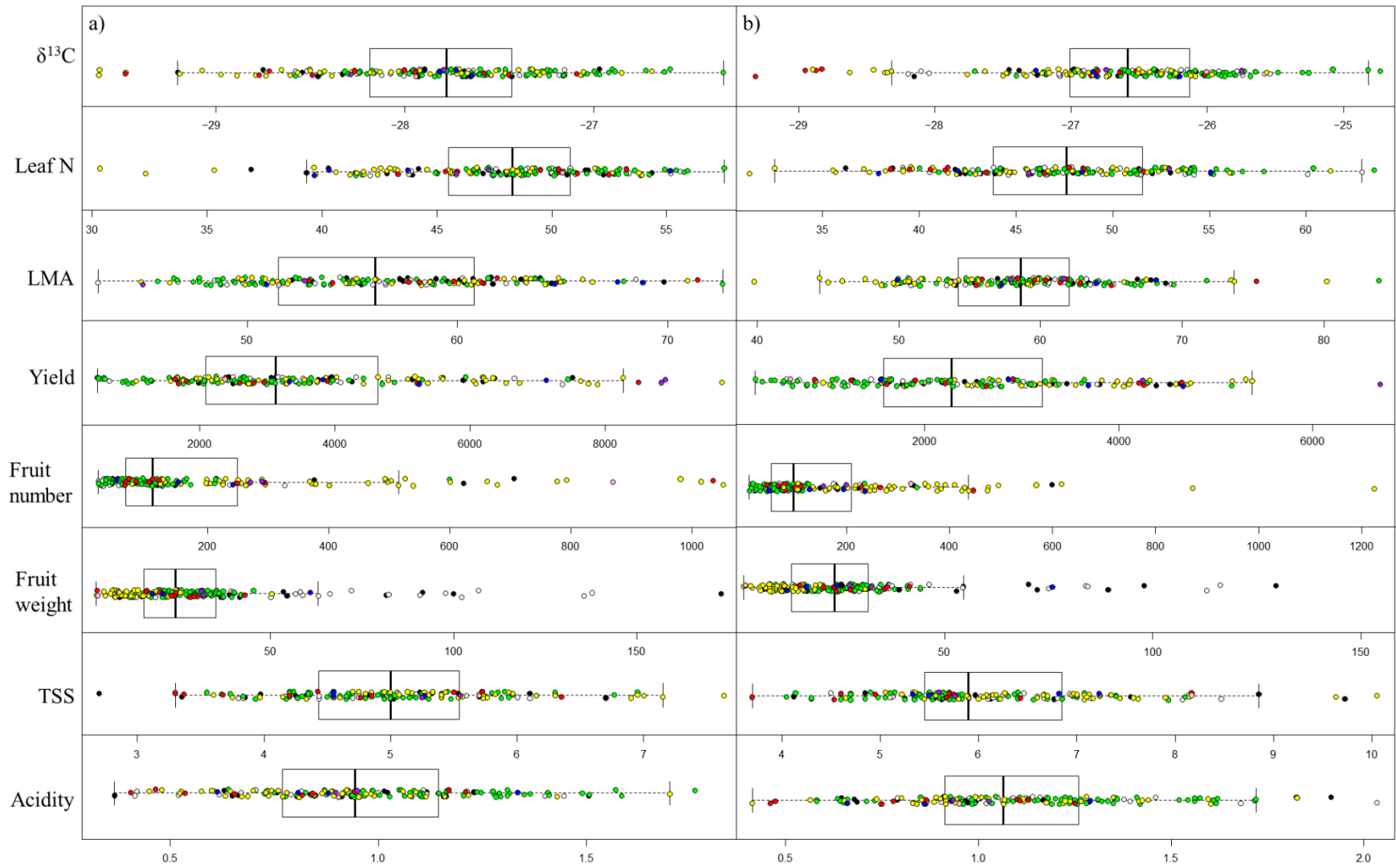
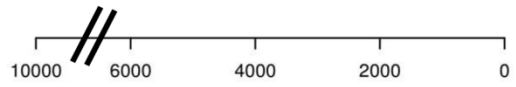
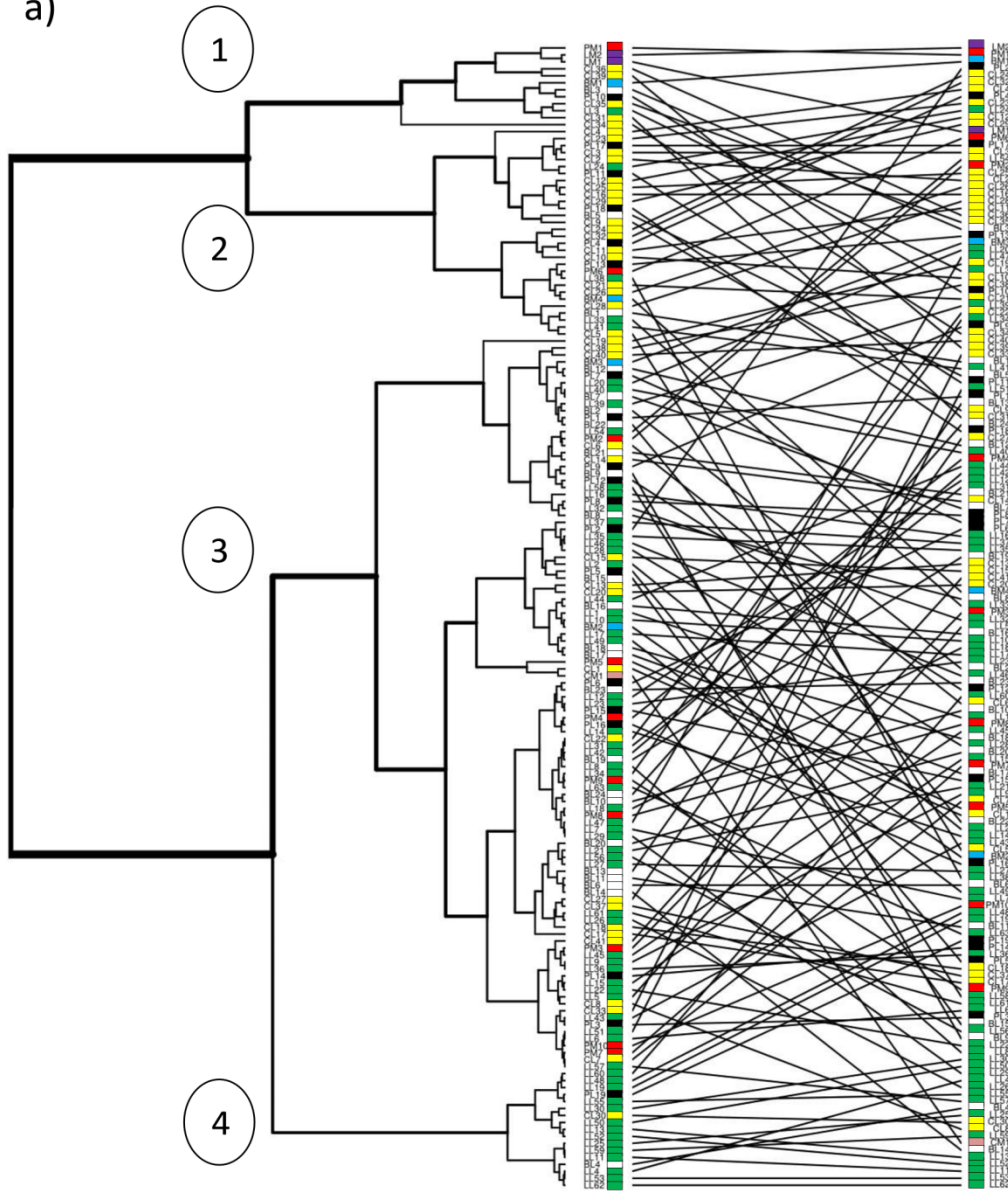


