Universitat
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PHENOTYPIC DIVERSITY AND FUNCTIONAL RESPONSES TO WATER DEFICIT ACROSS MEDITERRANEAN LANDRACES OF TOMATO

A RESOURCE TO ENHANCE CROP'S RESILIENCE TO DROUGHT

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Doctoral Programme in Plant Biology

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Mateu Fullana Pericàs

Thesis Supervisor: Jeroni Galmés Galmés
Thesis Supervisor: Miquel À. Conesa Muñoz
Thesis Tutor: Jeroni Galmés Galmés

Doctor by the Universitat de les Illes Balears

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Dr. Jeroni Galmés Galmés, Catedràtic de Fisiologia Vegetal de la Universitat de les Illes Balears i Dr. Miquel À. Conesa Muñoz, Contractat Doctor Interí de l’àrea de Producció Vegetal de la Universitat de les Illes Balears

DECLAREM:

Que la tesi doctoral que porta per títol “Phenotypic diversity and functional responses to water deficit across Mediterranean landraces of tomato. A resource to enhance crop’s resilience to drought” presentada per Mateu Fullana Pericàs per a l'obtenció del títol de doctor, ha estat dirigida sota la meva supervisió i que compleix amb els requisits necessaris per optar al títol de Doctor Internacional.

I perquè quedi constància d'això signem aquest document.

Signatura

Dr. Jeroni Galmés Galmés Dr. Miquel À. Conesa Muñoz

Palma, 16 de novembre del 2020

Als meus pares

Agraïments

No idoi si, això ja és cuit!

Tot i ser la primera secció de la tesi, aquestes són les darreres paraules que n'escric. I és que des del primer dia que vaig començar aquesta aventura fins al darrer, han estat moltes les persones que m'han ajudat, directa o indirectament. Sense ells aquesta fita no hagués estat possible, i per això vull els vull agrair tota la seva estima.

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Symbols and abbreviations

Symbols and abbreviations used along this Thesis *:

Symbol	**Meaning**
ABA	Abscisic acid
A_N	Net CO_2 assimilation rate
C/N	Carbon to nitrogen ratio
C_a	CO_2 ambient concentration
C_c	Chloroplastic CO_2 concentration
Chl	Chlorophyll
C_i	Substomatal CO_2 concentration
CPA	Canopy projected area
$\delta^{13}C$	Leaf carbon isotope composition
ε	Bulk modulus of elasticity
E	Transpiration rate
ET_C	Crop evapotranspiration
ET_O	Reference evapotranspiration
ETR	Electron transport rate
F'_M	Maximum fluorescence
FOV	Field of view
F_s	Steady-state fluorescence in the light
F_v/F_m	Maximum quantum efficiency of photosystem II
GCP	Ground control point
GH	Greenhouse
g_m	Leaf mesophyll conductance to CO_2
GNDVI	Green normalized difference vegetation index
g_s	Stomatal conductance
g_{total}	Leaf total conductance to CO_2
J_{max}	Maximum rate of electron transport
K_c	Crop coefficient
LA	Leaf area
LD	Leaf density
Leaf N	Leaf nitrogen content
LMA	Leaf mass per area
LSL	Long shelf-life
LT	Leaf thickness
Max Ø rootstock	Maximum diameter of the stem below the graft
Max Ø scion	Maximum diameter of the stem above the graft
NDVI	Normalized difference vegetation index
NPQ	Non-photochemical quenching
NUE	Nitrogen-use efficiency
OF	Open field

PAR	Photosynthetic active radiation
PDB	Pee Dee Belemnite standard
PET	Potential evapotranspiration
PPFD	Photosynthetic photon flux density
ϕPSII	Quantum efficiency of photosystem II
qP	Photochemical quenching
R_D	Rate of mitochondrial respiration at darkness
RF	Rain-fed
RGB	Red-blue-green bands
R_L	Rate of mitochondrial respiration in light
RLA	Rate of leaf appearance
RMSE	Root-mean-square error
ROS	Reactive oxygen species
RSE	Root stem elongation
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RuBP	Ribulose-1,5-biphosphate
RWC	Relative water content
S_c	Chloroplasts surface exposed to intercellular air spaces
$S_{c/o}$	Rubisco specificity factor
Scion FW	Scion fresh weight
SR	Simple ratio index
TPU	Use of triose-P
TSS	Total soluble solids
UAV	Unmanned Aerial Vehicles
V_{cmax}	Maximum velocity of Rubisco carboxylation
VI	Visual index
WD	Water deficit
WS	Water stress
WUE	Water-use efficiency
WUE_i	Intrinsic water-use efficiency
WW	Well-watered
Γ*	Chloroplast CO_2 compensation point
Ψ_{PD}	Leaf pre-dawn water potential
Ψ_W	Leaf water potential

* Note that, in Chapters 3 and 4, symbols and abbreviations may differ to the list presented above due to Journal Editorial decisions. Genotype grouping abbreviations are defined within each article.

Publications list

Publications derived from the present Thesis

The present Doctoral Thesis is presented as a compendium of seven manuscripts, either published or submitted:

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Fullana-Pericàs M, Conesa MÀ, Soler S, Ribas-Carbó M, Granell A, Galmés J (2017) Variations of leaf morphology, photosynthetic traits and water-use efficiency in Western-Mediterranean tomato landraces. *Photosynthetica* 55:121-133

Fullana-Pericàs M, Conesa MÀ, Douthe C, El Aou-ouad H, Ribas-Carbó M, Galmés J (2019). Tomato landraces as a source to minimize yield losses and improve fruit quality under water deficit conditions. *Agricultural Water Management*, 223:105722.

Fullana-Pericàs M, Conesa MÀ, Gago J, Ribas-Carbó M, Galmés J. High-throughput phenotyping of a large tomato collection under water deficit: combining UAVs' remote sensing with conventional leaf-level physiologic and agronomic measurements (in preparation)

Fullana-Pericàs M, Conesa MÀ, Pérez-Alfocea F, Galmés J (2020). The influence of grafting on crops' photosynthetic performance. *Plant Science*, 295:110250.

Fullana-Pericàs M*, Ponce J*, Conesa MÀ, Juan A, Ribas-Carbó M, Galmés J (2018). Changes in yield, growth and photosynthesis in a drought-adapted Mediterranean tomato landrace (*Solanum lycopersicum* 'Ramellet') when grafted onto commercial rootstocks and *Solanum pimpinellifolium*. *Scientia Horticulturae*, 233:70-77.

Fullana-Pericàs M, Conesa MÀ, Ribas-Carbó M, Galmés J (2020). The Use of a Tomato Landrace as Rootstock Improves the Response of Commercial Tomato under Water Deficit Conditions. *Agronomy*, 10(5):748.

* These authors contributed equally to the present study

CONTENT

Three tomatoes are walking down the street.
Papa Tomato, Mama Tomato and Baby Tomato.
Baby Tomato starts lagging behind,
and Papa Tomato starts getting really angry.
Goes back and squishes him
and says: 'Ketchup'

Mia Wallace
Pulp Fiction (1994)

Summary

Tomato (*Solanum lycopersicum* L.) is the most consumed horticultural crop and with the highest economic impact in the world. Along tomato domestication process and the successive selection and breeding steps, there has been a strong selection for those alleles favouring plant fruit production and fruit weight instead of fruit quality under non-limiting water conditions. However, in the next years most high-yield genotypes may experience a large decrease in their agronomic performance because of climate change effects, which include changes in temperature and precipitations regimes. Hence, it is necessary to prepare tomato crop to face the upcoming scenario, increasing tomato fruit production and quality resilience to extreme weather events as drought periods. In this sense, some Mediterranean genotypes have been traditionally cultivated under water shortage and selected based on their water-use efficiency (WUE) but have been neglected in tomato breeding programs. Similarly, the exploration of alternative techniques to breeding to improve drought resilience, as grafting, have not been largely investigated and the role that those drought-adapted genotypes could play is unknown.

Hence, the general objectives of this Thesis were: (1) to study the physiologic and agronomic variability among Mediterranean tomato landraces and their response to water deficit; and (2) to analyse the response of Mediterranean tomato landraces to grafting in physiologic and agronomic terms.

The results show that in the Mediterranean basin, tomato local selection criteria have been very variable, leading to a wide variation in fruit morphology and quality traits. Under non stress conditions, diverse Mediterranean landraces present clear differences compared to modern cultivars, mostly related to leaf morphology and photosynthetic traits, while no differences have been found regarding fruit production or quality. Results also highlight that better leaf CO_2 conductance might be a main factor determining the improvement of net CO_2 assimilation rate and WUE. A variable response to water deficit has been found among Mediterranean landraces, with differences depending on their fruit type. Interestingly, some landraces have similar agronomic performance than other high-productive modern genotypes under non-stress conditions, having a lower decrease in fruit production under water deficit. It has been observed that leaf carbon isotope composition ($\delta^{13}C$), generally used as a WUE indicator, determine the limit of tomato fruit production under both non and water deficit conditions. High-throughput indicators have been explored to easily phenotype large tomato collections and identify those with an enhanced response to water deficit. Results show that the differences in the leaf physiologic related parameters between tomato drought and non-drought adapted genotypes have been translated to aerial remote sensing measurements, leading to different regression models depending on the observed genotype. Also, this Thesis presents the first attempt to relate tomato fruit quality with different leaf- and plant-level phenotyping measurements in a large and variable tomato collection.

Regarding the use of grafting to improve crops response to drought stress, it has been found that grafting can be a useful technique to ameliorate plant photosynthetic performance under abiotic stress conditions, and that the rootstock selection for a specific environment is determinant for the variations in photosynthesis. The results of this Thesis highlight the potential of grafting to alter several physiologic traits of tomato landraces and their compatibility with the most used commercial rootstocks to improve their agronomic performance. Also, it has been described the potential of drought-adapted tomato landraces to be used as rootstocks in order to increase plant growth and fruit production under both well-watered and water deficit cultivation conditions.

Resum

La tomàtiga (*Solanum lycopersicum* L.) és el cultiu hortícola més consumit i amb el major impacte econòmic a nivell mundial. Durant les diferents etapes de domesticació i processos de selecció i millora de la tomàtiga, hi ha hagut una forta selecció dels al·lels que afavoreixen la producció de la planta i el pes del fruit en comptes de la qualitat del fruit, sempre en condicions no limitants d'aigua. No obstant, en els pròxims anys aquells genotips amb una major producció poden experimentar una gran caiguda en el seu rendiment agronòmic degut als efectes del canvi climàtic, que inclouen canvis en les temperatures i els règims de precipitacions. Així, és necessari preparar el cultiu de la tomàtiga per tal d'incrementar la resiliència de la producció i qualitat de la tomàtiga a esdeveniments climàtics extrems tals com la sequera. En aquest sentit, alguns genotips de tomatiguera del Mediterrani han estat tradicionalment cultivats en condicions de manca d'aigua i seleccionats en base a la seva eficiència en l'ús de l'aigua (EUA), però han estat omesos de manera general en els programes de millora de la tomàtiga. De manera similar, l'exploració d'altres tècniques alternatives a la millora per creuaments sexuals per incrementar la resiliència a la sequera, com pot ser l'empelt, no han estat àmpliament investigades i es desconeix el paper que hi poden jugar aquests genotips adaptats a la sequera.

Així, els objectius generals d'aquesta Tesi són: (1) estudiar la variabilitat fisiològica i agronòmica entre varietats locals de tomàtiga de la Mediterrània i la seva resposta al dèficit hídric; i (2) analitzar la resposta de varietats locals de tomàtiga a l'empelt pel que fa als seus trets fisiològics i agronòmics.

Els resultats obtinguts mostren que a la conca Mediterrània el criteris de selecció local de la tomàtiga han estat molt variable, propiciant una elevada variabilitat pel que fa a la morfologia de fruit i a la seva qualitat. En condicions de no estrès, diverses varietats locals de la Mediterrània han presentat clares diferències respecte cultivars moderns, sobretot en aquells paràmetres relacionats amb la morfologia foliar i les característiques fotosintètiques, mentre que no s'han trobat diferències relacionades amb la producció i la qualitat del fruit. Els resultats també destaquen que una millor conductància del CO_2 pot ser un factor important a l'hora de determinar la millora de l'assimilació de CO_2 i la EUA. La resposta de les varietats locals de la Mediterrània al dèficit hídric ha estat variable, havent-hi diferències depenent del seu tipus de fruit. Curiosament, algunes de les varietats locals han tingut un rendiment agronòmic similar a l'observat a d'altres genotips moderns altament productius en condicions de no estrès, tenint una menor reducció de la producció en condicions de dèficit hídric. S'ha observat que la composició isotòpica de carboni de la fulla ($\delta^{13}C$), usada de manera general com un indicador de la EUA, ha determinat el límit de la producció tant en condicions de no estrès com de dèficit hídric. S'han examinat indicadors d'alt rendiment per tal de poder fenotipar de manera senzilla grans col·leccions de tomàtiga i identificar aquelles amb una millor resposta al dèficit hídric. Els resultats mostren que les diferències observades en els paràmetres fisiològics de la fulla entre

genotips de tomàtiga adaptats a la sequera i genotips no adaptats es traslladaren a mesures de teledetecció aèria, donant peu a diferents models de regressió depenent del genotip observat. A més, aquesta Tesi mostra el primer intent per relacionar la qualitat del fruit de la tomàtiga amb diferents mesures de fenotipat a nivell de fulla i de planta a una col·lecció gran i variable de tomàtiga.

Pel que fa a l’ús de l’empelt per tal de millorar la resposta dels cultius a l’estrès hídric, s’ha trobat que l’empelt pot ser una tècnica útil per tal de reduir l’impacte dels estressos abiòtics sobre el rendiment fotosintètic, i que l’elecció del peu és determinant per les variacions en la fotosíntesi. Els resultats d’aquesta Tesi destaquen el potencial de l’empelt per alterar diversos paràmetres fisiològics de les varietats locals i la seva compatibilitat amb la gran majoria de peus comercials per tal millorar el seu rendiment agronòmic. Finalment, s’ha descrit el potencial de les varietats locals de tomàtiga adaptades a la sequera per ser usades com a peu per tal d’incrementar el creixement i la producció de fruit tant en condicions òptimes de reg com de dèficit hídric.

Resumen

El tomate (*S. lycopersicum*) es el cultivo hortícola más consumido y con un mayor impacto económico en el mundo. Durante las diferentes etapas de domesticación y procesos de selección y mejora del tomate, ha habido una fuerte selección de los alelos que favorecen la producción de la planta y el peso del fruto en lugar de la calidad de éste, siempre en condiciones no limitantes de agua. No obstante, en los próximos años aquellos genotipos con una mayor producción pueden experimentar una caída en su rendimiento agronómico debido a los efectos del cambio climático, que incluyen cambios en las temperaturas y los regímenes de precipitaciones. Así, se hace necesario preparar el cultivo del tomate para el próximo escenario, incrementando la resiliencia de la producción y la calidad del tomate a eventos climáticos extremos tales como la sequía. En este sentido, algunos genotipos del Mediterráneo han sido tradicionalmente cultivados en condiciones de falta de agua y seleccionados en base a su eficiencia en el uso del agua (EUA), pero han sido omitidos de manera general en los programas de mejora del tomate. De manera similar, la exploración de otras técnicas alternativas a la mejora por cruzamientos sexuales para incrementar la resiliencia a la sequía, como puede ser el injerto, no han sido detalladamente investigadas y se desconoce el papel que pueden jugar estos genotipos adaptados a la sequía.

Así, los objetivos generales de esta Tesis son: (1) estudiar la variabilidad fisiológica y agronómica entre variedades locales de tomate del Mediterráneo y su respuesta al déficit hídrico; y (2) analizar la respuesta de variedades locales de tomate al injerto en lo que se refiere a sus características fisiológicas y agronómicas.

Los resultados muestran que en la cuenca Mediterránea el criterio de selección local del tomate ha sido muy variable, propiciando una elevada variabilidad por lo que se refiere a la morfología del fruto y a su calidad. En condiciones de no estrés, varias variedades locales del Mediterráneo han presentado claras diferencias en comparación con cultivares modernos, básicamente en parámetros relacionados con la morfología de foliar y sus características fotosintéticas, mientras que no se han encontrado diferencias relacionadas con la producción y la calidad del fruto. Los resultados también destacan que una mejor conductancia del CO_2 puede ser un factor importante a la hora de determinar la mejora de la asimilación de CO_2 y la EUA. La respuesta de las variedades locales de la Mediterránea al déficit hídrico ha sido variable, dependiendo de su tipo de fruto. Curiosamente, algunas de las variedades locales han tenido un rendimiento agronómico similar al observado en otros genotipos modernos altamente productivos en condiciones de no estrés, teniendo una menor reducción de la producción en condiciones de déficit hídrico. Se ha observado que la composición isotópica de carbono de la hoja ($\delta^{13}C$), usada de manera general como un indicador de la EUA, ha determinado el límite de la producción tanto en condiciones de no estrés como de déficit hídrico. Se han examinado indicadores de alto rendimiento con el objetivo de poder fenotipar de manera sencilla grandes colecciones de tomate e identificar aquellas con una mejor respuesta al

déficit hídrico. Los resultados muestran que las diferencias observadas en los parámetros fisiológicos de la hoja entre genotipos de tomate adaptados a la sequía y genotipos no adaptados se trasladan a las medidas de teledetección aérea, dando lugar a diferentes modelos de regresión dependiendo del genotipo observado. Además, esta Tesis presenta una primera aproximación para relacionar la calidad de fruto del tomate con diferentes medidas de fenotipados a nivel de hoja y de planta en una colección grande y variable de tomate.

Respecto al uso del injerto para mejorar la respuesta de los cultivos al estrés hídrico, se ha encontrado que el injerto puede ser una técnica útil para reducir el impacto de los estreses abióticos sobre el rendimiento fotosintético, y que la elección del pie es determinante para las variaciones en fotosíntesis. Los resultados de esta Tesis destacan el potencial del injerto para alterar diversos parámetros fisiológicos de las variedades locales de tomate y su compatibilidad con la mayoría de pies comerciales, que permiten aumentar su rendimiento agronómico. También ha descrito el potencial de las variedades locales de tomate adaptadas a la sequía para ser usadas como pie con el objetivo de incrementar el crecimiento y la producción de fruto tanto en condiciones óptimas de riego como de déficit hídrico.

Chapter 1

General Introduction

1.1. Tomato: from poison to obsession

Tomato (*Solanum lycopersicum* L.) was considered a poisonous plant in several regions in the world even some centuries after its introduction in Europe from the Andean South America region. Nowadays, it is the most consumed horticultural crop in the world, constituting a fundamental part of human diet and it is cultivated all over the planet, indicating its versatility and capacity to adapt to very different scenarios. The fundamental basis for this is a large diversity of genotypes adapted to different -cultivation- conditions originated due to variable and parallel selection criteria at local scale, mainly corresponding to the tomato landraces.

1.1.1. There and back again: tomato travel around the world in six hundred years

The first reports of tomato in Europe date from the sixteenth century, announcing its recent introduction into the Old Continent. In 1544, the naturist Pietro Andrea Mattioli describes for the first time tomato and eggplant, defining them as mandrake-like species (Mattioli, 1544). In a later edition dating from 1554, Mattioli gives for the first time a common name to tomato: ‘Pomi d’oro’ (*Mala aurea* in Latin). He describes tomato as a fruit similar to an apple, that changes from green to golden coloration and that was eaten fried in oil with salt and pepper.

Although the work of Mattioli is considered the first tomato evidence in botanical literature, questions such as who, when and from where tomato was first introduced in Europe remain unanswered. It was not until 1572 when Guilandini di Padua assigned America as the tomato’s native place (Padua, 1572). In his historical research of the first written tomato reports, Jenkins (1948) debates between two possible importation locations: Mexico and Peru; suggesting that tomato was first introduced in Europe from Mexico soon after conquest. Although there are no evidences of tomato cultivation in Mexico during Spanish conquest, the time difference between Mattioli’s first tomato description in Europe and the conquest of Mexico (approx. 1519), and the description of Mattioli of several tomato fruit sizes, colours and shapes (some of them with large fruits, far from the cherry-like sizes found in most wild relatives) indicate that tomato had reached an advanced stage of domestication before being imported to Europe (Rick, 1978).