Figure 1. Boxplot graphs illustrating the variability of leaf, yield and fruit quality parameters in a) well-watered (WW) and b) water deficit (WD) conditions. Each box illustrates the 25% (Q1) and 75% (Q3) quartiles (left and right of box) and median values (vertical bar). Left and right lines of each box (whiskers) calculated as: $Q1 - 1.5 \cdot IQR$ and $Q3 + 1.5 \cdot IQR$ respectively, where IQR refers to the interquartile range. Dots represent mean of each genotype. Colors as follows: black for PRO-L, white for BIG-L, green for LSL-L, yellow for CHE-L, red for PRO-M, blue for BIG-M, purple for LSL-M and pink for CHE-M (see Table 1 for labels).

a)



b)

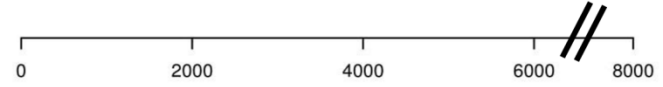
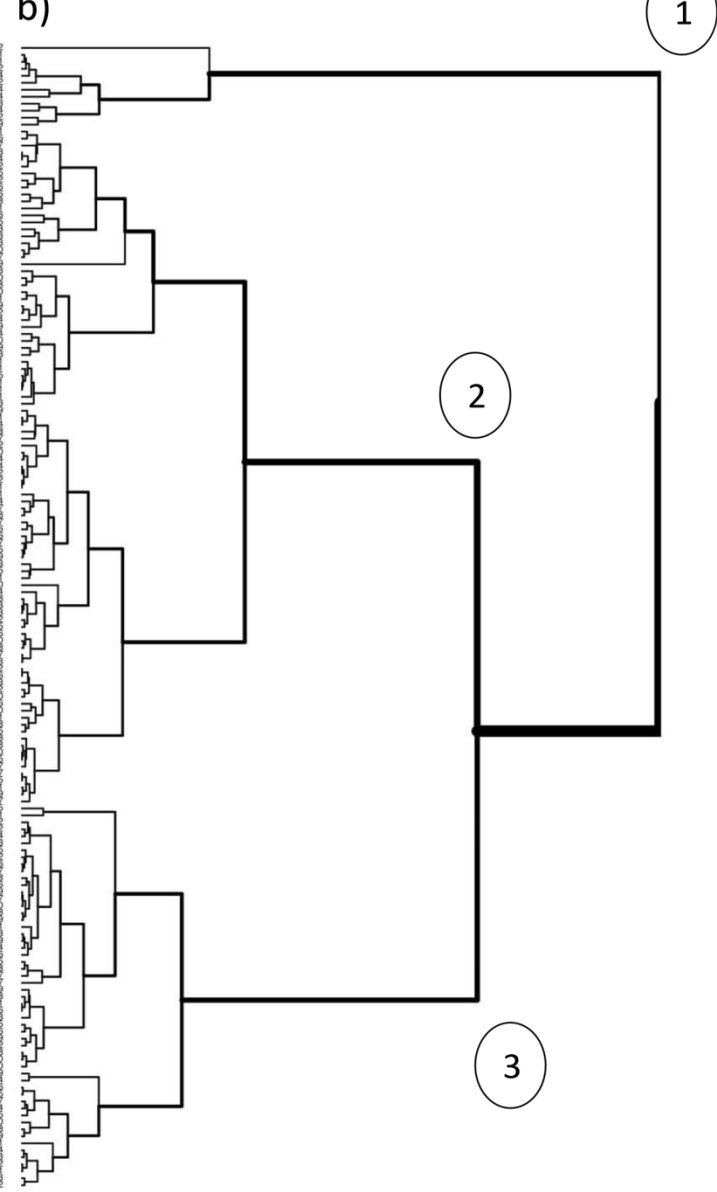


Figure 2. Dendrogram of genotypes under (a) WW and (b) WD conditions resulting from the cluster analyses based on the following parameters: yield, fruit number, fruit weight, total soluble solids (TSS) and acidity. Dark lines link the same genotype between both figures. Numbers indicate the different clusters for each plot when cut the dendrogram at a height of 4000. Colors as Fig. 1. Labels as follows: PL for processing landraces, BL for big-sized landraces, LL for long-shelf life landraces, CL for cherry landraces, PM for processing modern, BM for big-sized modern, LM for long-shelf life modern and CM for cherry modern genotypes.

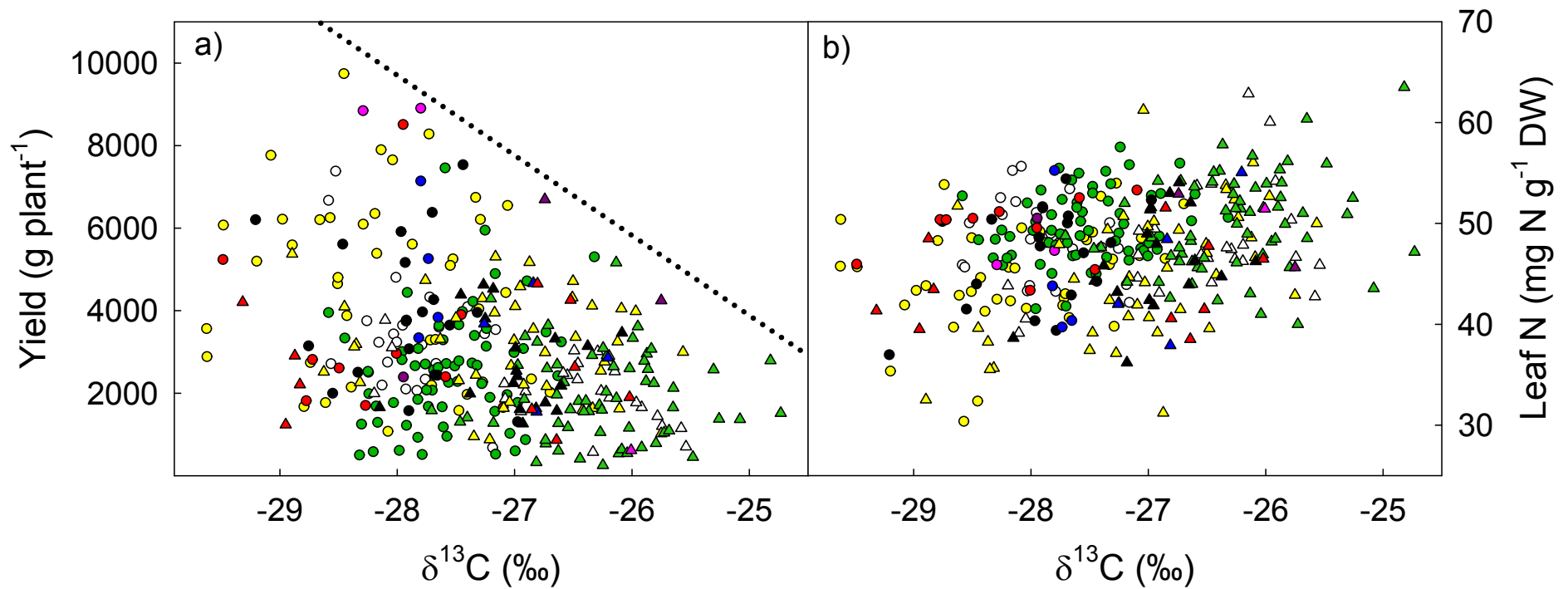


Figure 3. Relationship between leaf carbon isotope composition ($\delta^{13}\text{C}$) and a) yield (g plant^{-1}) and b) leaf nitrogen content (leaf N). Data are means. SE is not shown for clarity, but it is available in Supplementary Data Set. Dots refer to well-water (WW) and triangles to water deficit (WD) genotypes. Colors as in Fig. 1. Dotted line in figure a) sets the limitation of $\delta^{13}\text{C}$ to yield.

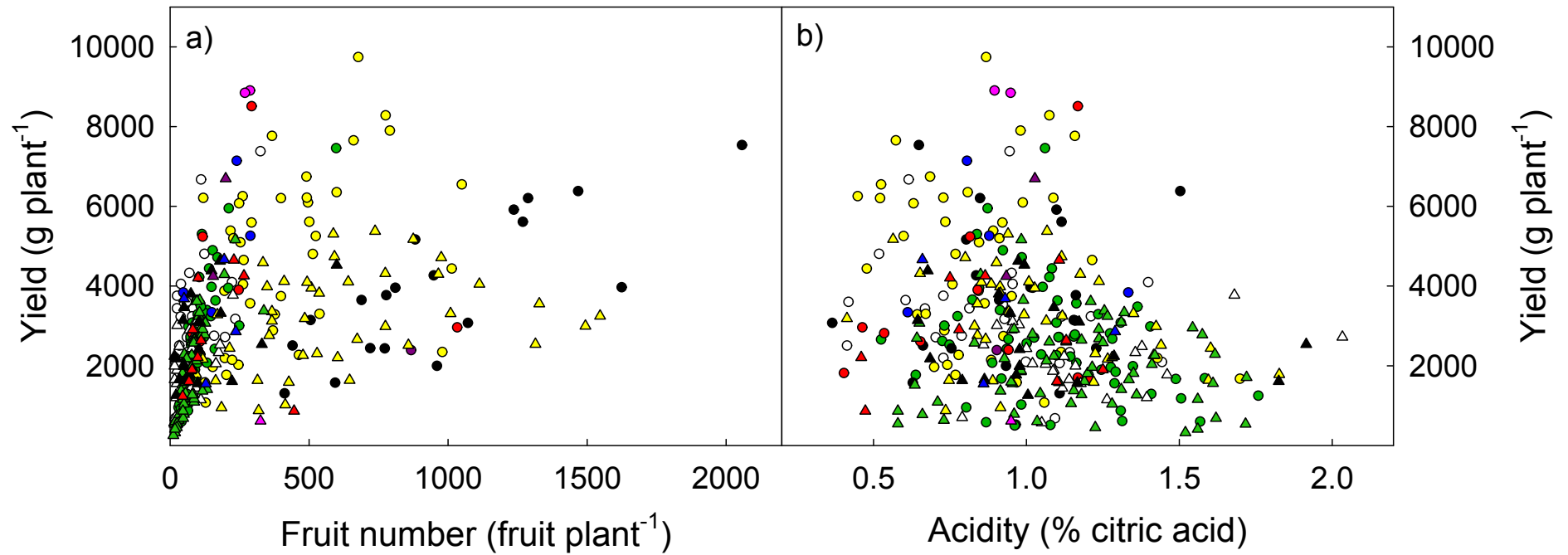


Figure 4. Relationship between yield and a) fruit number (g plant⁻¹), and b) acidity (% citric acid). Data are means. SE is not shown for clarity, but it is available in Supplementary Data Set. Dots refer to well-water (WW) and triangles to water deficit (WD) genotypes. Colors as in Fig. 1.