It is well known that tomato wild relatives are native from western South America, being *Solanum pimpinellifolium* L. considered the closest wild ancestor to cultivated tomato (Peralta et al., 2008; Rick and Fobes, 1975). Despite tomato wild relatives are well known and described, the original domestication site and the events involved in that process are still unclear. Two hypotheses have been proposed to explain tomato domestication. The first suggests that the South American *S. lycopersicum* var. *cerasiforme* (Dunal) Spooner, G.J. Anderson & R.K. Jansen, native from the Andean Ecuador and Peru regions, is an intermediate evolutionary step between *S. pimpinellifolium* and the cultivated *S. lycopersicum* (Jenkins, 1948; Rick and Fobes, 1975). A second hypothesis suggests that *S. lycopersicum* var. *cerasiforme* is a hybrid between *S. pimpinellifolium* and the cultivated *S. lycopersicum*, and therefore it was originated after tomato complete domestication (Nesbitt and Tanksley, 2002; Ranc et al., 2008). Blanca et al. (2015) performed a detailed study of the genomic variation in tomato that supports the first hypothesis and suggests that tomato followed a two-steps domestication: a first pre-domestication in South America and a second step in Mesoamerica. Also, in a previous study, the same authors confirmed that the genetic basis of European vintage varieties arrived from Mesoamerica region (Blanca et al., 2012). This is in accordance with the hypothesis proposed by Jenkins 70 years earlier, explaining that tomato was probably imported from Mexico.

There are no records of tomato in Spain neither before 1554 nor several years after. However, it is clear that tomato had to be transported from America to Europe through Spanish ships, entering Europe through Sevilla (Long, 1995). The illustrations of Fuchs in 1549, where tomato plants with different tomato fruit shapes, colours and sizes are represented, highlight two main issues: the high tomato fruit variability present in Europe in the mid sixteenth century; and that tomato was not a very well-known plant since those drawings represent chimeric plants (Daunay et al., 2007). Tomato was quickly spread over different European countries, as described by the English botanist John Gerard in 1597, who reported the reception of tomato seeds from Italy and Spain among other countries (Gerard, 1597). However, tomato use was quite different depending on the regions. Gerard described that tomato was consumed in Southern Europe boiled and in sauces. Contrarily, in other European regions tomato was only cultivated as a curiosity, ornamental or even for its supposed medicinal properties (since at the beginning tomato was related to the nightshade poisonous family) (Rick, 1978).

Therefore, the suitable agro-climatic conditions for its cultivation added to its early introduction in the local cuisine facilitated the tomato expansion over the Mediterranean basin, considered a secondary centre of diversification (García-Martínez et al., 2006; Mazzucato et al., 2010). Hence, farmers started to unconsciously select genotypes adapted to the local conditions, appearing a large number of landraces, most of them nowadays still cultivated (Casañas et al., 2017; Zeven, 1998). An example of these landraces can be found in paintings existing in the Balearic Islands, dated from mid seventeenth century, where there are represented leaves and fruits of the ‘de Ramellet’ tomato (Sa Nostra, 1994). Once tomato culinary properties started to be known in other European regions, tomato quickly spread over the continent, being also selected for farmers to be cultivated under different conditions (Peralta et al., 2008). After its expansion over Europe, tomato travelled back to the American continent during mid-late eighteenth century. Particularly, it was spread along North America due to British colonization (Bergougnoux, 2014). It is notorious that tomato in North America followed a similar route than in Europe, with an initial rejection to its consumption. In that case, the main reasons were that some prejudices about its toxicity were still maintained, and that settlers prioritized other staple crops available year-round as corn or wheat (Hoenig, 2018). Nevertheless, immigrants continued introducing new tomato genotypes and farmers selected at local scale their own tomato genotypes, considering fruit taste, size, and curious shape as the main selection parameters instead of its adaptation to local growth conditions. Hence, North American regions (mainly USA) became another centre of tomato diversity, characterized by a high organoleptic quality and ornamental interest, being such genotypes commonly labelled as “heirloom” (Rodríguez-Burruezo et al., 2005). Tomato expansion was not limited to Europe and North America, but during the seventeenth and up to late eighteenth centuries tomato was widely spread by settlers arriving to far places such as Southern Asia, the Caribbean islands, Africa and Alaska regions, indicative of its easiness to be adapted to different climates (Peralta et al., 2008).

The industrialization in Europe and USA also affected tomato expansion and particularly its genotypic selection. Several factors, including the standardization of diet and feeding, the incorporation of women to factories, and war periods lead to an increase in the demand of canned supplies, including tomato (Jordan, 2007). Therefore, tomato production moved from local to a mass-production scale, favouring the use of genotypes easy to cultivate, with fast growth and high production instead of genotypes with enhanced fruit quality. Despite tomato selection has been performed from the first domestication step until nowadays, it was not until the twentieth century when public and private institutions get involved in tomato breeding. The goals of these breeding programs were to increase tomato yield and tolerance to biotic and abiotic stresses, reducing production costs (Bai and Lindhout, 2007).

Nowadays, tomato is one of the most important horticultural crop commercialized in the world, being China, India, and the Mediterranean basin the regions with the highest tomato production. The main reason why tomato is the horticultural crop most consumed and with the highest economic impact in the world probably relies on the large number of available genotypes (more than 83000) (FAO, 2020). Therefore, over the last centuries, there has been a tremendous work selecting and breeding for new genotypes to meet farmers' and consumers' preferences.

1.1.2. Adapting tomato to worldwide cultivation: tomato selection and breeding

As previously explained, after its introduction in Europe, tomato found one of its secondary centres of diversification. Cultivated tomato is a diploid ($2n = 2x = 24$) and self-pollinated crop, being homozygous for most of its traits (Causse et al., 2019; Chen et al., 2007; Foolad, 2007a). In this sense, Rick (1995) proposed that tomato domestication and a strong artificial selection implied drastic changes in stigma position. While most wild relatives tend to have exserted stigma, cultivated tomato has the stigma inserted in the anther tube. It is highly probable that sixteenth century farmers did not select their plants considering the stigma length but selecting those plants with increased fruit set. In the absence of appropriate pollinators, those plants with exserted stigma had lower fruit set percentage and were -automatically- discarded for the next grown season.

In this sense, landraces are the clearest example of farmers' selection. Over centuries, they selected their own tomato genotypes, and stored the seeds of tomato fruits for the next growth season considering very diverse criteria, as their capacity to be cultivated during large drought periods, under different soils or nutrient availability (i.e., calcareous or volcanic soils); considering fruit storage properties (to be stored as a fresh or processed product) or their culinary preferences (differences in their quality depending on the main dishes of the zone). It is worth denoting again that selection towards such adaptative traits responds to unconscious selection (Meyer et al., 2012; Zohary, 2006), given that each particular environment limited the fruit production or survivorship of the less suitable genotypes, thus being selected against as seed providers for the next season crop. Along the Mediterranean basin, several landrace collections have been identified: in the Iberian Peninsula (Cebolla-Cornejo et al., 2013; Cortés-Olmos et al., 2015a, 2015b; García-Martínez et al., 2013), the Balearic Islands (Bota et al., 2014; Ochogavía et al., 2011), Southern Italy and Sicily (Corrado et al., 2014; Sacco et al., 2017) and Greece (Terzopoulos et al., 2009; Terzopoulos and Bebeli, 2008), among others. Most of these landraces, particularly those from Eastern Iberian Peninsula, the Balearic Islands, and Southern Italy and Sicily are considered as drought resilient genotypes since they were selected to produce under Mediterranean summer conditions (Galmés et al., 2011; Patanè et al., 2016).

Despite the large autogamy level in domesticated tomato genotypes, there are several studies reporting phenotypic and genotypic variability in landraces (Cebolla-Cornejo et al., 2013; Corrado et al., 2014; Di Paola Naranjo et al., 2016; Terzopoulos and Bebeli, 2010) and also in heirloom genotypes (Flores et al., 2017; Glogovac et al., 2010; Gonçalves et al., 2009; Gonçalves et al., 2008) all over the world. It is remarkable that for landraces, most of them showed a large intra-population heterogeneity in fruit related traits (such as size or flowering phenology), despite being selected under the same conditions (Bota et al., 2014; Terzopoulos and Bebeli, 2010). One explanation to this phenomenon is that all the farmers of a region had unavoidably to selected for the same high pressure trait (cultivation under drought, high temperatures, poor soil nutrients,…), but individually selected fruit traits depending on particular interests, or even chance, added to poor seed exchange with other farmers (i.e., own seed storage for next season), resulting in very large variability in fruit traits (Fig. 1.1.).

Figure 1.1. Variability in fruit size, colour and shape in a large tomato collection including landraces and heirloom genotypes. Adapted from Fullana-Pericàs et al. (2019).

It was not until the beginning of the twentieth century when modern tomato breeding starts, being most of the traits selected in that decades the ones we can find nowadays in modern tomato genotypes (Jones et al., 2007). Some of the first breeding programs were focused on spontaneous mutations. For instance, the recessive self-pruning mutation (*sp*) was found in Florida in 1914. This mutation is associated with a concentrated flowering, fruit firmness, resistance of mature fruits to over-ripening and with a determinate growth habit of the plant, being perfect for mechanical collection (Razdan and Mattoo, 2005). Private companies also looked for promote and protect their new genotypes to obtain higher economic profits and started developing hybrid genotypes. Such commercial F_1 genotypes constitute an easy way to combine traits from different genotypes in a single, highly heterozygous but also highly homogeneous generation, which can also express traits related to hybrid vigour. Apart from the agronomic benefits, the seed produced by such plants segregates and thus, seed companies ensure that growers need to buy new seed each season. The first F_1 commercial hybrid tomato genotype was the ‘Single Cross’, released in 1946 (Dorst, 1946). The commercial success of these genotypes was that high that nowadays most of the new tomato genotypes released for fresh and transforming industry are F_1 hybrids (Lindhout, 2005).

More than 1000 spontaneous mutations have been identified in the domesticated tomato, involved in plant architecture, yield, fruit shape or shelf-life among other traits (Rick and Chetelat, 1993). The most used way to incorporate a desired trait to a target genotype is by an initial hybridization between donor and target genotypes, followed by several backcrosses of the product with the target genotype, selecting in each generation the plants carrying the desired trait. Despite the number of described mutations, and the new mutations that nowadays are still being characterized, the hybridization and breeding among cultivated genotypes provides limited variability. Due to the different genetic bottlenecks that tomato undergoes from domestication to its worldwide expansion, the genetic variability among cultivated tomato is really poor as compared to wild relative species, representing less than 5% of the total genetic variation found in their wild relatives (Miller and Tanksley, 1990). The *Solanum* sect. *Lycopersicon* includes 12 wild species and the domesticated tomato (*Solanum lycopersicum* L.). The wild species occur in the western slopes of the Andean region, from Ecuador to northern Bolivia and Chile (including also the Galapagos Islands), and inhabit very different environments, from dry desert or pre-desert to humid habitats (Peralta et al., 2008). This environmental spectrum, added to the fact that most are interfertile, also with the domesticated crop, makes wild relatives a notorious genetic resource for tomato improvement. However, commercial tomato breeding with wild relatives did not start until the 1930’s decade. The resulting breeds led to the introduction of new tolerance and/or resistance genes into commercial tomato genotypes, ranging from disease or insect resistance to drought and other abiotic stresses resilience (Foolad, 2007a).

However, it was not until the 1940’s decade when the geneticist and botanist Charlie Rick (University of California) organized several expeditions to the Andean region and started the creation of a germplasm collection of wild tomato species. The creation of the Tomato Genetics Resource Centre (TGRC) in Davis (California, USA) opened the doors to the *ex-situ* conservation and exploration of tomato wild relatives and the creation of introgression lines between cultivated and wild species (Canady et al., 2005; Doganlar et al., 2002; Eshed and Zamir, 1995; Monforte and Tanksley, 2000). Although wild relatives represented an extraordinary source for breeders to improve tomato crop, it often involves major difficulties. Several backcrosses are required to successfully fix the desired trait in the target genotype, which can take up to 15 years of selection (Foolad, 2007a). Also, some desirable traits can be closely associated with loci for undesirable traits, that mask the expression of the favourable trait (Swamy and Sarla, 2008; Zhang et al., 2017), and its expression or interaction can cause pleiotropic effects (Rose et al., 2011). Alternatively, landraces have been barely explored in breeding programs, despite representing a less problematic donor material in terms of pleiotropic effects and might be an excellent source for abiotic stress resilience.

Knowledge on the genetic background allowed breeders to identify genetic markers associated to selective traits, increasing the speed and efficiency of the breeding proves, with no need to wait to the phenotypic expression. Further, the existence of genetic maps can assist in the determination of the chromosomal location of particular traits, the number of genes involved in a particular phenotype, the quantitative trait loci (QTLs), and the possible interaction among genes and QTLs affecting the desirable phenotype (Foolad, 2007a; Tanksley, 1993). To increase the knowledge of specific genes and improve tomato genome editing, tomato genome sequencing started in 2005 with 14 countries involved. Using ‘next generation’ equipment, the inbreed tomato cultivar ‘Heinz 1706’ was sequenced, covering 760 megabases (Mb) of the 900 Mb previously estimated genome size. Also, the genome of *S. pimpinellifoilum* LA1589 was sequenced in parallel, with an estimated divergence between wild and domesticated genomes of 0.6% (The Tomato Genome Consortium, 2012). Not only for breeders, but tomato genome sequencing provided priceless information about genetic architecture and evolutionary history of modern tomato (Causse et al., 2019). In 2014, the genome of *S. pennellii* Correll (particularly, accession LA0716) was published, and up to 389 potential stress-related genes were described (Bolger et al., 2014). Despite transgenic tomatoes are currently unavailable in the market, the first genetically engineered commercialized food was tomato (‘FLAVR SAVR’, Calgene, California, USA). The most common process for genetic transformation in tomato is the *Agrobacterium*-mediated process, but in recent years the development of genome-editing tools as the CRISPR/Cas9 are widely used (Causse et al., 2019; Gerszberg et al., 2015). Nevertheless, the restrictive laws regulating transgenic and CRISPR edited plant in Europe make unlikely the commercialization of these plants at the short- and mid-term, discouraging tomato improvement for commercial purposes through these techniques. However, notorious scientific advances are being obtained via gene edition techniques by using tomato as a model species, particularly for fleshy fruit studies (Gerszberg et al., 2015; Gerszberg and Hnatuszko-Konka, 2017; Kortbeek et al., 2016; Krishna et al., 2019).

Along the domestication process and the successive selection and breeding steps, there has been a strong selection for alleles favouring plant yield and fruit weight instead of fruit quality, leading to the emergence of highly productive modern genotypes (Tieman et al., 2017). However, in the next years, most high-yield genotypes may experience a large decrease in their agronomic performance because of climate change effects. Several models predict an increase of temperatures and changes in precipitations regimes that will increase extreme weather events as drought periods (Battisti and Naylor, 2009; Fischer and Knutti, 2014; Gornall et al., 2010; Koutroulis, 2019). Particularly, it is predicted that climate change will affect temperate and semi-arid zones as Eastern Asia, North America, and the Mediterranean basin, which are the regions concentrating worldwide tomato production (Grillakis, 2019; Hertig and Tramblay, 2017; Raymond et al., 2019; Schlaepfer et al., 2017). Increase of heat and water stress are expected to reduce growing seasons, reducing in turn tomato fruit production (Olesen and Bindi, 2002; Rosenzweig and Tubiello, 1995). Also, it should be considered that extremely high temperatures and drought periods are the main abiotic stresses limiting fruit production (Nankishore and Farrell, 2016; Saadi et al., 2015; Zhou et al., 2019, 2015).

Hence, it is necessary to prepare tomato crop for the upcoming scenario. As will be explained in section 1.4., grafting is an agronomic tool that can be successfully used to improve crops tolerance to biotic and abiotic stresses and enhance crop's fruit production and quality. Concerning breeding, wild relatives have been used as a source to improve tomato, but the possible pleiotropic effects involved in their use entail a handicap for breeders. Alternatively, drought-tolerant landraces are proposed as a notorious genetic resource for plant breeding, with plenty of genotypes highly adapted to local environment and pests. In this sense, European Commission, through the Horizon 2020 European Union programme, has recently funded several projects to explore tomato landraces and heirloom genetic variability. The main aims of these projects are to preserve the current variability and avoid the dramatic genetic erosion in most crops and particularly tomato, which is intrinsically associated to a cultural lost (Casals et al., 2011; Rocchi et al., 2016; San-San-Yi et al., 2008). For instance, TRADITOM (http://traditom.eu/) or TomGEM (https://tomgem.eu/) had the objective to valorise the genetic diversity stored in traditional tomato varieties and provide new breeding and management strategies to improve the crop. This Thesis is framed within the TOMRES (https://www.tomres.eu/) H2020 project (*A novel and integrated approach to increase multiple and combined stress tolerance in plants using tomato as a model*), whose aim is to enhance resilience to combined water and nutrient stress in tomato and to maximize water (WUE) and nutrient use efficiency (NUE) by designing and testing in the field (open and protected) novel combinations of genotypes and management practices reducing the environmental impact of agricultural activities.

1.2. Determinants of the agronomic performance and fruit quality in tomato and the impact of water deficit

Tomato crop faces two main problems: the lack of fruit quality in modern genotypes, and the need to be adapted to the conditions derived from climate change, especially water shortage. The former is a consequence of decades of improvement focused in fruit production, and quality is now being increasingly demanded by consumers (Tieman et al., 2017). The latter is demanded by growers to reduce production costs and is needed to maintain yield rates in areas expected to be less suitable for cultivation in next decades. Among the large diversity of available tomato genotypes, Mediterranean landraces represent an untapped genetic resource to enhance tomato drought resilience, but also to improve fruit quality. In fact, diverse studies and cultural practices demonstrate the increased fruit quality traits in landraces and heirloom genotypes (Klee and Tieman, 2013; Tieman et al., 2012), and the positive impact on quality of cultivation under mild stress (Dorais et al., 2001; Mitchell et al., 1991; Saito and Matsukura, 2015). So, genotypes with higher stress resilience may allow to breed for novel tomato plants minimizing yield reduction under stress, and with increased fruit quality.

1.2.1. On the determinants of tomato fruit production and quality

Fruit shape and size are the main parameters driving consumers' choice. This is probably the main reason explaining the enormous variability existing in the domesticated tomato fruit phenotypes (e.g., Fig. 1.1). Hence, the fruit variation observed among the wild relative species (*Solanum* sect. *Lycopersicon*) is much lower, which seems to be in contradiction with the low genetic variability found in cultivated tomato as compared to its wild relatives. In this regard, two main reasons can be invoked. First, most variation in fruit size and shape is controlled by very few genes (e.g., *SUN*, *OVATE*, *FAS*, *LC* for shape; Rodriguez et al., 2011) and thus, such a large phenotypic diversity in fruit arises from only few mutations. Anthropic selection promoted allelic variation in those genes and, hence, the domestication process seems to have also originated some of the mutations. Thus, contrary to *OVATE*, *FAS* and *LC*, mutations in *SUN* seem to have appeared in Europe after the domestication process (Rodriguez et al., 2011). Similarly, it is feasible that selecting for larger fruits was prioritized in order to facilitate harvest and probably to increase fruit production per plant, promoting also increased fruit size mutations (reviewed in Tanksley 2004). Second, despite some of the mutations related to fruit shape and size might exist in wild germplasm, their expression may be selected against by natural selection and thus, with low frequency in wild populations (e.g., Grandillo et al. 1999; Tanksley et al. 1996). Fruit texture and firmness are other two quality parameters that influence consumer preference and determine the use of that fruit (fresh consumption or processing industry) (Kader et al., 1977). Very diverse factors are involved in defining tomato fruit texture, as cell wall degradation (Toivonen and Brummell, 2008), fruit anatomical traits (Aurand et al., 2012) or fruit turgor and water loss (Saladie et al., 2007).