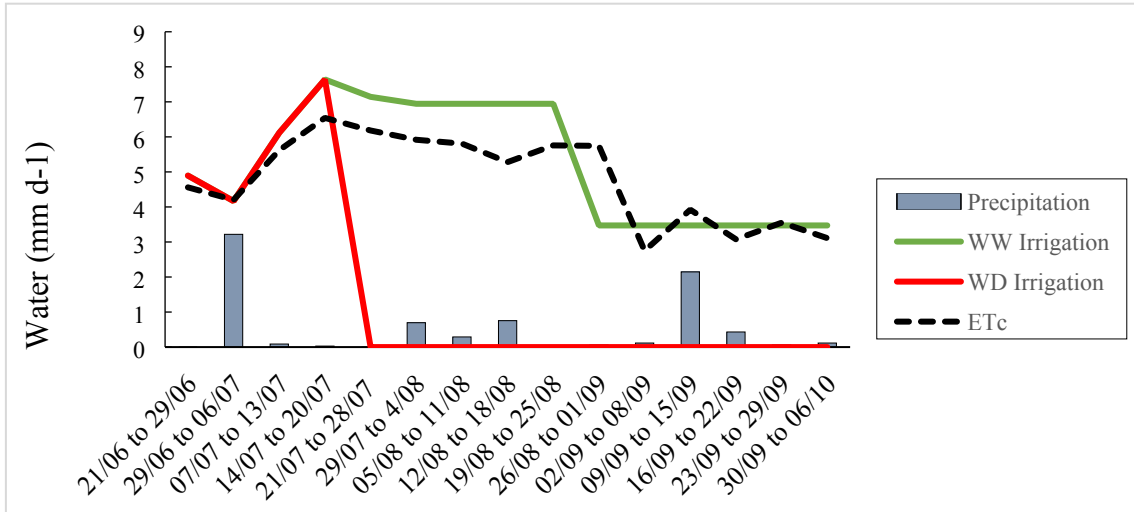


Figure S1. Weekly values for precipitation, irrigation in WW and WD blocks and the crop evapotranspiration (ET_c) over all the growing season