Regarding "non-visual" parameters, tomato nutritional value, taste and flavour are determined by its chemical composition (Paolo et al., 2018). Tomato fruit dry matter is mainly composed by sugars (reducing sugars, glucose and fructose), organic acids (citric and malic acids), free aminoacids (glutamic acid, γ-aminobutyric acid, glutamine and aspartic acid) and minerals (potassium and phosphate) (Yilmaz, 2001). Tomato fruit contains more than 400 volatile compounds, despite only 30 have been found to contribute significantly to tomato taste (Tieman et al., 2017). Sugar content is the major responsible for tomato fruit quality, and represents between 50 and 65% of total solids of the fruit (Paolo et al., 2018; Zhao et al., 2016). The concentration of organic acids is another major determinant of tomato fruit quality, whereas the ratio sugar to acids plays a crucial role determining consumer's quality perception (Malundo et al., 1995). The amount of sugar and acid (and other components as secondary metabolites, carotenoids, or polyphenols) depends on the genetic background, but also its interaction with environmental factors and cultural practices during cultivation. Several efforts have been done to find genes and genome regions related to fruit quality in order to be used by breeders to improve tomato taste (Causse et al., 2002; Klee and Giovannoni, 2011; Klee and Tieman, 2013; Lecomte et al., 2004; Tieman et al., 2017). However, most attempts to increase tomato quality modifying a particular gene or gene groups failed due to the complexity involving fruit ripening and quality (Giovannoni, 2004; Moore, 2002).

In recent decades, tomato shelf-life has been also a target for breeders to improve fruit quality. In 1994, the FLAVR SAVR tomato was approved by the Food and Drug Administration (USA), becoming the first commercial transgenic food. The FLAVR SAVR tomato had a 99% decrease in polygalacturonase (PG) protein content, which confers a delayed softening to the fruit, increasing the shelf-life (Kramer and Redenbaugh, 1994). There are several modern tomato genotypes including mutations related with delayed fruit ripening, found as spontaneous mutations or identified in wild relatives and transferred to cultivated tomato through breeding, as the *Colorless non-ripening* (*Cnr*), *Green-ripe* (*Gr*), *high-pigment* (*hp-1* and *hp-2*), *Never-ripe* (*Nr*), *non-ripening* (*nor*) and *ripening-inhibitor* (*rin*) mutations (Giovannoni, 2007). Most of such mutations delay fruit deterioration through a delayed or incomplete ripening, allowing fruits to last a few weeks and up to 1-2 months (Kitagawa et al., 2005; Kopeliovitch et al., 1979; Liu et al., 2016), although in most cases cause pleiotropic effects. Hence, consumers have criticized the lower flavour of these mutants as compared to other tomato genotypes, as in the case of the ‘Daniela’ tomato (Guzmán et al., 2009; Jones, 1986; McGlasson et al., 1987). On the contrary, several Mediterranean landraces bear the long shelf-life (LSL) phenotype. In those landraces, ripening is complete and on the vine, rarely has pleiotropic effects, and these phenotype allows tomato fruits to be stored up to 12 months after harvest without physical deterioration, being still palatable. In fact, the popular names of LSL landraces are usually related to the conservation period or to the cultural practices used to store the fruits, since in most places the fruits were disposed in bunches to be hung. Thus, names as ‘de Ramellet’ (referring to bunch in Catalan), ‘da Serbo’ (referring to preserve in Italian) and ‘de Penjar’ and ‘da Appendere’ (referring to hung in Catalan and Italian, respectively) can be found. The genetic basis of the LSL phenotype has been related to the *alcobaça* (*alc*) mutation in the *NAC-NOR* region (Casals et al., 2012; Conesa et al., 2014; Mutschler, 1984), although it seems this mutation is absent in some others (Tranchida-Lombardo et al., 2018).

There is a general negative correlation between fruit size and sugar content (e.g., Causse et al., 2001; Kalloo, 1988). Wild relatives have been explored in order to find genes that can break this trend, and some genes related to sugar content have been found to be more efficient in those species than in cultivated tomato (reviewed in Causse et al. 2019). However, as highlighted before, pleiotropic effects suppose a major impairment in wild-involved breeding programs. Grafting is also an effective tool to enhance fruit quality under non-stress and abiotic stress conditions (Rouphael et al., 2010; Schwarz et al., 2013) (see section 1.4. below). In this regard, tomato landraces and heirloom genotypes constitute an alternative that has been barely used to improve fruit quality. Despite these genotypes were used as basis in some modern tomato breeding programs, nowadays the fruit production of modern genotypes largely overcome landraces production. There is almost no information available about the use of

Mediterranean landraces to improve fruit production, quality or to extend tomato shelf-life, being these genotypes practically ignored in breeding programs. Considering the large variability in fruit shape, size, quality and shelf-life described in Mediterranean landraces (Andreakis et al., 2004; Bota et al., 2014; Figàs et al., 2018, 2015; Lisanti et al., 2008; Sinesio et al., 2007), these genotypes might constitute an unspoiled germplasm source to improve tomato crop.

1.2.2. Water deficit: a major impairment to fruit production but an ally to enhance fruit quality

Tomato is a high water-demanding crop (214 L kg^{-1} fresh tomato, Mekonnen and Hoekstra 2011), having water deficit a huge impact over plant growth and fruit production. For instance, in processing tomato genotype, drought stress not only decreases the number of fruits but also fruit size (Patanè and Cosentino, 2010). Aside of the genetic basis, fruit size depends on two main factors: production of new cells and cell growth and expansion. In turn, fruit cell growth depends on the balance between water inflow through xylem and phloem, and the outflow through fruit transpiration and water backflow to the plant through xylem (Bertin and Génard, 2018; Thompson, 2001). Therefore, changes in environmental conditions dramatically affect fruit size, being also dependent on the moment when the stress is applied (Cheniclet et al., 2005).

Not only in tomato, but in several species with agronomic interest, it has been reported that water deficit decrease plant growth and fruit production but increase fruit quality (Guichard et al., 2001; Ho, 1996; Ripoll et al., 2014). It has been largely discussed if the effect of drought stress on fruit quality is derived from a concentration effect, since water comprises about 95% of tomato fruit when ripened (reviewed in Beckles 2012). Therefore, increase of fruit quality under abiotic stress may not be related with an enhanced enzyme activity in the fruit but to solute concentration due to lower water content in the ripe fruit (Bertin et al., 2009; Gautier et al., 2010). Alternatively, increases in temperature and vapor pressure deficit (VPD) have been related with an enhanced activity of sucrose synthase activity (Bertin et al., 2000; Rosales et al., 2007). Nevertheless, the latter does not necessarily exclude the former hypothesis, and fruit quality can be a variable rate of both processes depending on the stress severity and the species or variety of the crop.

The goal under the climate change scenario is to be able to maintain a stress level enhancing fruit quality, but mild enough for the plant to avoid significant decreases in growth and fruit production. Consequently, the latter makes necessary to increase crop drought resilience. Drought resilience is a complex process, regulated by many and diverse genes, and is influenced by diverse environmental factors and the plant developmental stage. A prime in the adaptation of crops to drought conditions is increasing their WUE, that is, increasing the growth and fruit production per drop of irrigated water or, alternatively, minimizing the impact of the water shortage on growth and fruit production. Despite the efforts to increase WUE through efficient crop management techniques, there is also a need to obtain genotypes with an enhanced response to water deficit in terms of fruit production (Foolad, 2007b; Kumar et al., 2012). Some authors pointed out that drought resilient breeds had lower fruit production than drought-susceptible genotypes when both were cultivated under non-stress conditions (Rahman et al., 1999; Rosielle and Hamblin, 1981). However, Guida et al. (2017) observed no significant decrease in fruit production in two Italian drought-tolerant landraces genotypes when cultivated under full irrigation and rain-fed conditions, having under full irrigation a comparable fruit production than other similar tomatoes (Fanasca et al., 2007). Similarly, Andreakis et al. (2004) found similar fruit production under well-watered conditions between cherry drought-tolerant tomatoes and hybrid elite genotypes. Therefore, Mediterranean landraces not only represent a genetic resource to improve tomato fruit quality, but also to increase crop WUE and enhance their response to drought stress. However, further efforts are needed to fully understand their resilience mechanisms and to develop tools to easily phenotype tomato plants to identify the most promising genotypes.

1.3. From leaf to whole plant: the use of physiologic and remote sensing measurements to screen for drought adapted tomato genotypes

In recent decades, farmers started to introduce several high-throughput measurements allowing fast and precise phenotyping of high number of plants in their fields, which can be performed even in a recurrent manner during the crop cycle. By knowing the crop status along the cultivation period, farmers can treat their field as divided management zones adjusting the necessary inputs, instead of managing it as a homogeneous zone. This kind of crop management is known as precision agriculture (Chlingaryan et al., 2018; Zhang et al., 2002). The use of these techniques also allows to easily identify not only those plants under stress (biotic or abiotic), but also to detect outstanding plants with an enhanced agronomic performance. To do so, it is necessary to collect data about the plant physiologic status, from leaf level to whole plant, sometimes in a recurrent manner during the plant cycle.

1.3.1. Classical measurements at leaf level to determine crop stress

Since the leaf is the main photosynthetic organ in a plant, most physiologic monitoring parameters are focused on measuring leaf related traits. Leaf destructive measurements as leaf mass per area (LMA), relative water content (RWC) and water potential (Ψ) provide reliable information about plant physiologic status (reviewed in Sack and Holbrook, 2006). Particularly, changes in LMA are considered of high relevance when analysing the adaptation of species to their environment (de la Riva et al., 2016; Poorter et al., 2019; Wright et al., 2004). In tomato, fluctuations in LMA have been observed at short and long term as response to variations in the source-sink relationship (Bertin, 1998; Bertin et al., 1999). All these adaptations are of high relevance since they can affect leaf gas-exchange and photosynthetic performance, as well as plant carbon balance, thus with an impact on growth capacity and WUE (Easlon and Richards, 2009; Galmés et al., 2013; García et al., 2007).

Crop growth capacity is intrinsically linked to plant carbon balance and carbon allocation. In turn, plant carbon balance primarily depends on the plant capacity to assimilate atmospheric CO_2 via the photosynthetic process. At leaf level, the most informative parameter in this sense is the net CO_2 assimilation rate (A_N). At a given time, A_N is the difference between the gross CO_2 assimilation rate and the respiratory processes leading to CO_2 loss (i.e. photorespiration and mitochondrial respiration). At saturating light intensities, the rate of photosynthetic CO_2 assimilation is limited by the velocity of CO_2 diffusion from the atmosphere to the carboxylation sites in the cell chloroplasts, and the capacity of the photosynthetic machinery to convert light energy to biochemical energy to fix CO_2 into sugars (Flexas et al., 2012). On the one hand, CO_2 entrance into the leaf, as well as water vapor loss to the atmosphere, are regulated by the aperture of stomatal pores, and are frequently reported as stomatal conductance (g_s). Once in the substomatal cavity, CO_2 moves through the leaf mesophyll to be finally delivered at the stroma of the chloroplast at a rate determined by the leaf mesophyll conductance to CO_2 (g_m). On the other hand, the biochemical capacity to fixate the delivered CO_2 is mainly determined by the catalytic properties of the enzyme ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco). Under non-stress conditions, at the current atmospheric CO_2 concentration (ca. 400 ppm) and at saturating light, photosynthesis is metabolically limited by the Rubisco carboxylation capacity (Lambers et al., 2008). Also, ribulose-1,5-biphosphate (RuBP) regeneration and the velocity to convert triose phosphates into other sugars are important limitations to photosynthesis (Sharkey, 1989; Yang et al., 2016). However, under mild to moderate water stress conditions, the main limitation is usually the CO_2 availability at the Rubisco fixation site and thus, improvement of the CO_2 diffusion pathways, that is, g_s and g_m, plays a key role in plant -and crop- resilience to water shortage (Flexas et al., 2012, 2004; Tomás et al., 2013).

The relationship between the amount of fixed CO_2 per water vapour transpired at leaf level (i.e., A_N/g_s), known as intrinsic water-use efficiency (WUE_i), is a fundamental parameter defining crop water status and has been widely used by breeders to select genotypes with increased drought tolerance (Condon et al., 2002; Condon, 2004; Long et al., 2015). Aside of WUE_i, there are other parameters that allow to monitor plant water use not as an instantaneous measurement but integrating the entire life of the leaf. In this sense, leaf carbon isotope composition ($\delta^{13}C$) has been identified as a reliable and integrative WUE indicator (Condon et al., 1990; Farquhar and Richards, 1984; Impa et al., 2005; Martin et al., 1999; Martin and Thorstenson, 1988; Seibt et al., 2008). Moreover, in recent years different attempts have been done to scale WUE measurements from leaf-level to whole-plant level. Tomás et al. (2012) observed that whole-plant WUE was a promising method to detect the most suitable grapevine genotypes to be cultivated under water deficit conditions. However, the method presents different limitations, existing a gap between leaf and whole-plant WUE related to the leaf position and the respiration in the dark (Douthe et al., 2018; Medrano et al., 2015).

Several efforts have been done to breed for a parallel increase of both WUE and fruit production (Tardieu, 2013; Wu et al., 2019), despite some authors maintain that are antagonistic parameters (Blum, 2009, 2005). What is totally clear is that over centuries drought-adapted landraces have been selected to maximize fruit production under drought conditions, with a consequent increase of WUE as compared to drought-sensitive landraces and most modern breeds. For instance, Galmés et al. (2013) observed leaf anatomical responses to drought in landraces, enhancing CO_2 diffusion and improving photosynthetic performance. Still, Moles et al. (2018) and Landi et al. (2017) showed that the more efficient PSII photochemistry and the expression of specific enzymes involved in the reactive oxygen species (ROS) detoxification improved the response to water deficit in landraces as compared to a modern genotype.

1.3.2. Aerial high-throughput measurements to estimate stress level in crops

Most of the parameters described in the previous section have demonstrated their reliability in plant stress phenotyping. However, plant-by-plant measurements are time consuming, especially those which depend on the stabilization of the equipment before each measurement. Additionally, environmental conditions could vary significantly among measurements, compromising the comparison between genotypes or treatments. Moreover, plant-by-plant measurements are unaffordable for most farmers in terms of monitoring a whole crop field status in a continuous manner. In the last decades, remote sensing has been proposed as an effective high-throughput tool since it can provide high-quality information on plant physiologic parameters in different spatial scales and time periods (Zhang and Kovacs, 2012). Despite satellites have been used for remote sensing for almost 50 years (Bauer and Cipra, 1973; Doraiswamy et al., 2003), their limitations in terms of weather (they are only available in cloud-free days) and data accessibility promoted the use of more cheap and easy to use tools as the unmanned aerial vehicles (UAVs) (Maes and Steppe, 2018; Mulla, 2013). There are mainly four types of sensors, covering almost all remote sensing applications: RGB (red-green-blue), multispectral, hyperspectral and thermal sensors; being each of them more suitable depending on the application (reviewed in Maes and Steppe 2018). Nevertheless, one of the main limitations of remote sensing to assess plant stress is to precisely correlate the data retrieved from the UAVs sensors with leaf-level physiologic measurements, which might be also variable depending on the species, the crop management and the environmental conditions. Hence, further studies linking remote sensing and leaf- or plant-level are required to overcome most of these limitations.

Regarding the use of UAVs to assess plant status, multispectral and hyperspectral data showed good correlations with leaf nitrogen and chlorophyll content across grain, horticultural and fruit tree crops (Maresma et al., 2016; Padilla et al., 2015; Perry et al., 2018). Elvanidi et al. (2018) found that hyperspectral and multispectral data can be used to detect nitrogen deficit in tomatoes grown under well irrigated conditions. Moreover, since transpiration is an energy demanding process that modifies leaf temperature, thermal imaging has been described as a reliable measurement to detect plants under drought stress (Gago et al., 2015; Maes and Steppe, 2012). Biotic and abiotic stresses can alter crops physiologic performance. For instance, it is well known that drought stress induces several physiologic responses, including changes in leaf chlorophyll content and fluorescence (Chen et al., 2015; Munné-Bosch et al., 2001; Munné-Bosch and Alegre, 2004), being remote sensing an appropriate tool to detect those plants with an improved or worsened response to the stress or monitor plants response. In this sense, Ihuoma and Madramootoo (2019) found that several multispectral parameters significantly correlated with different water status parameters, including the RWC.

Aside of assessing plant status, remote sensing data has been widely used to monitor and predict fruit production in different crops, including tomato (Aparicio et al., 2000; Cairns et al., 2012; Duan et al., 2019; Gizaw et al., 2018; Marino et al., 2015), and in recent years the prediction of fruit quality in different woody crops, with promising results (Meyers et al., 2020; Uribeetxebarria et al., 2019). Most of these studies use visible indexes (VI) to estimate plant vigour, generally showing that as the more vigorous is the plant more fruit production is expected. Despite NDVI is nowadays widely used in precision agriculture (Manfreda et al., 2018), there is still a large pathway to cover to understand the relationship between remote sensing and fruit production. For instance, most of prediction models developed until nowadays cannot be applied in consecutive years or in different locations, being necessary also to increase the genotypic variability studied to enhance model reliability (Maes and Steppe, 2018). Moreover, the inclusion of drought-resilient genotypes, as some tomato Mediterranean landraces, in regression models to assess crop physiologic status and fruit production has not been tested yet and might cause notorious model deviations as compared to those for non-resilient plants. The inclusion of these genotypes in precision agriculture and high-throughput phenotyping is necessary mainly because: (1) the identification of VI high-throughput traits in these genotypes may be determinant to define which traits should be phenotyped when looking for drought-resilient genotypes, and (2) facilitate the implementation of precision agriculture in Mediterranean landrace’s fields to effectively increase their agronomic performance.

1.4. Grafting: an ancient biotechnological technique to improve crops’ performance

Different to genotype selection and breeding, in which a single genotype is being improved, grafting is generally based in the merging of two different genotypes in a single plant (chimerical organism), one as the productive variety (scion) and the other as the root (rootstock), each one maintaining its characteristics and adaptive traits. This is an ancient agronomic technique widely used in horticulture to confer resistance and tolerance to different biotic and abiotic stresses and to enhance fruit production and quality.

Grafting relies on the ability to use genotypes (scions) obtained through selection and breeding but improving its performance by adding the rootstock properties. Thus, grafting-related improvement -through selection and breeding- is also important on rootstock genotypes and pursues a double objective: improvement of the rootstock genotypes towards biotic and abiotic stresses, while enhancing the compatibility and tuning between rootstock and scion in order to increase the scion performance. In fact, recent grafting research focuses on the interaction between scion and rootstock in order to understand the physiologic and molecular basis of the tuning and the genotype communication pathways (Gautier et al., 2018; Goldschmidt, 2014; Martínez-Ballesta et al., 2010).

1.4.1. Roots and beginnings: grafting origin and use generalization in horticultural crops

Despite grafting is considered as one of the most ancient horticultural techniques involving deliberate manipulation, it occurs in natural populations of some species (Warschefsky et al., 2016). An example of natural grafting can be found in parasitic plants, which connect their xylem to the host's xylem and act as a sink to uptake nutrients, minerals and water (Melnyk and Meyerowitz, 2015).

It is clear that grafting was first performed in China, but there is still controversy over whether if it was originated during 'Warring States' China's history period (475 – 221 BC) or much earlier, prior to 7000 BC (Mudge et al., 2009; Wang, 2011). From then, several reports can be found along history and in different cultures (extended grafting history has been reviewed in Mudge et al. 2009). Across centuries, grafting's first aim was to asexually propagate woody cultivars (Baron et al., 2019; Warschefsky et al., 2016). However, during the nineteenth century grafting became a key technique to overcome pests and diseases in main economic crops. For instance, grafting was used to manage the phylloxera (*Dactylosphaera vitifolii*) pest invasion originated in grapevines in Europe in 1864, while it was also introduced as a standard procedure in commercial citrus orchards in order to stop the spread of fungal (*Phytophthora*) and virus (Tristeza) diseases (Mudge et al., 2009). Also, grafting has been widely used in several crops to correct the effects of soil mineral deficiencies over the scion (Köse et al., 2016; Lazare et al., 2020; Prado and Alcantara-Vara, 2011).