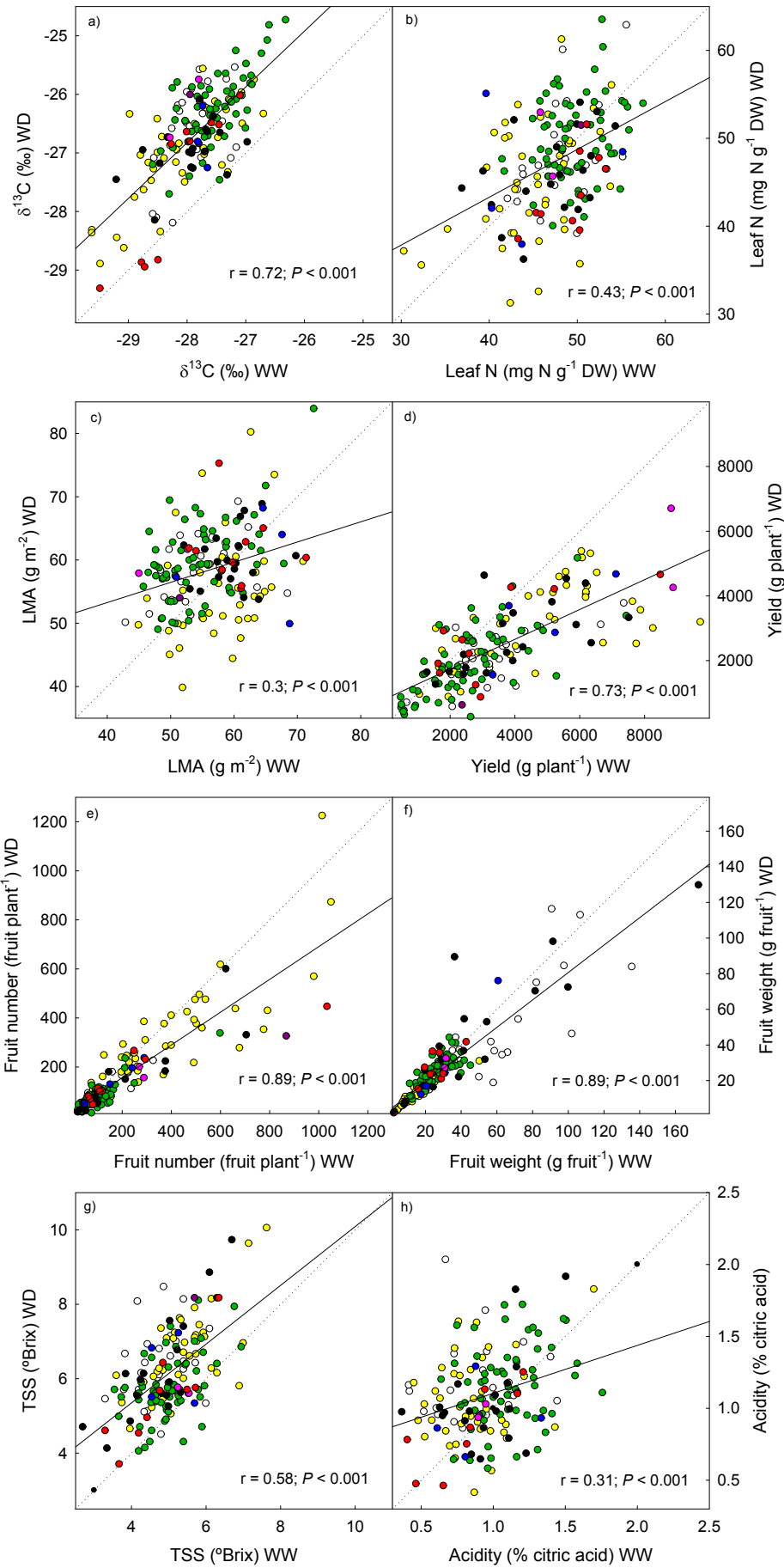


Figure S2. Relationship between the values obtained in WD and WW for each genotype in a) leaf carbon isotope composition ($\delta^{13}\text{C}$), b) leaf nitrogen content (Leaf N), c) leaf mass per area (LMA), d) yield (g plant^{-1}), e) fruit number (fruit plant^{-1}), f) fruit weight (g fruit^{-1}), g) total soluble solids (TSS) and g) acidity (%citric acid). For all plots, y-axis refers to WD and x-axis to WW values. Data are means. Colors as follows: black for PRO-L, white for BIG-L, green for LSL-L, yellow for CHE-L, red for PRO-M, blue for BIG-M, purple for LSL-M and pink for CHE-M (see Table 1 for labels). Dotted line represent the 1:1 relationship between WD and WW, and the solid line the actual correlation between treatments.

Table S1. List of the used genotypes, including their growth habit, fruit and cultivar type, origin, variety name and the seed origin. For seed origin, HUI refers to Hebrew University of Jerusalem, UN to University of Naples, UIB to University of the Balearic Islands, COMAV to Centre de Conservació i Millora de l'Agrodiversitat Valenciana and US to University of Sassari.

Individual code	Fruit type	Cultivar type	Origin	Variety name	Seed origin
PRO-L1	PRO	Landrace	Catalonia	LC 433 Pera Girona	HUI
PRO-L2	PRO	Landrace	Italy	San Marzano	HUI
PRO-L3	PRO	Landrace	Italy	Pera Abruzzo	HUI
PRO-L4	PRO	Landrace	Italy	Piennolo Rosso	HUI
PRO-L5	PRO	Landrace	Italy	Acampora	HUI
PRO-L6	PRO	Landrace	NA	Brandywine	HUI
PRO-L7	PRO	Landrace	NA	BRIANNA	HUI
PRO-L8	PRO	Landrace	NA	Chih-Mu-Tao-Se	HUI
PRO-L9	PRO	Landrace	Russia	Cosmonaut Volkov Red	HUI
PRO-L10	PRO	Landrace	USA	Costoluto Genovese	HUI
PRO-L11	PRO	Landrace	USA	Earliana	HUI
PRO-L19	PRO	Landrace	USA	Green Zebra	HUI
PRO-L12	PRO	Landrace	USA	Hillbilly	HUI
PRO-L13	PRO	Landrace	USA	Japanese Black Trifele	HUI
PRO-L14	PRO	Landrace	NA	JOHN'S BIG ORANGE	HUI
PRO-L15	PRO	Landrace	USA	Nyagous	HUI
PRO-L16	PRO	Landrace	NA	OPALKA	HUI
PRO-L17	PRO	Landrace	Italy	S. Marzano Terra Asciutta	UN
PRO-L18	PRO	Landrace	Italy	22/030-1	UN
PRO-M1	PRO	Modern	Control	Moneymaker	HUI
PRO-M2	PRO	Modern	Control	Ailsa Craig	HUI

PRO-M3	PRO	Modern	Control	M82	HUJ
PRO-M4	PRO	Modern	Italy	20 SMEC-3	HUJ
PRO-M5	PRO	Modern	Control	DZ52	HUJ
PRO-M6	PRO	Modern	Control	m82	HUJ
PRO-M7	PRO	Modern	USA	Red Zebra	HUJ
PRO-M8	PRO	Modern	NA	B27	UN
PRO-M9	PRO	Modern	NA	N182	UN
PRO-M10	PRO	Modern	USA	Processing	UIB
BIG-L1	BIG	Landrace	Greece	Areti	HUJ
BIG-L2	BIG	Landrace	Greece	Makedonia	HUJ
BIG-L3	BIG	Landrace	Greece	Santorini	HUJ
BIG-L4	BIG	Landrace	Catalonia	LC 95 Montserrat	HUJ
BIG-L5	BIG	Landrace	Valencian Country	Muchamiel	HUJ
BIG-L6	BIG	Landrace	Valencian Country	Valenciano	HUJ
BIG-L7	BIG	Landrace	France	Marmande	HUJ
BIG-L8	BIG	Landrace	France	Saint Pierre	HUJ
BIG-L9	BIG	Landrace	France	Outre (Coeur de Boeuf)	HUJ
BIG-L10	BIG	Landrace	USA	Ace	HUJ
BIG-L11	BIG	Landrace	Guatemala	Belmonte	HUJ
BIG-L12	BIG	Landrace	USA	Black	HUJ
BIG-L13	BIG	Landrace	NA	BRANDYWINE	HUJ
BIG-L14	BIG	Landrace	USA	Caro Rich	HUJ
BIG-L15	BIG	Landrace	Germany	Condine Red	HUJ
BIG-L16	BIG	Landrace	Italy	Cuor di bue	HUJ
BIG-L17	BIG	Landrace	USA	Dixie Golden Giant	HUJ
BIG-L18	BIG	Landrace	Turkey	Dolmalik	HUJ