Regarding horticultural grafting, the first reports are in cucurbits in Korea during the late seventeenth century (Lee and Oda, 2002). Horticultural grafting was expanded worldwide during late 1950's and was commercially introduced in Europe and USA in 1990's decade (Lee et al., 2010). The use of grafting in horticultural crops is focused on managing soil-borne diseases, pests, induce resilience to several abiotic stresses or even modify plant yield and fruit properties (Rouphael et al., 2018). In the Iberian Peninsula, one of the principal tomato production zones in Europe, between 50 and 70 million grafted tomato plants are used annually, computing for about 40% of tomato production of that region (Grieneisen et al., 2018).

1.4.2. Rootstock diversity: rootstock-scion compatibility and rootstock selection

Taxonomic affinity between scion and rootstock is a requisite to ensure graft success. Hence, grafting scions onto rootstock of the same genotype, species or even different species from the same genus are commonly compatible (except for monocot plants, which are always incompatible). Contrarily, intra- and interfamilial graft combinations are rarely compatible (Goldschmidt, 2014). Graft effects can be observed even when scion and rootstock belong to the same genotype. Johkan et al. (2009) described how self-grafted pepper plants (*Capsicum annuum* L.) grafted in an older stage than other pepper plants self-grafted earlier had lower xylem connection and present drought induced symptoms as defoliation.

As for scions, rootstocks went through a domestication process, selecting for rootstocks that need less pruning, fertilization, and pesticide application. Most rootstock selection traits are related with root architecture, soil exploration and biotic or abiotic root tolerance. However, other rootstock selection parameters as shoot dwarfing can only be observed in the grafted scion, slowing the selection process (Warschefsky et al., 2016). In fact, high vigorous rootstocks are commonly related with an increased scion vegetative growth, but not necessarily with an increased fruit production. For instance, López-Marín et al. (2017) observed that non-stressed and water stressed peppers grafted onto a dwarfing rootstock had a more balanced vegetative growth and an increased fruit production when compared to those plants grafted onto high vigorous rootstocks. Similarly, other authors also found that the use of the commonly named ‘vegetative vs generative’ rootstocks, which alter the vegetative/reproductive balance, contributed to improve crop productivity and sustainability by reducing management costs, chemical use or increasing planting density (Atkinson and Else, 2001; Pérez-Alfocea, 2015; Prassinos et al., 2009). Therefore, rootstock breeding and selection process must not only consider rootstock properties, but also the direct/indirect effects over scion performance.

Tomato scions have shown high survival rates when grafted onto other tomato genotypes, wild relatives or other solanaceous species like eggplant (*S. melongena* L.), but not pepper (de Paula Farias et al., 2013; Ibrahim et al., 2001; Kawaguchi et al., 2008; King et al., 2010; Petran and Hoover, 2013). Anyhow, interspecific tomato hybrids between domesticated and wild species (mostly involving *S. habrochaites* S. Knapp & D.M. Spooner) are the most common genetic resource to obtain tomato rootstocks (King et al., 2010). Among them, ‘Maxifort’ and ‘Beaufort’ (deRuiter Seeds, The Netherlands) are the most popular rootstocks in Europe and USA and are reported to be resistant to a large amount of soil-borne diseases and increase scion vigour. Although it is widely used, the effect of ‘Maxifort’ over scion yield and vigour is no homogeneous, depending on the scion genotype (reviewed in Grieneisen et al. 2018). The analysis of the interactions between scion and rootstock may explain some of the underlying causes of this dissimilar behaviour, being nowadays partially unknown.

1.4.3. Graft formation and rootstock-scion interactions: limitations of crop improvement by grafting and the impact of stressful cultivation conditions in tomato

Since grafting disrupts vascular connections, vasculature reconnection is necessary to maintain normal water and nutrient flow. After cutting and joining scion and rootstock, ruptured cells collapse, and intact cells close to the graft junction start adhering to the opposite tissue. Graft junction is hardened with depositions of polysaccharides, while starts a mass production of pluripotent cells named callus. Callus differentiation gives way to phloem and xylem tissues. A properly alignment of the vascular cambium of both scion and rootstock is important to improve graft success. In fact, the lack of success of grafting in monocot plants is mainly due to their lack of vascular cambium (Melnyk and Meyerowitz, 2015; Wang, 2011).

The needed time to establish the vascular connection after grafting between scion and rootstock largely varies among species, taking longer in woody than herbaceous species, and being in tomato fully developed after 15 days (Fernández-García et al., 2004; Goldschmidt, 2014). Melnyk et al. (2018) observed a differential gene expression in *Arabidopsis* (*Arabidopsis thaliana* L.) that indicates the possible existence of recognition mechanisms between scion and rootstock. Nevertheless, little is known about hormonal signalling during graft formation. Grafting induces the synthesis of auxin, which accumulates near the graft junction. In turn, auxin triggers the biosynthesis and accumulation of gibberellins in the graft union, which promote cell expansion and help to seal the wound. However, the role of abscisic acid (ABA), jasmonic acid or ethylene is still not clear (Aloni et al., 2010; Nanda and Melnyk, 2018; Yin et al., 2012). Moreover, use of particular rootstocks can also affect the shoot-root signalling of other molecules as RNA, mitochondrial DNA, or proteins (Agüero et al., 2005; Berger et al., 2018; Gurdon et al., 2016; Wang et al., 2017).

Overall, a successful graft formation could determine the hydraulic capacity of the scion, and in turn its agronomic development. There is an open debate about the presence of a certain level of resistance to water movement once the graft union is established in compatible grafts (Gregory et al., 2013; Webster, 2004) or not (Clearwater et al., 2004; Nardini et al., 2006). The existence of different "compatibility levels" between scion and rootstocks should partially explain the different effect of the 'Maxifort' rootstock mentioned in the previous section. Therefore, there are some unknown issues about graft compatibility that should alter plant development, and plant response to abiotic stresses (for instance, water deficit).

Despite it is well described that the rootstock has the capability to modify the scion phenotype and performance, there is a gap of information about these underlying mechanisms. Use of vigorous rootstocks could increase root length and soil exploration, being able to capture more nutrients and water and transport them to the scion, probably enhancing the scion drought tolerance (Oztekin et al., 2009; Suchoff et al., 2017; Venema et al., 2008). However, the use of high vigorous rootstocks is not always related with enhanced scion growth. When the 'Piccolino' cherry tomato cultivar was grafted onto 'Maxifort' under low potassium (K) supply, grafted plants had higher scion growth and fruit production as compared to self-grafted plants due to a larger soil exploration. Nevertheless, under optimal K supply, the strong and vigorous root growing of grafted plants changed assimilate portioning in favour of the roots, showing a significant fruit production decrease (Schwarz et al., 2013). Consequently, despite the existence of commercial rootstocks suitable for most varieties in a crop and under a wide range of conditions, the selection of a compatible rootstock enhancing the scion under the expected growing conditions is a prime, especially if some degree of stress is expected. Additionally, grafting has been largely used to enhance nutrient uptake and translocation of different molecules (Martínez-Ballesta et al., 2010). In this sense, grafting supposes a useful technique to cultivate horticultural crops in salinized soils, avoiding salt tolerant rootstocks the translocation of Na^+ to the scion holding the ions in the root, while others directly avoid the incorporation of Na^+ and chlorine (Cl^-) in the roots (reviewed in Colla et al. 2010).

Development of drought-tolerant tomato rootstocks has been neglected in recent years. In a recent review, Kumar et al. (2017) describe the scientific advances in the last years regarding the role of grafting to maintain fruit production under drought stress conditions in horticultural crops. Several transgenic and mutant rootstocks have been developed to study how changes in hormonal signalling could increase drought resilience. For instance, the use of the ‘Procera’ tomato mutant as rootstock, with a constitutive response to gibberellin, prevented reduction of growth and stomatal conductance under drought stress, inducing also an increase in ABA content (Gaion et al., 2018). Similarly, in cucumber (*Cucumis sativus* L.) Liu et al. (2016) demonstrated that grafting onto luffa (*Luffa cylindrica* Roem.) enhanced the ability to respond to changes of moisture in the root-zone and anticipating the synthesis of ABA, reducing scion stomatal conductance and increasing WUE and biomass accumulation under drought stress. Also, introgression lines between cultivated tomatoes and wild relatives have been tested as rootstock to improve drought tolerance, improving scion’s stomatal regulation under drought stress (Poudyala et al., 2015). Mediterranean tomato landraces represent an enormous genetic resource to obtain drought resilient rootstocks, but are still poorly explored. Considering that the compatibility level should be higher than with introgression lines or hybrids with other species, and that have been selected to maximize WUE under drought periods, Mediterranean landraces represent an unexplored resource to obtain new drought resilient rootstocks.

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Chapter 2

Objectives and Thesis Outline

2.1. Objectives

As presented in the general introduction section, tomato is a widely distributed crop that has gone through different selection processes to increase the diversity in fruit traits, to be cultivated under diverse growing conditions, and to overcome most frequent biotic and abiotic stresses during cultivation. Among the latter, water deficit is a major impediment to tomato physiologic and agronomic successful development. In this regard, length and intensity of the drought periods are expected to increase in the next years under the climate change scenario. Therefore, increasing tomato resilience to water deficit and further associated stresses are a prime in tomato.

In this Thesis, the physiologic and agronomic variability of Mediterranean landraces under commercial field conditions has been explored, with the aim to investigate their potential as a useful source to improve tomato crop under water deficit conditions. This Thesis considered two different approaches for it, by identifying traits and genotypes more suitable to be introduced in breeding programs, and by the use of grafting to improve Mediterranean landraces, even examining the use of such landraces as a source to obtain new drought tolerant rootstocks.

Thus, the present Thesis had two general objectives: (1) to study the physiologic and agronomic variability among Mediterranean tomato landraces and their response to water deficit; and (2) to analyse the response of Mediterranean tomato landraces to grafting in physiologic and agronomic terms.

The general objectives were approached through 7 specific objectives:

1. To search for the underlying mechanisms determining the variability in the photosynthetic performance among Mediterranean landraces.
2. To compare the response to water deficit among Mediterranean landraces and modern genotypes.
3. To investigate the use of phenotyping measurements to monitor the effect of water deficit over physiologic and agronomic tomato performance.
4. To identify the most resilient genotypes to water deficit studied in this Thesis.
5. To determine the capability of grafting to modify the photosynthetic performance and alleviate abiotic stress effects.
6. To determine the efficiency of grafting to enhance the agronomic performance of Mediterranean drought-adapted landraces’ when using commercial and experimental rootstocks.
7. To study the suitability of drought-adapted landraces to obtain drought-resilient rootstocks.

2.2. Thesis Outline

The present Thesis is organized in the following 6 chapters:

Chapter 1: General introduction

This chapter provides a background and a framework for this Thesis. From the introduction of tomato in Europe from South America, to the techniques to measure tomato crop status, this section provides a general overview about tomato history, selection and breeding, and the main relevant parameters related with fruit production and quality. The section also provides detailed information about the grafting technique, its physiologic implications, and the utility to enhance the crop performance under stress.

Chapter 2: Objectives and thesis outline

This chapter describes the general and specific objectives, as well as the outline of the Thesis.

Chapter 3: Diversity and importance of the drought stress response in Mediterranean tomato landraces: a notorious genetic resource to improve crop performance

In this chapter, a detailed review about the origin, diversity and selective traits of Mediterranean long shelf-life landraces is provided. Also, it focuses on the physiologic and agronomic variability of these genotypes, their response to water deficit and the suitability of high-throughput parameters to phenotype them.

The general objective 1 and specific objectives 1, 2 and 3 are addressed in this chapter.

Chapter 4: Use of grafting as an alternative to traditional breeding to improve Mediterranean landraces: tomato as a case study

This chapter includes an extensive review about the role of grafting in modifying photosynthetic performance and crops' response to abiotic stresses. It also provides information about the changes in water-use efficiency, fruit production and quality of Mediterranean landraces grafted onto different rootstocks and the suitability of these landraces to be used as rootstocks.

The general objective 2 and specific objectives 5, 6 and 7 are addressed in this chapter.

Chapter 5: General discussion

This chapter contains a general overview of the most relevant findings of this Thesis, relating the main outcomes with other studies of the field of work. The specific objective 4 is addressed in this chapter.

Chapter 6: Conclusions

This chapter presents a list of the main conclusions derived from the present Thesis in relation to the general and specific objectives.

Chapter 3

Diversity and importance of the drought stress response in Mediterranean tomato landraces: a notorious genetic resource to improve crop performance

Chapter 3.1.

Mediterranean long shelf-life landraces: an untapped genetic resource for tomato improvement

Miquel À. Conesa[1]*, **Mateu Fullana-Pericàs[1]**, Antonio Granell[2] and Jeroni Galmés[1]

[1] Department Biologia-INAGEA, Universitat de les Illes Balears, Balearic Islands
[2] Instituto de Biología Molecular y Celular de Plantas, CSIC-UPV, Valencia

* Corresponding author

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Chapter 3.2.

Variations of leaf morphology, photosynthetic traits and water-use efficiency in Western-Mediterranean tomato landraces

M. Fullana-Pericàs[1], M.À. Conesa[1], S. Soler[2], M. Ribas-Carbó[1], A. Granell[3], and J. Galmés[1],*

[1] Research Group on Plant Biology under Mediterranean Conditions, Department of Biology, Universitat de les Illes Balears, Carretera de Valldemossa km 7.5, 07122 Palma, Spain
[2] Institut de Conservació i Millora de l'Agrodiversitat Valenciana, Universitat Politècnica de València, Camí de Vera 14, 46022 València, Spain
[3] Institut de Biologia Molecular i Cel·lular de Plantes, Consejo Superior de Investigaciones Científicas, Universitat Politècnica de València, Camí de Vera 14, 46022 València, Spain

* Corresponding author

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Chapter 3.3.

Tomato landraces as a source to minimize yield losses and improve fruit quality under water deficit conditions

M. Fullana-Pericàs[1], M.À. Conesa[1], C. Douthe[1], H. El Aou-ouad[1], M. Ribas-Carbó[1], J. Galmés[1]*

[1] Research Group on Plant Biology under Mediterranean Conditions-INAGEA, Universitat de les Illes Balears, Balearic Islands

* Corresponding author

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Chapter 3.4.

High-throughput phenotyping of a large tomato collection under water deficit: combining UAVs' remote sensing with conventional leaf-level physiologic and agronomic measurements

M. Fullana-Pericàs[1]*, M.À. Conesa[1], J. Gago[1], M. Ribas-Carbó[1], J. Galmés[1]

[1] Research Group on Plant Biology under Mediterranean Conditions-INAGEA, Universitat de les Illes Balears, Balearic Islands, Spain

* Corresponding author

In preparation

Title: High-throughput phenotyping of a large tomato collection under water deficit: combining UAVs' remote sensing with conventional leaf-level physiologic and agronomic measurements

Authors: Mateu Fullana-Pericàs*, Miquel À. Conesa, Jorge Gago, Miquel Ribas-Carbó, Jeroni Galmés

Research Group on Plant Biology under Mediterranean Conditions-INAGEA. Universitat de les Illes Balears, Balearic Islands.

*Corresponding author:

Tel: +34971259556;

E-mail: mateufullana@gmail.com

Abstract

Field high-throughput phenotyping studies are highly needed to study water use efficiency (WUE), stress tolerance capacities, and fruit production and quality in tomato to improve crop breeding strategies and adapt them to the climatic change scenario. In this study, we combined leaf-level physiologic and agronomic measurements with the use of UAV high-throughput remote sensing techniques for phenotyping 91 tomato genotypes. These genotypes include long shelf-life (LSL) and non-LSL (CON) Mediterranean landraces, cultivated under well-watered (WW, covering 100% crop evapotranspiration demands) and water deficit (WD, irrigation stopped one month after plantlet transplantation to field) conditions. Aerial remote sensing (including multispectral imaging), leaf gas-exchange, leaf carbon isotope composition ($\delta^{13}C$), carbon to nitrogen ratio (C/N), and fruit production and quality measurements were performed. LSL and CON genotypes differed at whole-canopy and leaf level measurements in response to WD. For the same NDVI value, LSL genotypes showed lower A_N and much minor g_s than CON, and therefore higher intrinsic water use efficiency (WUE). However, CON showed a better performance than LSL regarding fruit production, having for the same canopy projected area (CPA) higher fruit production than LSL genotypes. Also, tomato fruit quality was approached through remote sensing measurements, being correlated with multispectral indices but not with CPA. Thus, the response of each genotype or genotype group to WD drove the relationships among remote sensing, leaf-level physiologic and agronomic measurements. Overall, our results indicated that UAV high-throughput data are reliable measurements to phenotype large genotype tomato collections at agriculture field conditions, and in combination with leaf-level physiologic and agronomic parameters let to improve our understanding of tomato genotypic performance in response to water deficit.

Keywords: Field phenotyping, fruit quality landraces, NDVI, photosynthesis, remote sensing, WUE

Highlights

- UAV remote sensing is a reliable technology to phenotype large tomato collections under water deficit at field conditions
- Multispectral vegetation indices were more related with leaf-level physiologic parameters
- Fruit production was highly correlated with canopy projected area
- Fruit quality was approached through multispectral measurements
- Combining techniques from UAV high-throughput phenotyping to leaf physiology and fruit level improve genotypes’ characterization under drought

1. Introduction

Global climate models based into the Climatic Change predict increases in the annual mean temperature for the next decades, and especially in the summer season (Battisti and Naylor, 2009). In the Mediterranean basin, the increase in temperature will be accompanied by reductions in the rainfall from 25 to 50% (Giorgi and Lionello, 2008; Hertig and Tramblay, 2017; Raymond et al., 2019). Considering this scenario, improving water use efficiency (WUE) and stress tolerance in crops becomes a challenge to meet global food demand at the lowest agricultural water consumption. Thus, there is an urgent need to check the performance of large numbers of genotypes under field conditions with increased WUE and drought tolerance, but sustaining acceptable commercial fruit production and quality (Mickelbart et al., 2015). For this purpose, the use of high-throughput phenotyping technologies is very convenient, adding valuable information to plant-level measurements in order to drive genetic crop breeding (Araus et al., 2018).

In this sense, in the last years the use of aerial remote sensing techniques based into the use of Unmanned Aerial Vehicles (UAVs) to monitor crop fields has revolutionized field phenotyping (Adão et al., 2017; Araus et al., 2018; Gago et al., 2015; Salas Fernandez et al., 2017). Usually, UAVs employed to monitor vegetation are equipped with red-green-blue (RGB) or multi-spectral cameras to collect data about vegetation coverage, size and plant height, or the use of vegetation indices (VIs) based in canopy reflectance (Gago et al., 2015). These VIs have been used for plant phenotyping to assess the plant physiological status under abiotic stresses in different crops as wheat, maize or tomato (Babar et al., 2006; Cairns et al., 2012; Comar et al., 2012; Gianquinto et al., 2011; Padilla et al., 2015; Zarco-Tejada et al., 2012). Among them, probably the normalized difference vegetation index (NDVI) is the most commonly used to estimate biomass production, plant vigor, stress levels, yield, and even as a proxy to photosynthesis (Fortes et al., 2015, 2014; Gamon et al., 2015; Steltzer and Welker, 2006; Virlet et al., 2015). UAV high-throughput phenotyping technology can overcome some of the previous spatial and temporal limitations of the traditional leaf-level physiologic techniques. However, remote sensing technologies are still limited by the physiological information that can be retrieved (Araus et al., 2018; Gago et al., 2015). Integrative approaches combining high-throughput UAV phenotyping technologies and plant-truth eco-physiologic techniques are therefore required to improve our understanding of the different genotypes' performance at real field conditions.

For instance, leaf gas-exchange parameters as net CO_2 assimilation rate (A_N), stomatal conductance (g_s) and their ratio, known as intrinsic water use efficiency (WUEi, as A_N/g_s), are widely used as dynamic references of plant performance, physiological stress status, growth dynamics and fruit production, and are commonly related to aerial remote sensing data (Araus et al., 2018; Flexas and Medrano, 2002; Gago et al., 2017; Zarco-Tejada et al., 2016). Carbon isotope composition in leaf tissues ($\delta^{13}C$) has been defined as an integrative physiological stress and WUE indicator (Dhanapal et al., 2015; Farquhar and Richards, 1984), providing information at different levels and time scales (Flanagan and Farquhar, 2014; Tambussi et al., 2007). Despite the correlation between $\delta^{13}C$ and WUE_i is widely defined in literature, their relationship may be affected by the interaction between environment and genotypic variability (Condon, 2004). Although both leaf gas-exchange traits and $\delta^{13}C$ provide highly valuable information to evaluate crop breeding performance, their measurement is time-consuming. Additionally, they are mostly focused on leaf rather than plant-level, and difficult to implement in field trials with hundreds/thousands of plants that should be measured at the same time and/or for monitoring purposes along the season (Araus and Cairns, 2014; Gago et al., 2015).

Tomato (*Solanum lycopersicum* L.) is one of the most produced vegetables worldwide and its production has doubled in the last 20 years (FAO, 2019). Despite tomato crop is widely distributed and adapted to an important range of climates (Cuartero and Fernández-Muñoz, 1999), it is mainly cultivated in temperate regions, and particularly the Mediterranean basin. At open-field, tomato is a spring-summer high water-demanding crop, requiring more than 3 L per plant and day at maturity (Harmanto et al., 2005). Considering the predicted climate scenario, it becomes essential to explore the tomato genotypic variability to find the most resilient genotypes under stress conditions, which may also became valuable genetic resources to improve WUE in the tomato crop and sustain fruit production and quality under harsh conditions. In this regard, it has been described that some long shelf-life (LSL) landraces have improved drought tolerance as compared to modern genotypes (Fullana-Pericàs et al., 2019; Galmés et al., 2011; Guida et al., 2017; Tranchida-Lombardo et al., 2018). The LSL phenotype, characterized by their extended fruit post-harvest conservation, exists in several West-Mediterranean landraces like the ‘de Ramellet’ tomato from the Balearic Islands (Bota et al., 2014; Conesa et al., 2014) and the ‘de Penjar’ tomato from the Eastern Iberian peninsula (Casals et al., 2012). Also, the LSL phenotype can be found in some Italian landraces (Sacco et al., 2017; Sinesio et al., 2007), and in Greek landraces (Terzopoulos and Bebeli, 2010) (extended review of LSL landraces distribution and traits can be found in Conesa et al. 2020).

In this study, the physiologic and agronomic performance of 91 tomato genotypes under well-watered and deficit irrigation conditions was assessed using high-throughput UAV phenotyping technologies combined with conventional leaf-based physiologic measurements at plant level. The screened genotypes included 68 Western-Mediterranean LSL landraces, and 23 non-LSL landraces and modern inbreeds of very diverse origin and fruit types, with evidences for improved tolerance to open-field summer cultivation conditions. We hypothesized a differential performance of the genotypes regarding productivity and drought adaptation that should emerge at canopy and leaf levels. Thus, our objectives were: (1) to compare the use of different phenotyping measurements to monitor the effect of water deficit over a large tomato collection, and (2) to investigate if the relationships between remote sensing and leaf-based physiologic measurements and agronomic traits were different depending on the tomato genotype group.

2. Material and methods

2.1. Plant material

A total of 91 tomato genotypes (*Solanum lycopersicum* L.) were evaluated in this study. Two major groups were differentiated, control genotypes (CON, 23 genotypes) and long-shelf life landraces (LSL, 68 genotypes). The CON group included non-LSL landraces from the Mediterranean basin and the M82 and OH8245 genotypes, which were included as two non-Mediterranean control genotypes. The LSL group included genotypes from different Mediterranean regions and was subdivided depending on the origin of these landraces, thus LSL landraces from the Italic peninsula, Sicily and Sardinia (ITA), 'de Penjar' genotypes from Catalonia and Valencian Country (CVC), and 'de Ramellet' genotypes from the Balearic Islands (BAL) (Table 1). Seeds were obtained from the Hebrew University of Jerusalem, University of Naples, University of the Balearic Islands, Centre de Conservació i Millora de l'Agrodiversitat Valenciana and University of Sassari (Table S1).

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

2.2. Experimental design and treatments

Seeds from all genotypes were germinated in polystyrene trays filled with peat-based substrate under greenhouse conditions. One-month old seedlings were transplanted to a field for commercial production of tomato in Ariany (Mallorca, Balearic Islands, latitude

39º38’N, longitude 3º08’E, altitude 79 m a.s.l.) in late June. The field soil was fumigated (50% metam sodium anhydrous, 50% p/v) at a rate of 300 L ha^{-1}, rototilled and enriched with 250 kg ha^{-1} of a granulated fertilizer (composition of 12% of total N, 8% of P_2O_5 and 16% of K_2O) prior transplantation. The soil was clay, with an electric conductivity as saturated past of 0.55 mS cm^{-1} and a pH of 8.4.

Two treatment blocks were designed, the well-watered (WW), and the water deficit (WD), with five plants per genotype and treatment grown in a random distribution within each block. Blocks were separated by a non-cultivated area (6 m wide) to prevent water infiltration among blocks. Plant beds (0.30 m width) were covered with an opaque plastic film to avoid weeds and to maintain soil humidity. Irrigation was applied via drip tape (AzudPro, 0.33 m emitter spacing, 1 mm thickness, 2.15 L h^{-1} at 100 kPa). Water applied by irrigation was recorded by volumetric rotatory piston water meters (Genebre SA, Barcelona). Dripping lines were 80 m long, separated 2 m from each other, and plants were separated 0.8 m within lines. In order to avoid differences due to management, plants were grown freely, without sustain structures and with no pruning all over the experiment. Pests and weeds were treated following typical commercial practices.

During the first month after field transplantation, both WW and WD blocks were irrigated covering the daily crop evapotranspiration (ET_C). Afterwards, irrigation in the WD treatment was stopped until the end of the experiment, meanwhile the irrigation of the WW treatment was maintained covering the daily ET_c demands (Fig S1, Table S2).

Weekly reference evapotranspiration was calculated according to FAO-56 (Testa et al., 2011) using data obtained by two nearby weather stations. Crop evapotranspiration (ET_c) was obtained as the product of ET_o and the crop coefficient (K_c) at each growth stage (Allen et al., 2006). Over all the cultivation period, WW treatment received 606 l m^{-2} and WD treatment 215 l m^{-2} (Fig. S1). Over all the experiment, the per month averages of the daily average, daily maximum (day) and daily minimum (night) temperatures in the field were (in ºC), respectively, 24.1, 31.6 and 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 and 14.3 in September. The average relative air humidity was 70.45 ± 1.05 % throughout the experiment. Precipitations per month were (in mm), respectively: 0.0 in June, 6.0 in July, 8.3 in August and 19.0 in September.

2.3. Leaf gas exchange and chlorophyll fluorescence

Leaf gas exchange and chlorophyll *a* fluorescence were measured 50 days after field transplantation (20 days after treatment application) simultaneously with an open infrared gas-exchange analyzer system equipped with a leaf chamber fluorometer (Li-6400-40, Li-Cor Inc., USA). Measurements were performed from 09:00 to 14:00 for eight days.

Environmental conditions in the leaf chamber consisted of a photosynthetic photon flux density of 1500 μmol m^{-2} s^{-1} (with 10% blue light), and a leaf temperature of 32 °C. Measurements were performed after inducing steady-state photosynthesis for at least 5 min at an ambient CO_2 concentration (C_a) of 400 μmol CO_2 m^{-2} s^{-1}.

The quantum efficiency of the photosystem II (PSII)-driven electron transport was determined using the equation (1):

$$(1)\ \Phi PSII = \frac{F'_M - F_s}{F'_M}$$

where F_s is the steady-state fluorescence in the light (PPFD 1500 μmol photon m^{-2} s^{-1}) and F'_M the maximum fluorescence obtained with a light-saturating pulse (8500 μmol photon m^{-2} s^{-1}) (Genty et al., 1989). As ΦPSII represents the number of electrons transferred per photon absorbed by PSII, the rate of electron transport (ETR) can be calculated as (2):

$$(2)\ ETR = \Phi PSII \cdot PPFD \cdot \alpha \cdot \beta$$

where α is the leaf absorbance, and β is the distribution of absorbed energy between the two photosystems. The values of α and β were obtained from Fullana-Pericàs et al. (2017).

2.4. Leaf $\delta^{13}C$ isotope composition and nitrogen content

Leaf carbon isotope composition ($\delta^{13}C$) and leaf nitrogen and carbon content were determined from a young fully expanded leaf per plant replicate. Leaves were dried at 60 ºC until constant weight (*ca.* 72 h), ground to fine powder and sampled for analysis. Samples were combusted in an elemental analyzer (Thermo Flash EA 1112 Series, Bremen, Germany), and CO_2 and N_2 were directly injected into a continuous-flow isotope ratio mass spectrometer (Thermo-Finnigan Delta XP, Bremen, Germany) for isotope analysis. Leaf nitrogen content was calculated from the area obtained for isotope analysis on mass 28, while carbon content from the area obtained for isotope analysis on mas 46. Peach leaf standards (NIST 1547) were run every six samples. The standard deviation of the analysis was below 0.1‰. Results for $\delta^{13}C$ are presented as δ vs. PDB.

2.5. Fruit production and quality measurements

Fruit production was measured per plant 79, 92, 96, 107 and 114 days after field transplantation. Fruit quality parameters were measured from 8 healthy fruits per plant. Fruits were squashed and homogenized using an electric mixer (LM310E10, Moulinex, Alençon, France). Total soluble solids (TSS) and acidity were determined from the obtained juice. A digital re- fractometer and electrical conductimeter (PAL-BXACID F5, Atago, Tokyo, Japan) with a 0.2°Brix and with a 0.10% citric acid precision was used to evaluate TSS (results expressed as ºBrix) and acidity (results expressed as % of citric acid).

2.6. Aerial image analysis

The images of the study were acquired using an unmanned aerial vehicle (UAV) (FV8, Atyges, Malaga, Spain). The UAV was controlled by an autopilot for autonomous flying (AP04, UAV Navigation, Madrid, Spain) and followed a flight plan using waypoints to acquire imagery from all study field. Aerial measurements were performed 65 days after field transplantation and were performed during the solar noon to avoid plant shadows that could hinder the image analysis.

The UAV was equipped with a Parrot Sequoia sensor (Parrot SA, Paris, France). The Parrot Sequoia sensor imaged with one 16 megapixel rolling shutter RGB camera at 4608 x 3456 pixel resolution and four 1.5 megapixel global-shutter single band cameras imaging at 1280 x 960 pixel resolution in green (550 nm), red (660 nm), red-edge (735 nm) and near infrared (790 nm) spectral bands. Sensors were calibrated before the flight by a reflectance panel provided by the manufacturer just before the flight in the takeoff site. This equipment includes a light sensor (that was placed in the top of the UAV) that measures the incoming sun radiation during the flight and corrects the reflectance data from the 4 sensors by the fluctuating irradiance. The image resolution (ground pixel size) was of 1.65 cm/pixel at typical established flight altitude of 15 m above the terrain.

The normalized difference vegetation index (NDVI) was calculated as Rouse et al. (1974):

$$(3)\ \mathrm{NDVI} = \frac{\mathrm{NIR-RED}}{\mathrm{NIR+RED}}$$

Using the same multispectral bands, the simple ratio index (SR) was calculated as:

(4) $\mathrm{SR} = \frac{\mathrm{NIR}}{\mathrm{RED}}$

The green normalized difference vegetation index (GNDVI) was calculated using the green band (500-550 mm) as:

(5) $\mathrm{GNDVI} = \frac{\mathrm{NIR-GREEN}}{\mathrm{NIR+GREEN}}$

Canopy projected area (CPA) was measured using a 16 mm lens RGB camera (Alpha 5000, Sony, Tokyo, Japan) on board measuring the area covered by each plant. The field of view (FOV) was 25.5º, which delivered high-RGB image resolution (ground pixel size) of 0.86 cm/pixel at typical established flight altitude of 30 m above the terrain. Image post-processing was carried out using Pix4DPro (ver. 3.3.29, Pix4D, Lausanne, Switzerland). A total of 25 ground control points (GCP´s) were used for geo-referencing of the images using this software. All GCP`s were build covering a 20 x 10 cm steel plate with aluminum foil to ease its visualization in images. Error was assessed using the root-mean-square error (RMSE) of GCP's with values <0.05 m. Obtained maps were mounted in ArcMap module of ArcGIS (version 10.3.1, ESRI Inc., USA), where individual plant shape was manually extracted. Following this, the different spectral bands were extracted as a mean of the selected region, and multispectral indices were calculated according to the previous formulas. Similarly, CPA was extracted using the individual shapes.

2.7.Statistical analyses

One-way ANOVA was performed to all measured parameters to reveal differences between treatments or within treatments for the genotype groups (*P*-value < 0.05 after Duncan *post-hoc* test). Pearson's correlations (r) were calculated to determine the relationships among the studied parameters. ANCOVA analysis was performed to evaluate if there were differences in intercept and slopes between different regression analysis. All statistical analyses were performed using R software (ver. 3.2.2.; R Core Team, Vienna, Austria).

3. Results

3.1 Variability in leaf-level physiologic parameters and correlations among them

The traits indicative of leaf physiological status are presented in Table 2 for the different genotype groups under well-watered (WW) and water deficit (WD) conditions. There were no significant differences in the net CO_2 assimilation rate (A_N) and stomatal conductance (g_s) between control (CON) and long shelf-life (LSL) or among LSL genotype groups under WW conditions (Table 2). All genotype groups had lower A_N and g_s and higher intrinsic water-use efficiency (WUE_i) under WD as compared to WW. Under WD, average values of LSL for A_N and g_s were lower than those of CON. Also, LSL genotypes from Italic Peninsula, Sicily and Sardinia (ITA) had the lowest A_N, whereas ITA and LSL genotypes from Balearic Islands (BAL) had lower average g_s values than CON. Regarding WUE_i, LSL presented lower average values than CON under WW but higher under WD. Under WW, CON had higher WUE_i than ITA and LSL genotypes from Catalonia and Valencian Country (CVC), while under WD CON had lower values than ITA and BAL (Table 2).

For leaf carbon isotope composition ($\delta^{13}C$), all genotype groups had higher $\delta^{13}C$ under the WD treatment. Regardless of the treatment, CON had the lowest, CVC and BAL the highest and ITA intermediate values. Globally, the LSL group had higher $\delta^{13}C$ average values than CON under both WW and WD. Despite this, no significant differences were observed between LSL and CON for the carbon to nitrogen ratio (C/N), while among LSL genotype groups ITA had the highest values under both WW and WD values. Only BAL increased C/N under WD as compared to WW (Table 2).

Regarding the correlations among leaf physiological measurements, A_N and g_s showed a positive relationship when considering all data, having CON and LSL a similar behavior (Fig. 1a). The electron transport rate (ETR) to net CO_2 assimilation rate ratio

(ETR/A_N; a physiological indicator of stress) was negatively correlated with g_s (Fig. 1b). Similarly, a negative correlation was found between WUE_i and g_s (Fig. 1c). All these relationships were also significant when considering CON and LSL separately, but ANCOVA analysis did not reveal any difference between such groups in the slope or intercept (*P*-value > 0.05).

A negative correlation was observed between $\delta^{13}C$ and both A_N and g_s (Fig. 1d,e), with differences between CON and LSL regressions. ANCOVA analysis revealed that LSL had higher A_N and g_s than CON at low $\delta^{13}C$ values. On the contrary, there was a positive relationship between $\delta^{13}C$ and WUE_i when considering all data, although this relationship was only significant for LSL when considering genotype groups individually (Fig. 1f).

3.2.Variability in remote sensing parameters

The normalized difference vegetation index (NDVI) and the canopy projected area (CPA) showed similar trends in response to water treatments among genotype groups. As a general pattern, LSL had significantly higher NDVI and CPA than CON regardless of the treatment (Table 2). Specifically, ITA and BAL had higher NDVI than CON and CVC under WW. Interestingly, BAL had the highest NDVI under WD. In terms of CPA, ITA and BAL groups showed also higher CPA under both WW and WD than the remaining groups. Except for ITA, all genotype groups significantly reduced their NDVI and CPA under WD (Table 2). A significant positive correlation was found between both parameters ($r = 0.59$; *P*-value < 0.001, Fig. S2).

3.3. Relationships between leaf-level physiologic and remote sensing measurements

We further compared the information obtained through the high-throughput phenotyping technique employing the UAV with the leaf-level physiologic measurements. Contrasting results were obtained when examining the relationship between NDVI and CPA with leaf gas-exchange, carbon isotope composition and C/N ratio (Fig. 2). NDVI was positively correlated with both A_N and g_s, either when considering all genotypes and treatments together, and for CON and LSL separately (Fig. 2a,b). In both treatments, a negative relationship of NDVI was found with water use efficiency-related traits, considering either WUE_i and $\delta^{13}C$, for all genotypes together and separately in groups (Fig. 2c,d). For all the relationships previously described, ANCOVA analyses revealed significant differences between CON and LSL regressions in their intercepts (P-value < 0.05) but not in their slopes. Contrarily, a significant correlation between NDVI and C/N was only observed for LSL (Fig. 2e).

In general, as compared to the NDVI, CPA showed weaker or non-significant relationships with the leaf-level physiologic parameters. Significant correlations with CPA were only observed for A_N, g_s and WUE_i when considering all genotypes together (Fig. 2f,g,h). For CON genotypes, CPA significantly correlated with g_s and WUE_i, while for LSL, significant correlations were found with all leaf-level parameters (Fig. 2f-j). For the correlations with g_s and WUE_i, where both CON and LSL regressions were significant, ANCOVA analysis revealed differences in their intercepts (P-value < 0.05) but not in their slopes.

Other vegetation indices were obtained from UAV measurements, as the simple ratio index (SR) and the green normalized difference vegetation index (GNDVI). When considering all genotypes and treatments, both SR and GNDVI significantly correlated with all ground-based parameters (i.e., A_N, g_s, WUE_i, $\delta^{13}C$ and C/N; Table 3) showing a similar behavior than the previously observed for NDVI.

3.4. Variability in fruit related traits and the relationship with remote sensing parameters

A large variability was observed in fruit production and fruit quality parameters among genotype groups (Table 4). When comparing among groups, ITA had significantly the highest and CVC the lowest fruit production, under both WW and WD conditions. Given the large variability among groups within LSL, there were no significant differences between LSL and CON. Similarly, ITA had the highest TSS regardless of the treatment, having CON the lowest values under WW and with no significant differences among the other genotype groups under WD. CON also had the lowest acidity values under WW conditions and CVC the highest, while ITA had the lowest acidity under WD. Therefore, different to production, under WW conditions there were differences in TSS and acidity between LSL and CON, with higher values in the former group. Except for CVC, all genotype groups decreased their fruit production and increased TSS under WD as compared to WW. On the other hand, only CON increased acidity under WD (Table 4).

We further explored the relationships obtained from the UAV remote sensing data with the fruit production and fruit quality parameters. Fruit production was positively correlated with NDVI when considering all genotypes and treatments together and genotype groups separately (Fig. 3a). Similar regression coefficients with fruit production were observed when using SR (Fig. 3b) and GNDVI (Table S3). However, higher correlation coefficients were obtained when fruit production was correlated with CPA (Fig. 3c). Despite NDVI and GNDVI were significantly correlated with TSS when considering all genotypes and treatments (Fig, 3d, Table S3), the correlation of TSS with SR showed higher correlation coefficient and was significant regardless of the genotype group (Fig. 3e). On the other hand, correlation between CPA and TSS was only significant for LSL genotypes (Fig. 3f). Any of the UAV high-throughput parameters was significantly correlated with acidity, except CPA, only when considering LSL genotypes (Table S3).