BIG-L19	BIG	Landrace	USA	Kellogg's Breakfast	HUJ
BIG-L20	BIG	Landrace	France	Marmande	HUJ
BIG-L21	BIG	Landrace	France	Marmande VFA	HUJ
BIG-L22	BIG	Landrace	USA	Red Calabash	HUJ
BIG-L23	BIG	Landrace	Italy	Tramatticasa tundasa a siccu	US
BIG-L24	BIG	Landrace	Italy	Tamatta siccada	US
BIG-L25	BIG	Landrace	Italy	Tamatta groga de appiccai	US
BIG-M1	BIG	Modern	Control	Monalbo	HUJ
BIG-M2	BIG	Modern	Control	9466 jj	HUJ
BIG-M3	BIG	Modern	USA	Beefsteak	HUJ
BIG-M4	BIG	Modern	NA	Hawaii 7998	HUJ
LSL-L1	LSL	Landrace	Valencian Country	De Penjar	HUJ
LSL-L2	LSL	Landrace	Italy	Da Serbo	HUJ
LSL-L3	LSL	Landrace	Italy	Principe Borguese	HUJ
LSL-L4	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L5	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L6	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L7	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L8	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L9	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L10	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L11	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L12	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L13	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L14	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L15	LSL	Landrace	Balearic Islands	Ramellet	UIB

LSL-L16	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L17	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L18	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L19	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L20	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L21	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L22	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L23	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L24	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L25	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L26	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L27	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L28	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L29	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L30	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L31	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L32	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L33	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L34	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L35	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L36	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L37	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L38	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L39	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L40	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L41	LSL	Landrace	Balearic Islands	Ramellet	UIB

LSL-L42	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L43	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L44	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L45	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L46	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L47	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L48	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L49	LSL	Landrace	Balearic Islands	Ramellet	UIB
LSL-L50	LSL	Landrace	Catalonia	Penjar-Catalonia	COMAV
LSL-L51	LSL	Landrace	Catalonia	Penjar-Catalonia	COMAV
LSL-L52	LSL	Landrace	Catalonia	Penjar-Catalonia	COMAV
LSL-L53	LSL	Landrace	Catalonia	Penjar-Catalonia	COMAV
LSL-L54	LSL	Landrace	Catalonia	Penjar-Catalonia	COMAV
LSL-L55	LSL	Landrace	Catalonia	Penjar-Catalonia	COMAV
LSL-L56	LSL	Landrace	Valencian Country	Penjar-Valencia	COMAV
LSL-L57	LSL	Landrace	Valencian Country	Penjar-Valencia	COMAV
LSL-L58	LSL	Landrace	Valencian Country	Penjar-Valencia	COMAV
LSL-L59	LSL	Landrace	Valencian Country	Penjar-Valencia	COMAV
LSL-L60	LSL	Landrace	Valencian Country	Penjar-Valencia	COMAV
LSL-L61	LSL	Landrace	Valencian Country	Penjar-Valencia	COMAV
LSL-L62	LSL	Landrace	Balearic Islands	Ramellet ("Gallardí")	UIB
LSL-L63	LSL	Landrace	Balearic Islands	Commercial Ramellet ("Ariany")	UIB
LSL-M1	LSL	Modern	Balearic Islands	Commercial Ramellet ("Palamós")	UIB
LSL-M2	LSL	Modern	Balearic Islands	Commercial Ramellet ("Palamós") grafted on commercial rootstock ("Emperador")	UIB
CHE-L1	CHE	Landrace	NA	ABC POTATO LEAF	HUJ
CHE-L2	CHE	Landrace	USA	Amish Salad	HUJ