4. **Discussion**

The need for efficient high-throughput field phenotyping techniques is claimed as a major constraint for genetic crop breeding programs (Araus and Kefauver, 2018 and references therein). Despite remote sensing has important advantages related to high automation and reproducibility of samplings over time, the challenge is still the reliability with common leaf-based physiologic parameters or fruit related traits. Moreover, most of the studies attempting to correlate remote sensing with those measurements include low genetic variability in the screened plant material, which biases the results of the correlation to genotype-related responses (e.g., Duan et al., 2019; Fortes et al., 2015; Wu et al., 2008). Here, where 797 plants from 91 different tomato genotypes were screened, we aim to test the importance of remote sensing and high-throughput measurements to predict plant stress response in open field tomato crops.

4.1. Leaf-level physiologic differences among genotypes are detected with remote sensing measurements

Significant correlations were observed between NDVI and A_N, g_s, WUE_i and $\delta^{13}C$ when considering all genotypes and treatments (Fig. 2a-d). This is in accordance with previous studies using tomato, corn, or orange orchards, where plants with higher A_N had higher NDVI values and drought induced reductions in parallel in A_N and NDVI (Fig. 2a) (Marino et al., 2015; Tan et al., 2013; Zarco-Tejada et al., 2016).

ANCOVA analysis revealed different performance of CON and LSL genotypes in these relationships, denoting a different physiologic behavior. In this sense, for the same NDVI value, LSL had lower A_N and g_s than CON (Fig. 2a,b), leading in turn to a higher WUE_i (Fig. 2c). The higher WUE_i of LSL was achieved through a larger reduction in g_s as compared to the reduction in A_N, as previously reported in other tomato landraces with enhanced drought tolerance (Galmés et al., 2013; Giorio et al., 2018; Guida et al., 2017). Also, when considering LSL genotype groups, ITA and CVC showed higher ETR/A_N (18.12 ± 2.8 and 16.90 ± 1.4 respectively) than CON (15.05 ± 0.62) under WD condition, indicating that LSL genotypes had an increased ratio between the electrons generated in the photosynthetic electron transport and the electrons consumed in A_N that would provoke higher ROS production and oxidative stress (Flexas and Medrano, 2002; Salazar-Parra et al., 2012) (Fig. 1b). This is in agreement with the stronger reductions showed in g_s by both ITA and CVC in response to WD. Hence, it possible that their improved water use efficiency is accompanied by primary and secondary antioxidant and osmoprotection metabolism as suggested before for other LSL genotypes and model species (da Fonseca-Pereira et al., 2019b, 2019a; Landi et al., 2017; Patanè et al., 2016).

Interestingly, CON under WD had the same $\delta^{13}C$ than BAL under WW, with almost no CON genotype reaching the elevated WUE levels of LSL under WD, denoting the different behavior in WUE among genotype groups (Fig. 1f). This contrasting performance explain the differences in the relationship of $\delta^{13}C$ with leaf gas-exchange parameters between genotype groups, having LSL higher A_N and g_s than CON for the same $\delta^{13}C$ (Fig. 1d,e), which in turn explains the higher NDVI for LSL genotypes for the same $\delta^{13}C$ values (Fig. 2d).

Regarding CPA, weaker correlations with leaf-level physiologic measurements were observed if compared with NDVI (Fig. 2). It is worthy to note that no correlation of CPA with $\delta^{13}C$ was observed for CON, but a negative relationship was found for LSL (Fig. 2i). Several studies related CPA with crop physiologic status, growth, and leaf water evapotranspiration (Enciso et al., 2019; Haboudane et al., 2004; Mukherjee et al., 2010). Hence, the higher CPA and lower g_s of ITA and BAL as compared to CVC and CON under WD (Fig. 2g,h) indicates that the constrained g_s in these groups (thus, driving higher WUE) do not impose a detriment in plant growth (Table 2).

4.2. Fruit production and quality can also be approached using remote sensing measurements in large tomato collections

All the included remote sensing measurements included in this study were significantly correlated with fruit production (Fig. 3, Table S3). However, and similar to the observed in the relationships between leaf-level physiologic and remote sensing measurements, different regressions were found for CON and LSL.

Regarding multispectral indices, previous studies in tomato showed that NDVI positively correlate with fruit production, but only including a single genotype in their studies (Campillo et al., 2019; Fortes et al., 2014; Ihuoma and Madramootoo, 2019). In this study, where 91 genotypes were screened, higher fruit production was found for CON than for LSL genotypes for the same NDVI and SR value (Fig. 3a,b). That different regressions between CON and LSL could be derived from their different physiologic behavior and response to water deficit. In fact, a weak positive relationship was found between A_N and fruit production ($r = 0.17$, P-value < 0.001, Fig. S3), having again CON and LSL different slopes. However, the relationship between A_N and fruit production is still and open discussion due to the different source-sink carbon partitioning (Génard et al., 2008; Ho, 1996; Osorio et al., 2014), and other authors did not found any correlation between both parameters in tomato (Fullana-Pericàs et al., 2018; Wei et al., 2016)

Furthermore, and opposite to the observed in the relationships between leaf-level physiologic measurements and remote sensing, stronger correlations of fruit production were found with CPA than with multispectral indices (Fig. 3c). These results suggest that those tomato varieties with enhanced vigor, plant growth and more open canopies (i.e., more exposed zenithally) can sustain higher fruit production. Nevertheless, ANCOVA analysis revealed different regressions for CON and LSL between fruit production and CPA, hindering again the possibility to model the response to water deficit in terms of fruit production of a large tomato collection, and to identify the most resilient genotypes (since for the same CPA value different fruit production were found depending on the observed genotype).

Beyond the relationship between remote sensing and fruit production, the present study represents, at the best knowledge, the first attempt to relate remote sensing measurements with tomato fruit quality. The phenotyping of large tomato collections, as the included in this study, might suppose a handicap when trying to assess fruit quality through remote sensing, since those genotypes may have different ripening periods or different ripening responses to water deficit. When considering all genotypes, TSS and acidity were not related with CPA but with NDVI, GNDVI and SR, and stronger correlations of TSS were found with SR than with NDVI and GNDVI (Fig. 3 d-f, Table S3). In grapevines and fruit orchards changes in NDVI plant canopy have explored to monitor fruit maturation and estimate fruit quality, with promising results (Meyers et al., 2020; Overbeck et al., 2017; Stagakis et al., 2012; Uribeetxebarria et al., 2019). Therefore, our results suggest that in open-field tomato cultivation the use of UAVs equipped with multispectral cameras could be used to monitor the TSS, even when including a large variable collection.

4.3. Concluding remarks

We found that leaf physiology and fruit quality were better predicted by multispectral indices as NDVI, GNDVI and SR, whereas fruit production was closely related to CPA. Nevertheless, correlations between remote sensing and leaf-level physiologic measurements depended on the genotype group and its response to water deficit. The ample variability and high number of genotypes evaluated in this work highlight the potential in combining different remote sensing parameters (vegetation indices and canopy size) with leaf-level physiologic measurements. It also stresses the need to deepen in the improvement of UAV high-throughput phenotyping technologies to assess tomato plant stress responses at open-field, and finally fruit production and quality, which may be further extended to other crops.

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Tables and Figures

Table 1. Number of genotypes included in this experiment. From left to right columns indicate the genotype group label, their abbreviation and the number of genotypes included in that group. Detailed information of these genotypes can be found in Table S1.

Genotype group	Abbreviation	*n*
Control	CON	23
Long shelf-life landraces	LSL	
LSL from Italic Peninsula, Sicily and Sardinia	ITA	7
LSL from Catalonia and Valencian Country (‘de Penjar’)	CVC	12
LSL from Balearic Islands (‘de Ramellet’)	BAL	49

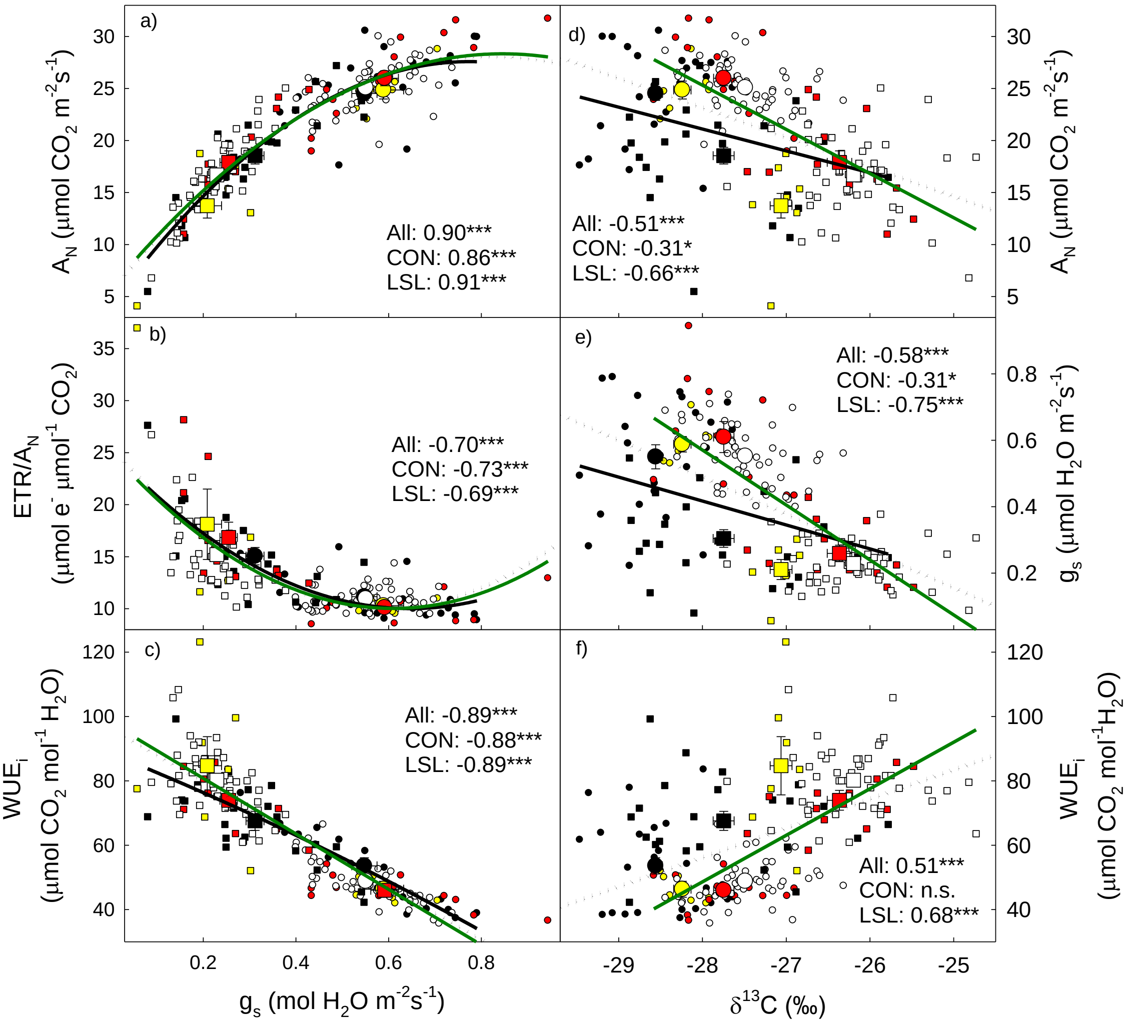

Figure 1. Relationship between stomatal conductance (g_s) and a) net CO_2 assimilation rate (A_N), b) electron transport rate (ETR) to net CO_2 assimilation rate ratio (ETR/A_N) and c) intrinsic water-use efficiency (WUE_i); and between leaf carbon isotope composition ($\delta^{13}C$) and d) net CO_2 assimilation rate (A_N), e) stomatal conductance (g_s) and f) intrinsic water-use efficiency (WUE_i). Dots refer to well-watered (WW) and squares to water deficit (WD) conditions for each of the genotypes. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Big-sized symbols indicate the genotype group average value ± SE. See Table 1 for group abbreviations and *n* specifications. Regression lines are shown when significant, where dotted black line represents the regression analysis considering all genotypes and treatments, black line the regression analysis considering only CON and green line considering only LSL genotypes. Pearson's correlation coefficient (r) is indicated, and asterisks mean significance level at * $P \leq 0.05$, ** $P \leq 0.01$ or ***$P \leq 0.001$; n.s. refers to non-significant.

Table 2. Differences in the normalized difference vegetation index (NDVI), canopy projected area (CPA), net CO_2 assimilation rate (A_N), stomatal conductance (g_s), intrinsic water-use efficiency (WUE_i), carbon isotope composition ($\delta^{13}C$) and carbon to nitrogen ratio (C/N) for the different genotype groups under well-watered (WW) and water deficit (WD) conditions. Data are means ± S.E. See Table 1 for *n* specifications and group abbreviations. Letters denote significant differences between groups within treatments, asterisks between treatments for each group and $^{¥}$ between CON and LSL for each treatment by one-way ANOVA after Duncan *post-hoc* test (*P*-value < 0.05).

	A_N µmol CO_2 $m^{-2}s^{-1}$	g_s mol H_2O $m^{-2}s^{-1}$	WUE_i µmol CO_2 mol^{-1} H_2O	$\delta^{13}C$ ‰	C/N	NDVI	CPA m^2 $plant^{-1}$
WW							
CON	24.53 ± 0.67 ^{a} *	0.55 ± 0.03 ^{a} *	53.59 ± 2.53 ^{a} *	-28.56 ± 0.01 ^{c} *	8.59 ± 0.12 ^{b}	0.75 ± 0.01 ^{b} *	0.97 ± 0.01 ^{b} *
LSL	25.21 ± 0.26	0.56 ± 0.01	48.12 ± 0.74 $^{¥}$	-27.61 ± 0.05 $^{¥}$	8.44 ± 0.06	0.78 ± 0.01 $^{¥}$	1.33 ± 0.01 $^{¥}$
ITA	24.85 ± 0.86 ^{a} *	0.59 ± 0.04 ^{a} *	46.32 ± 2.49 ^{b} *	-28.24 ± 0.10 ^{b} *	9.09 ± 0.25 ^{a}	0.78 ± 0.01 ^{a} *	1.34 ± 0.01 ^{a}
CVC	25.98 ± 0.72 ^{a} *	0.59 ± 0.03 ^{a} *	45.99 ± 1.36 ^{b} *	-27.75 ± 0.12 ^{a} *	8.55 ± 0.15 ^{b}	0.76 ± 0.01 ^{b} *	1.06 ± 0.01 ^{b} *
BAL	25.09 ± 0.29 ^{a} *	0.55 ± 0.01 ^{a} *	48.85 ± 0.90 ^{ab} *	-27.49 ± 0.06 ^{a} *	8.32 ± 0.07 ^{b} *	0.79 ± 0.01 ^{a} *	1.39 ± 0.01 ^{a} *
WD							
CON	18.54 ± 0.80 ^{a}	0.31 ± 0.02 ^{a}	67.58 ±2.95 ^{c}	-27.49 ± 0.13 ^{c}	8.78 ± 0.15 ^{b}	0.68 ± 0.01 ^{b}	0.72 ± 0.01 ^{b}
LSL	16.54 ± 0.41 $^{¥}$	0.23 ±0.01 $^{¥}$	79.74 ±1.75 $^{¥}$	-26.32 ± 0.06 $^{¥}$	8.79 ± 0.10	0.72 ± 0.01 $^{¥}$	1.04 ± 0.01 $^{¥}$
ITA	13.73 ± 1.19 ^{b}	0.21 ± 0.03 ^{b}	84.71 ± 9.05 ^{a}	-27.06 ± 0.13 ^{b}	9.95 ± 0.46 ^{a}	0.69 ± 0.01 ^{b}	1.17 ± 0.01 ^{a}
CVC	17.89 ± 1.12 ^{a}	0.26 ± 0.02 ^{ab}	73.96 ± 3.08 ^{bc}	-26.36 ± 0.15 ^{a}	8.83 ± 0.18 ^{b}	0.69 ± 0.01 ^{b}	0.75 ± 0.01 ^{b}
BAL	16.70 ± 0.47 ^{a}	0.23 ± 0.01 ^{b}	80.19 ± 1.79 ^{ab}	-26.20 ± 0.07 ^{a}	8.60 ± 0.10 ^{b}	0.72 ± 0.01 ^{a}	1.07 ± 0.01 ^{a}

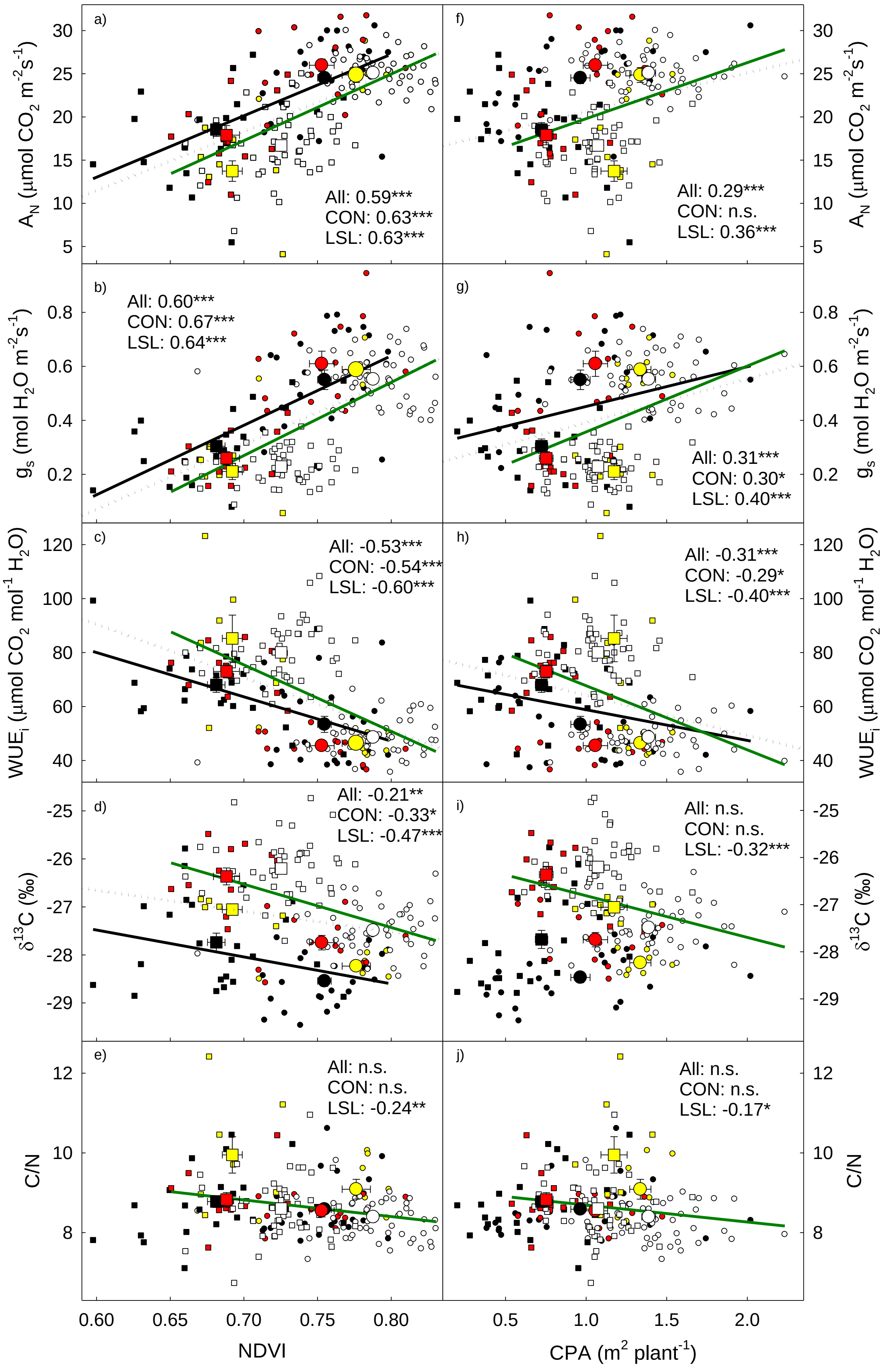
a)
All: 0.59***
CON: 0.63***
LSL: 0.63***
b)
All: 0.60***
CON: 0.67***
LSL: 0.64***
c)
All: -0.53***
CON: -0.54***
LSL: -0.60***
d)
All: -0.21**
CON: -0.33*
LSL: -0.47***
e)
All: n.s.
CON: n.s.
LSL: -0.24**
f)
All: 0.29***
CON: n.s.
LSL: 0.36***
g)
All: 0.31***
CON: 0.30*
LSL: 0.40***
h)
All: -0.31***
CON: -0.29*
LSL: -0.40***
i)
All: n.s.
CON: n.s.
LSL: -0.32***
j)
All: n.s.
CON: n.s.
LSL: -0.17*
A_N (µmol CO_2 $m^{-2}s^{-1}$)
g_s (mol H_2O $m^{-2}s^{-1}$)
WUE_i (µmol CO_2 mol^{-1} H_2O)
$\delta^{13}C$ (‰)
C/N
30
25
20
15
10
5
0.8
0.6
0.4
0.2
120
100
80
60
40
-25
-26
-27
-28
-29
12
10
8
0.60
0.65
0.70
0.75
0.80
NDVI
0.5
1.0
1.5
2.0
CPA (m^2 $plant^{-1}$)

Figure 2. Relationship between normalized difference visible index (NDVI) and a) net CO_2 assimilation rate (A_N), b) stomatal conductance (g_s), c) intrinsic water-use efficiency (WUE_i), d) leaf carbon isotope composition ($\delta^{13}C$) and e) leaf nitrogen to carbon ratio (C/N); and between canopy projected area (CPA) and f) net CO_2 assimilation rate (A_N), g) stomatal conductance (g_s), h) intrinsic water-use efficiency (WUE_i), i) leaf carbon isotope composition ($\delta^{13}C$) and j) leaf nitrogen to carbon ratio (C/N). Dots refer to well-watered (WW) and squares to water deficit (WD) conditions for each of the genotypes. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Big-sized symbols indicate the genotype group average value ± SE. See Table 1 for group abbreviations and *n* specifications. Regression lines are shown when significant, where dotted black line represents the regression analysis considering all genotypes and treatments, black line the regression analysis considering only CON and green line considering only LSL genotypes. Pearson's correlation coefficient (r) is indicated, and asterisks mean significance level at * $P \leq 0.05$, ** $P \leq 0.01$ or ***$P \leq 0.001$; n.s. refers to non-significant.

Table 3. Pearson's correlation coefficients (r) between simple ratio (SR) and green normalized difference vegetation index (GNDVI) and ground-based physiologic measurements when considering all genotypes and treatments together (All), only control genotypes (CON) and only long-shelf life genotypes (LSL). See Table 1 for *n* specification for each group. Significant correlations are highlighted in bold. Also, the significance level is indicated as: * *P*-value ≤ 0.05, ** *P*-value ≤ 0.01 and *** *P*-value ≤ 0.001.

		A_N	g_s	WUE_i	$\delta^{13}C$	C/N
SR	All	**0.65*** **	**0.68*** **	**-0.61*** **	**-0.3*** **	**-0.19** **
	CON	**0.67*** **	**0.73*** **	**-0.59*** **	**-0.35* **	0.03
	LSL	**0.68*** **	**0.7*** **	**-0.66*** **	**-0.52*** **	**-0.26** **
GNDVI	All	**0.58*** **	**0.58*** **	**-0.51*** **	**-0.17* **	**-0.19* **
	CON	**0.62*** **	**0.7*** **	**-0.58*** **	**-0.31* **	-0.03
	LSL	**0.61*** **	**0.59*** **	**-0.54*** **	**-0.39*** **	**-0.24** **

Table 4. Differences in fruit production, total soluble solids (TSS) and acidity for the different genotype groups under well-watered (WW) and water deficit (WD) conditions. Data are means ± S.E. See Table 1 for *n* specifications and group abbreviations. Letters denote significant differences between groups within treatments, asterisks between treatments for each group and ¥ between CON and LSL for each treatment by one-way ANOVA after Duncan *post-hoc* test (*P*-value < 0.05).

	Fruit production g plant^{-1}	TSS °Brix	Acidity % citric acid
WW			
CON	3214.7 ± 265.4 ^{b*}	4.56 ± 0.19 ^{c*}	0.80 ± 0.07 ^{c*}
LSL	2886.9 ± 152.4	5.01 ± 0.07 $^{¥}$	1.07 ± 0.03 $^{¥}$
ITA	4912.0 ± 576.5 ^{a*}	5.98 ± 0.22 ^{a*}	0.91 ± 0.06 ^{bc}
CVC	1804.9 ± 306.4 ^{c}	5.16 ± 0.25 ^{b}	1.17 ± 0.08 ^{a}
BAL	2793.4 ± 164.5 ^{b*}	4.83 ± 0.06 ^{bc*}	1.09 ± 0.03 ^{ab}
WD			
CON	2232.6 ± 179.0 ^{b}	5.92 ± 0.29 ^{b}	1.08 ± 0.07 ^{a}
LSL	2276.4 ± 118.1	5.88 ± 0.10	1.10 ± 0.03
ITA	3523.8 ± 346.9 ^{a}	7.20 ± 0.31 ^{a}	0.98 ± 0.09 ^{b}
CVC	1478.2 ± 227.5 ^{c}	5.72 ± 0.26 ^{b}	1.01 ± 0.08 ^{a}
BAL	2245.2 ± 137.6 ^{b}	5.67 ± 0.10 ^{b}	1.13 ± 0.03 ^{a}

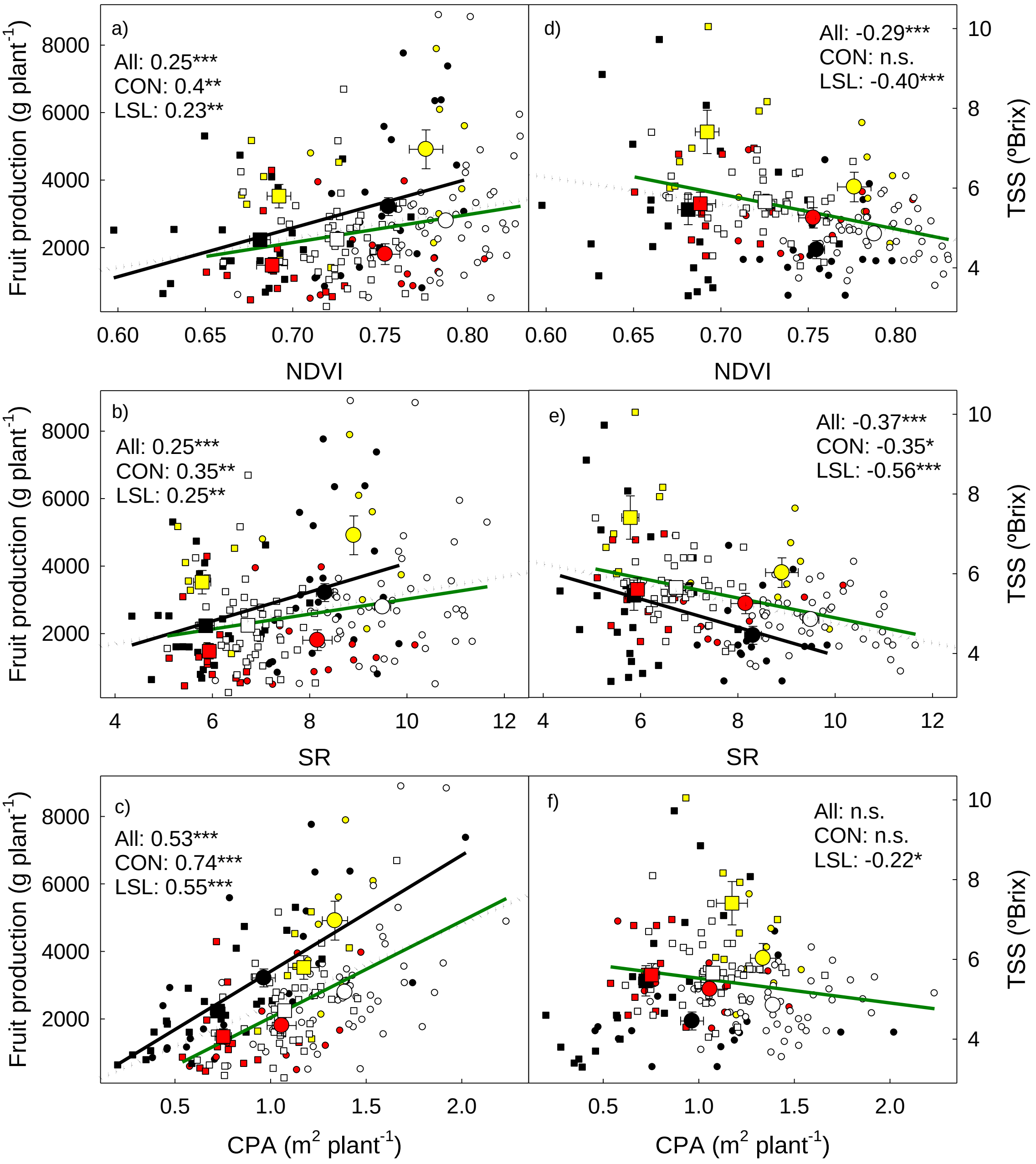

Figure 3. Relationship between fruit production (g plant^{-1}) and a) normalized difference visible index (NDVI), b) simple ratio (SR) and c) canopy projected area (CPA); and between total soluble solids (TSS) and d) normalized difference visible index (NDVI), e) simple ratio (SR) and f) canopy projected area (CPA). Dots refer to well-watered (WW) and squares to water deficit (WD) conditions. Dots refer to well-watered (WW) and squares to water deficit (WD) conditions for each of the genotypes. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Big-sized symbols indicate the genotype group average value ± SE. See Table 1 for group abbreviations and *n* specifications. Regression lines are shown when significant, where dotted black line represents the regression analysis considering all genotypes and treatments, black line the regression analysis considering only CON and green line considering only LSL genotypes. Pearson's correlation coefficient (r) is indicated, and asterisks mean significance level at * P≤0.05, ** P≤0.01 or ***P≤0.001; n.s. refers to non-significant

Supplementary Information

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

Genotype group	**Variety name**	**Seed origin**
Control	M82	HUJ
Control	OH-8245	UIB
Control	Marmande	HUJ
Control	Santorini	HUJ
Control	San Marzano	HUJ
Control	Pera Girona	HUJ
Control	Monalbo	UN
Control	N182	UN
Control	770P	UN
Control	990 P	UN
Control	22/030-1	UN
Control	Tramatticasa tundasa	US
Control	Tamatta sarda	US
Control	Tamatta groga	US
Control	DZ 88	HUJ
Control	IL12-4	UN
Control	B22	UN
Control	N176	UN
Control	N178	UN
Control	N179	UN
Control	N181	UN
Control	N201	UN
Control	N202	UN
LSL-ITA	Da Serbo	HUJ
LSL-ITA	Piennolo Rosso	HUJ
LSL-ITA	Vesuvio Foglia Riccia	UN
LSL-ITA	Vesuviano	UN
LSL-ITA	Corbarino MT/Crovarese Semiorto	UN
LSL-ITA	Lucariello	UN
LSL-ITA	Principe Borghese Selezione SAIS (IVALSA)	UN
LSL-CVC	Penjar-Catalonia	COMAV
LSL-CVC	Penjar-Catalonia	COMAV
LSL-CVC	Penjar-Catalonia	COMAV
LSL-CVC	Penjar-Catalonia	COMAV
LSL-CVC	Penjar-Catalonia	COMAV
LSL-CVC	Penjar-Catalonia	COMAV
LSL-CVC	Penjar-Valencia	COMAV
LSL-CVC	Penjar-Valencia	COMAV
LSL-CVC	Penjar-Valencia	COMAV
LSL-CVC	Penjar-Valencia	COMAV
LSL-CVC	Penjar-Valencia	COMAV
LSL-CVC	Penjar-Valencia	COMAV
LSL-BAL	Ramellet	UIB

LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
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LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Ramellet	UIB
LSL-BAL	Commercial Ramellet ("Palamós")	UIB
LSL-BAL	Commercial Ramellet ("Ariany")	UIB
LSL-BAL	Commercial Ramellet ("Palamós") GRAFTED ON commercial rootstock ("Emperador")	UIB

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

Week	ET_o ($l\ m^{-2}$)	K_c
21/06 to 29/06	53.19	0.6
30/06 to 06/07	49.03	0.6
07/07 to 13/07	43.71	0.9
14/07 to 20/07	39.82	1.15
21/07 to 28/07	37.63	1.15
29/07 to 4/08	36.02	1.15
05/08 to 11/08	35.35	1.15
12/08 to 18/08	32.14	1.15
19/08 to 25/08	35.04	1.15
26/08 to 01/09	34.96	1.15
02/09 to 08/09	16.74	1.15
09/09 to 15/09	23.87	1.15
16/09 to 22/09	18.73	1.15
23/09 to 29/09	21.61	1.15
30/09 to 06/10	18.93	1.15

Table S3. Pearson's correlation coefficients (r) between aerial and agronomic measurements when considering all genotypes and treatments together (All), only control genotypes (CON) and only long-shelf life genotypes (LSL). See Table 1 for *n* specification for each group. Significant correlations are highlighted in bold. Also, the significance level is indicated as: * *P*-value ≤ 0.05, ** *P*-value ≤ 0.01 and *** *P*-value ≤ 0.001.

		Fruit production	TSS	Acidity
NDVI	All	**0.25*** **	**-0.29*** **	-0.02
	CON	**0.4** **	-0.28	-0.23
	LSL	**0.23** **	**-0.4*** **	-0.05
CPA	All	**0.53*** **	0.01	0.06
	CON	**0.74*** **	0.26	0.22
	LSL	**0.55*** **	**-0.22* **	**-0.18* **
SR	All	**0.25*** **	**-0.37*** **	-0.07
	CON	**0.35* **	**-0.35* **	-0.27
	LSL	**0.25** **	**-0.56*** **	-0.09
GNDVI	All	**0.24** **	**-0.34*** **	-0.06
	CON	0.27	-0.3	-0.24
	LSL	**0.27** **	**-0.46*** **	-0.1

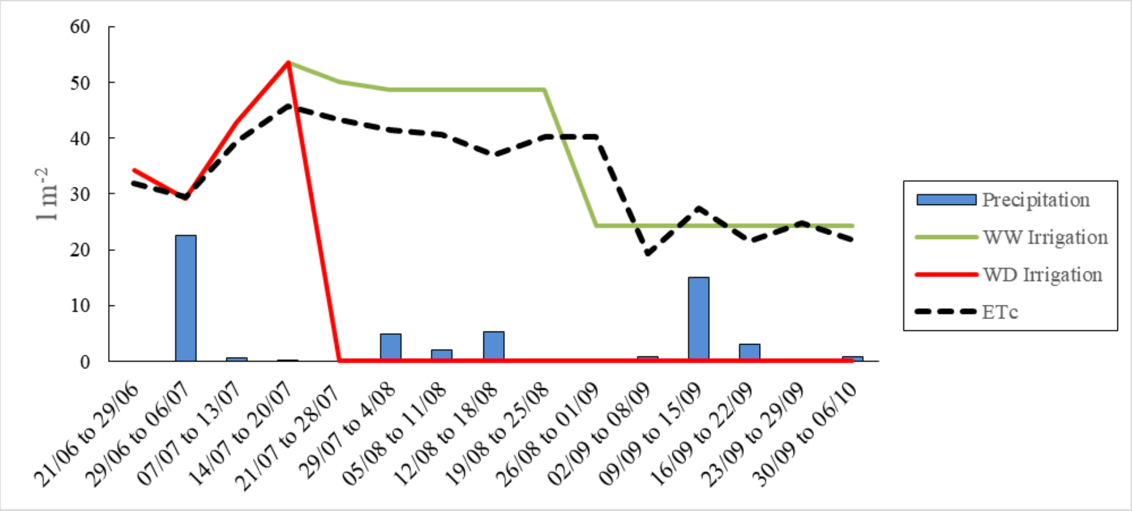

Figure S1. Weekly values for precipitation, irrigation in WW and WD blocks and the crop evapotranspiration (ET_c) over all the growing season

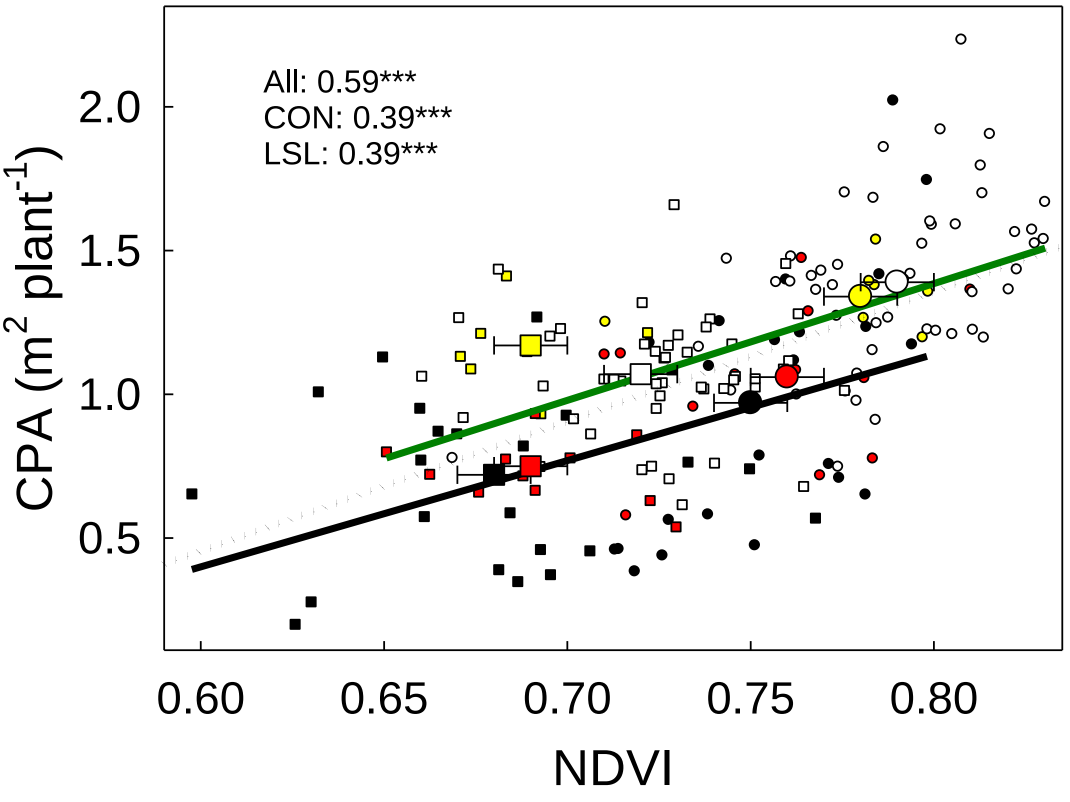

Figure S2. Relationship between canopy projected area (CPA) and normalized difference visible index (NDVI). Dots refer to well-watered (WW) and squares to water deficit (WD) conditions. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Dots refer to well-watered (WW) and squares to water deficit (WD) conditions for each of the genotypes. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Big-sized symbols indicate the genotype group average value ± SE. See Table 1 for group abbreviations and *n* specifications. Regression lines are shown when significant, where dotted black line represents the regression analysis considering all genotypes and treatments, black line the regression analysis considering only CON and green line considering only LSL genotypes. Pearson's correlation coefficient (r) is indicated, and asterisks mean significance level at * P≤0.05, ** P≤0.01 or ***P≤0.001; n.s. refers to non-significant.