CHE-L3	CHE	Landrace	USA	Bloody Butcher	HUJ
CHE-L4	CHE	Landrace	USA	Chocolate Cherry	HUJ
CHE-L5	CHE	Landrace	NA	GLACIER	HUJ
CHE-L6	CHE	Landrace	USA	Matina	HUJ
CHE-L7	CHE	Landrace	USA	Oaxacan Pink	HUJ
CHE-L8	CHE	Landrace	USA	Pink Ping Pong	HUJ
CHE-L9	CHE	Landrace	Italy	Cento scocche	UN
CHE-L10	CHE	Landrace	Italy	SM 1-38 SMEC	UN
CHE-L11	CHE	Landrace	Italy	Tondo col pizzo	UN
CHE-L12	CHE	Landrace	Italy	Vesuvio Foglia Riccia	UN
CHE-L13	CHE	Landrace	Italy	GiaGiù	UN
CHE-L14	CHE	Landrace	Italy	Parmitanella	UN
CHE-L15	CHE	Landrace	Italy	PI15250	UN
CHE-L16	CHE	Landrace	Italy	Black Plum Russia	UN
CHE-L17	CHE	Landrace	Italy	Cina	UN
CHE-L18	CHE	Landrace	Italy	y	UN
CHE-L19	CHE	Landrace	Italy	Rhodesia	UN
CHE-L20	CHE	Landrace	Italy	Siria	UN
CHE-L21	CHE	Landrace	Italy	Cina	UN
CHE-L22	CHE	Landrace	Italy	Seccagno PSC 1-1	UN
CHE-L23	CHE	Landrace	Italy	Allungato a fiasco	UN
CHE-L24	CHE	Landrace	Italy	Terrassutta (rosso alto)	UN
CHE-L25	CHE	Landrace	Italy	Rosso piccolo forma ovale	UN
CHE-L26	CHE	Landrace	Italy	Arsicolo (tondo piccolo)	UN
CHE-L27	CHE	Landrace	Italy	Piennolo Giallo Visciano	UN
CHE-L28	CHE	Landrace	Italy	Vesuviano	UN

CHE-L29	CHE	Landrace	Italy	Pollena	UN
CHE-L30	CHE	Landrace	Italy	Giallo Castel di Sasso	UN
CHE-L31	CHE	Landrace	Italy	770P	UN
CHE-L32	CHE	Landrace	Italy	990 P	UN
CHE-L33	CHE	Landrace	Italy	Casarbore	UN
CHE-L34	CHE	Landrace	Italy	Vesuviano Pizzo	UN
CHE-L35	CHE	Landrace	Italy	Vesuvio 2001	UN
CHE-L36	CHE	Landrace	Italy	Corbarino MT/Crovarese Semiorto	UN
CHE-L37	CHE	Landrace	Italy	Lucariello	UN
CHE-L38	CHE	Landrace	Italy	Principe Borghese Selezione SAIS (IVALSA)	UN
CHE-L39	CHE	Landrace	Italy	E103-SV	UN
CHE-L40	CHE	Landrace	Italy	520P IT025	UN
CHE-L41	CHE	Landrace	Italy	Regina Ostuni	UN
CHE-M1	CHE	Modern	Control	9457 cherry	HUJ

Table S2. Weekly values for potential evapotranspiration (ET_o) and crop coefficient (K_c) over all the growing season.

Week	ET _o (mm d ⁻¹)	K _c
21/06 to 29/06	7.60	0.6
30/06 to 06/07	7.00	0.6
07/07 to 13/07	6.24	0.9
14/07 to 20/07	5.69	1.15
21/07 to 28/07	5.38	1.15
29/07 to 4/08	5.15	1.15
05/08 to 11/08	5.05	1.15
12/08 to 18/08	4.59	1.15
19/08 to 25/08	5.01	1.15
26/08 to 01/09	4.99	1.15
02/09 to 08/09	2.39	1.15
09/09 to 15/09	3.41	1.15
16/09 to 22/09	2.68	1.15
23/09 to 29/09	3.09	1.15
30/09 to 06/10	2.70	1.15

Table S4 Pearson correlation matrix of the leaf, yield and fruit quality parameters. Values for genotypes grown in WW are found in the upper right side of the matrix. Values for genotypes grown in WD are found in the lower left side of the matrix for all genotypes cultivated in WW and WD conditions. Asterisks mean significance level at: * $P \leq 0.05$, ** $P \leq 0.01$ or *** $P \leq 0.001$.

	$\delta^{13}\text{C}$	LeafN	LMA	Yield	Fruit Number	Fruit Weight	TSS	Acidity
$\delta^{13}\text{C}$		0.32***	-0.09	-0.21**	-0.08	0.04	0.18*	0.2**
LeafN	0.48***		-0.34***	-0.35***	-0.24**	0.08	-0.2*	0.14
LMA	-0.12	-0.42***		0.04	-0.08	0.02	-0.02	-0.12
Yield	-0.27***	-0.22**	-0.18*		0.54***	-0.04	0.05	-0.26***
Fruit Number	-0.1	-0.21**	-0.35***	0.49***		-0.47***	0.33***	-0.26***
Fruit Weight	0.01	0.1	0.19*	-0.03	-0.49***		-0.19*	0.02
TSS	0	-0.14	-0.09	-0.03	0.29***	-0.35***		0.31***
Acidity	0.08	0.22**	-0.01	-0.19*	-0.16*	-0.02	0.37***	