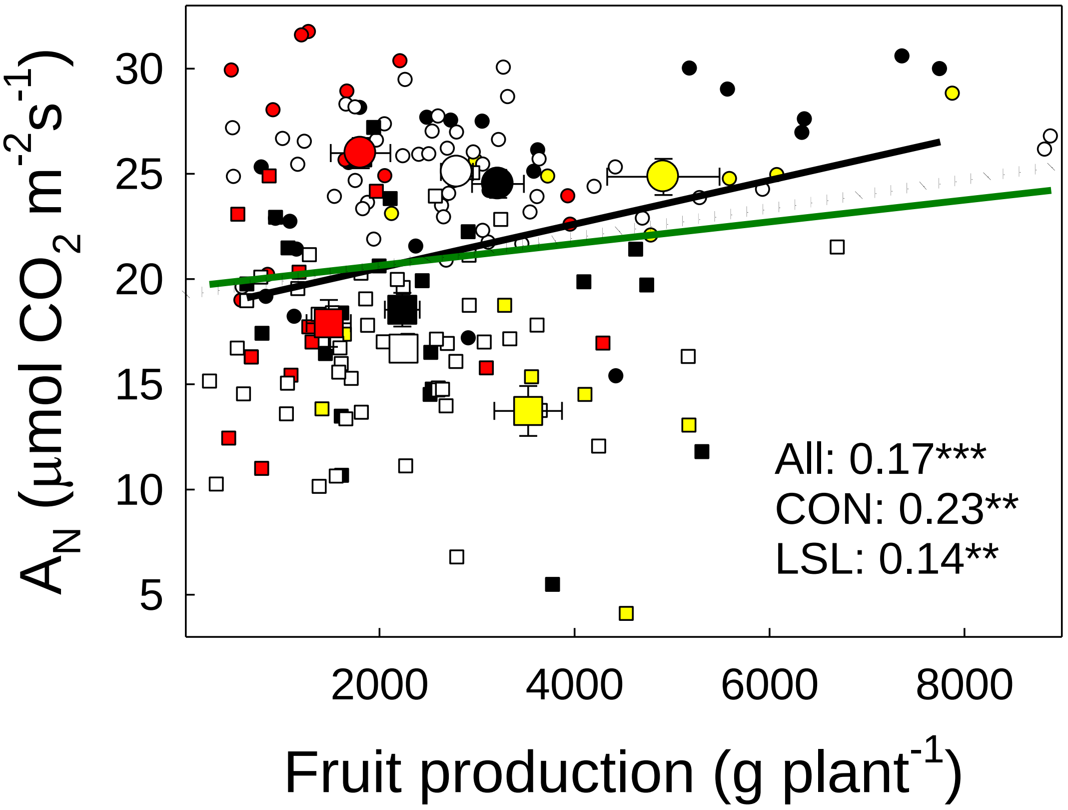

Figure S3. Relationship between fruit production (g $plant^{-1}$) and net CO_2 assimilation rate (A_N). Dots refer to well-watered (WW) and squares to water deficit (WD) conditions. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Major symbol indicate the genotype group average value ± SE. Dots refer to well-watered (WW) and squares to water deficit (WD) conditions for each of the genotypes. Black symbols refer to CON, yellow to ITA, red to CVC and white to BAL. Big-sized symbols indicate the genotype group average value ± SE. See Table 1 for group abbreviations and *n* specifications. Regression lines are shown when significant, where dotted black line represents the regression analysis considering all genotypes and treatments, black line the regression analysis considering only CON and green line considering only LSL genotypes. Pearson's correlation coefficient (r) is indicated, and asterisks mean significance level at * P≤0.05, ** P≤0.01 or ***P≤0.001; n.s. refers to non-significant.

Chapter 4

Use of grafting as an alternative to traditional breeding to improve Mediterranean landraces

Chapter 4.1.

The influence of grafting on crops' photosynthetic performance

M. Fullana-Pericàs[1], M.À. Conesa[1], F. Pérez-Alfocea[2], J. Galmés[1]*

[1] Research Group on Plant Biology under Mediterranean Conditions-INAGEA, Universitat de les Illes Balears, Balearic Islands

[2] Centro de Edafología y Biología Aplicada del Segura (CEBAS-CSIC), Department of Plant Nutrition, Campus Universitario de Espinardo, E-30100, Murcia

* Corresponding author

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Chapter 4.2.

Changes in yield, growth and photosynthesis in a drought-adapted Mediterranean tomato landrace (*Solanum lycopersicum* ‘Ramellet’) when grafted onto commercial rootstocks and *Solanum pimpinellifolium*

M. Fullana-Pericàs[1+], J. Ponce[1+], M.À. Conesa[1], A. Juan[2], M. Ribas-Carbó[1], J. Galmés*

[1] Research Group on Plant Biology under Mediterranean Conditions-INAGEA, Universitat de les Illes Balears, Balearic Islands

[2] Direcció General d’Agricultura i Ramaderia, Conselleria de Medi Ambient, Agricultura i Pesca, Govern de les Illes Balears, C/Reina de la Constança 4, 07006 Palma

* Corresponding author

[+] These authors contributed equally to the work

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Chapter 4.3.

The use of a tomato landrace as rootstock improves the response of commercial tomato under water deficit conditions

M. Fullana-Pericàs[1]*, M.À. Conesa[1], M. Ribas-Carbó[1], J. Galmés[1]

[1] Research Group on Plant Biology under Mediterranean Conditions-INAGEA, Universitat de les Illes Balears, Balearic Islands, Spain

* Corresponding author

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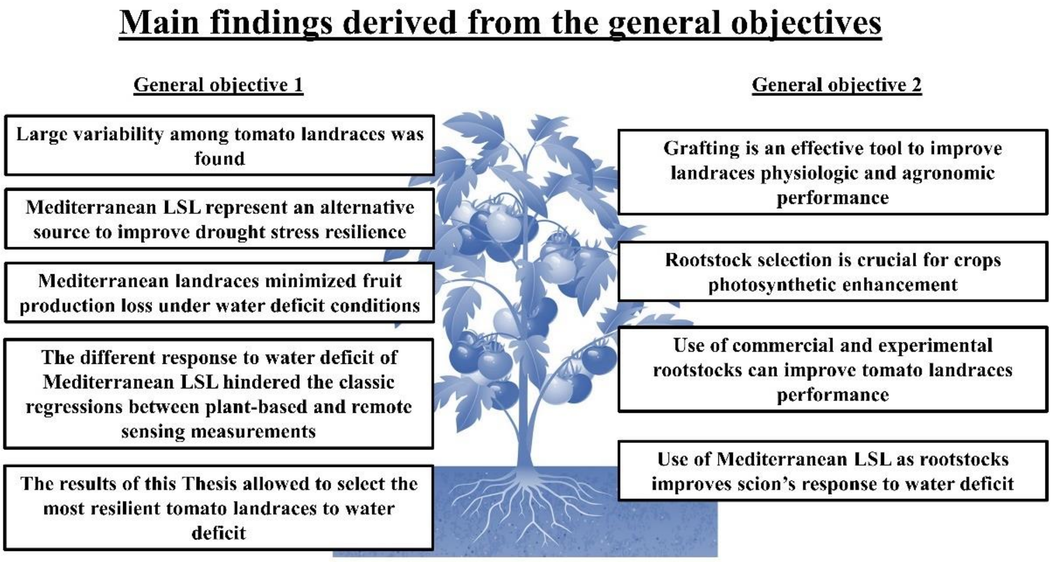
Chapter 5

General Discussion

The results of this Thesis have been structured in two chapters (Chapters 3 and 4). Each of the chapters contain different published or in preparation articles that deal with the general and secondary objectives (see ‘Publication list’ section in page “v” of the present Thesis for details). Since the findings are extensively discussed in each article, for proper discussion and specific answers to general and specific objectives, readers are addressed to the Discussion section in each article. Therefore, the present chapter provides an integrated overview of the most relevant findings of the Thesis, highlighting the main outcomes related to the objectives, which have been schematically represented in Figure 5.1, and are detailed in the following sections.



Large variability among tomato landraces was found

Mediterranean LSL represent an alternative source to improve drought stress resilience

Mediterranean landraces minimized fruit production loss under water deficit conditions

The different response to water deficit of Mediterranean LSL hindered the classic regressions between plant-based and remote sensing measurements

The results of this Thesis allowed to select the most resilient tomato landraces to water deficit

Grafting is an effective tool to improve landraces physiologic and agronomic performance

Rootstock selection is crucial for crops photosynthetic enhancement

Use of commercial and experimental rootstocks can improve tomato landraces performance

Use of Mediterranean LSL as rootstocks improves scion’s response to water deficit

Figure 5.1. Schematic representation of the main findings of this Thesis. The left boxes contain the main findings related with the General Objective 1 (and derived Specific Objectives 1, 2, 3 and 4), while the right boxes refer to the main findings related with the General Objective 2 (and derived Specific Objectives 5, 6 and 7).

5.1. The variability among Mediterranean tomato landraces represents a unique source to improve tomato drought resilience

Human population diet is mainly based on 12 crops, and barely more than 150 species are nowadays cultivated. Modern agriculture system prioritizes genotypes that can be widely cultivated, with uniform production patterns and high yield rates (Dwivedi et al., 2016; Esquinas-Alcázar, 2005; Frison et al., 2011). This mono-cropping system leads to a progressive agricultural biodiversity loss that threatens landraces variability. Landraces are heterogeneous genotype collections that have been selected in a certain ecogeographical area, adapted to its edaphic and climatic conditions, and linked to traditional management and uses (Casañas et al., 2017; Zeven, 1998). Hence, landraces represent the effort and work done during centuries to select and maintain genotypes with particular traits that allow them to be cultivated under specific biotic and abiotic stress conditions (Corrado and Rao, 2017). Consequently, the genetic erosion of landraces causes an important loss of unique gene combinations that can be used to improve crops’ biotic and abiotic resistance and/or tolerance to stress.

Along millennia, the Mediterranean basin has been the scenario of different civilizations and cultures, which cultivated their main staple foods and selected genotypes to grow under Mediterranean conditions. Mediterranean climate is generally defined by mild wet winters and warm to hot, dry summers (Lionello et al., 2006). Consequently, those crops selected for centuries under these conditions retained traits allowing to overcome many environmental-related stresses. For instance, several QTL's associated to the maintenance of yield under extreme drought, salt and high temperature stresses have been identified and mapped in Mediterranean barley and wheat landraces (Dwivedi et al., 2016). The Mediterranean basin has also been an important diversification point for several vegetables like aubergine (Cericola et al., 2013), pepper (Taranto et al., 2016), artichoke (Mauro et al., 2009) and tomato (Cebolla-Cornejo et al., 2007). Different to cereals, vegetables are mostly irrigated crops with significantly higher water consumption (Mekonnen and Hoekstra, 2011). Hence, identification of drought related traits in vegetables could be more challenging than in other rainfed crops. In fact, although several genes and metabolic processes in vegetable crops have been identified and related to drought tolerance mechanisms, there is still a long way to understand the regulation of all these pathways and to know how to effectively introduce them in vegetable germplasm to enhance drought resilience under commercial conditions (Gerszberg and Hnatuszko-Konka, 2017; Gong et al., 2010; Zhuang et al., 2014).

As exposed in the General Introduction chapter, along the numerous tomato landrace collections found in the Mediterranean basin, several landrace genotypes have been identified as drought resilient. This trait is in general the product of unconscious selection resulting from intrinsic selection of the plants able to produce under the stressful Mediterranean summer conditions, and the man-mediated selection of the most productive plants, which under stress may correspond to the most stress-adapted genotypes. In this Thesis, where a large number of Mediterranean tomato landraces have been studied under both well-watered (WW) and water deficit (WD) conditions, large variability has been found in leaf morphology and photosynthetic parameters among these genotypes. For some traits, this is magnified under stressful conditions. For instance, under WW conditions the variability in leaf nitrogen content (Leaf N) and leaf mass per area (LMA) was 2-fold, and 4-fold in net CO_2 assimilation rate (A_N) and stomatal conductance (g_s). Under WD conditions, variability in Leaf N and LMA was similar to WW, but it turned to 7-fold in A_N and g_s (Chapters 3.3. and 3.4.). It has been demonstrated that some parameters can be less variable or more resilient to change than others (Flexas et al., 2012; Wright et al., 2004). However, the obtained results suggest that the unconscious selection performed in Mediterranean tomato landraces has not been uniform along the Mediterranean basin. Probably, selection for different traits, with different selective pressure, and under variable conditions in each specific region, as different drought intensities, soil conditions and extreme temperatures among others, led to that large variability in physiologic parameters.

In many Mediterranean landraces, this selection has been performed in convergence with the long shelf-life (LSL) fruit phenotype. To some extent, this has been also unconscious in regions like the Balearic Islands, due to planting seed of the last fruits remaining for consumption, thus selecting genotypes with the longest shelf-life. Moreover, a different physiologic and agronomic behaviour between non-LSL and LSL drought resilient Mediterranean genotypes has been observed in the present Thesis, also having a different response to water deficit. In this sense, the three main locations in the Mediterranean basin previously identified as rich in tomato LSL landraces (Bota et al., 2014; Casals et al., 2012; Tranchida-Lombardo et al., 2018) have been screened: the Balearic Islands, West-Iberian Peninsula (Catalonia and the Valencian Country), and Southern-Italian Peninsula (including Sicily). The Table 5.1. summarizes the differences found in this Thesis among LSL landraces, depending on their origin and under WW and WD, for the different physiologic and agronomic parameters measured.

Table 5.1. Significant (YES) and non-significant (NO) differences among tomato Mediterranean LSL landraces depending on their origin location (the Balearic Islands, Catalonia and the Valencian Country, and southern-Italian Peninsula inlcuding Sicily) for the main physiologic and agronomic parameters measured in this Thesis under well-watered (WW) and water deficit (WD) conditions after a one-way ANOVA (*P* < 0.05). For parameters abbreviations see 'Symbols and abbreviations' section in page 'iii' of the present Thesis. NA means that the parameter was not tested under that treatment.

	Parameter	WW	WD
Leaf morphology	LA	YES	YES
	LMA	YES	YES
Leaf composition	$\delta^{13}C$	YES	YES
	Leaf N	YES	YES
	C/N	YES	YES
Leaf gas-exchange	A_N	NO	YES
	g_s	NO	NO
	WUE_i	NO	YES
	ΦPSII	NO	YES
	g_m	NO	NA
	g_m/g_s	NO	NA
	V_{cmax}	NO	NA
Whole-plant parameters	NDVI	YES	YES
	CPA	YES	YES
Agronomic traits	Fruit production	YES	YES
	Fruit weight	YES	YES
	Fruit number	YES	YES
	TSS	YES	YES
	Acidity	YES	YES

Differences in leaf morphology have been found under WW and WD conditions (Table 5.1.). In fact, both "tomato-leaf" (with five to nine homogeneous leaflets) and "potato-leaf" (with large trilobate terminal leaflet and two smaller leaflets) morphologies can be found in a single LSL landrace collection (as the 'de Penjar' or 'de Ramellet' landraces) (Galmés et al., 2011; Kessler et al., 2001; Ochogavía et al., 2011). Despite leaf anatomy has not been explored in the present Thesis, in the 'de Ramellet' LSL landrace, Galmés et al. (2013) related the increased water-use efficiency (WUE) under water deficit to changes in leaf anatomy, which led to an increased chloroplast area facing the mesophyll aerial spaces. However, this behaviour has not been reported in other Mediterranean landraces.

Under drought, plants close stomata partially or totally to avoid water loss, with a consequent reduction in A_N. However, maintenance of high photosynthetic rates during stomatal closure periods would lead to an increased intrinsic water-use efficiency (WUE_i). All LSL genotypes screened in this Thesis have very similar photosynthetic potential, i.e., similar values under WW conditions. However, as described in Chapter 3.4., under WD, genotypes from the Italic Peninsula and Sicily had lower A_N than landraces from the Balearic Islands and from Catalonia and the Valencia Country, with no significant differences in g_s. Similarly, differences under WD depending on the origin have been also found for leaf carbon isotope composition ($\delta^{13}C$), indicating the possibility of a different g_s behaviour among such landraces. This apparent incongruence between measurements of g_s and $\delta^{13}C$ (Table 5.1) suggests that differences do not exist at specific moments during the day, but may exist when considering the whole-day g_s. Aside of g_s¸ the mesophyll conductance (g_m) has been proposed as a key parameter defining plants photosynthetic performance and WUE (Flexas et al., 2013). Despite increases in g_m result in enhanced A_N, if they are not followed by a reduction or maintenance of g_s those changes may not be translated in higher WUE_i. In this Thesis, it has been observed that under WW conditions, Mediterranean tomato landraces' A_N was limited by diffusive parameters (stomatal conductance, mesophyll conductance and the combination of both) rather than by biochemical parameters. Moreover, increased g_m/g_s ratio is related to an increased WUE_i when plants are cultivated under WW conditions (Chapter 3.2.).

Unfortunately, no further bibliography is available about the underlying causes of the changes in leaf anatomy in the 'de Ramellet' landrace, and about the different physiologic behaviour under drought stress in Mediterranean landraces. Future research should focus on unravelling if these adaptations are linked to hormonal signalling, in which are the genes involved, and in exploring if other LSL-landraces developed similar strategies to increase WUE under drought periods.

The existence of different behaviours to face drought episodes described above would have implications to assess the common relationships between physiologic parameters, and the use of remote sensing to predict plant response to drought stress and fruit production. Nowadays, it is still not clear if, for the same crop, it is possible to create an universal regression model relating plant-level and remote sensing measurements valid for different locations and years (Maes and Steppe, 2018). In this Thesis, significant relationships between leaf-level physiologic and remote sensing measurements have been described (Chapter 3.4.). However, different regression models resulted depending on the observed genotype, based on their different leaf-level physiologic behaviour. Such different behaviour challenged modelling the response to WD in the screened genotypes, and the detection of the most resilient genotypes, through remote sensing. For instance, the genotypes LSL-L59, (from the Catalonia and Valencian Country group), LSL-L47 (from the Balearic Islands group) and BIG-M1 (a modern genotype) (codes in accordance with Chapter 3.3.), had similar NDVI values, but significantly different $\delta^{13}C$, A_N and/or fruit production. Considering that $\delta^{13}C$ did not efficiently predict fruit production under WW and WD conditions, but determined the maximum fruit production of a genotype (Chapter 3.3.), and considering the existence of different relationships between leaf-level physiologic and remote sensing parameters when considering large genotype groups (Chapter 3.4.), the results obtained in this Thesis point to a combination of leaf-level physiologic and remote sensing high-throughput measurements to not miscalculate remote sensing outputs and to reliably detect the most resilient genotypes to WD.

In this Thesis, weak or no correlation has been found between fruit production and A_N (Chapters 3.4 and 4.2). While some authors described a positive relationship between A_N and fruit production (Galmés et al., 2011; Zhu et al., 2012), other authors stated that increases in photosynthetic rates do not necessarily lead to increases in fruit production (de Oliveira Silva et al., 2018; Rossi et al., 2015). The lack of correlation could be derived from the different photosynthetic behaviour previously explained (Table 5.1.), but also from the large fruit shape and size diversity found among Mediterranean landraces (Chapters 3.1 and 3.3.). In fact, important differences in composition have been previously described in Mediterranean landraces and are related to the variability in fruit types (Casals et al., 2015; Causse et al., 2010; Figàs et al., 2018, 2015a, 2015b). That variability in fruit morphology also determined genotypes’ fruit production. Moreover, the fruit type partially drove the genotypes’ response to WD, being the reduction in fruit production lower in those genotypes with higher fruit number and lower fruit weight (Chapter 3.3.). Also, differences have been observed in fruit quality depending on genotypes’ fruit type and origin (Chapters 3.3. and 3.4.). Hence, the results in this Thesis do not only suggest that Mediterranean LSL tomato landraces’ response to WD is different depending on their origin, but also confirm differences in their fruit quality, probably derived from the final use of their fruit in the region, which is also variable. In consequence, the LSL phenotype seems to be unlinked to fruit quality, allowing for diverse fruit quality traits across LSL genotypes and even within a single landrace collection (Chapters 3.1., 3.3. and 3.4.).

Far from being an obstacle for crop improvement, the large variability in fruit morphology and quality found among drought-resilient landraces represents an exceptional opportunity for breeders to improve tomato drought resilience. While wild relatives, with small, non-edible and (usually) green fruits, might carry undesirable characteristics linked to drought tolerant traits (Foolad, 2007; Silva Dias, 2014), the inclusion of Mediterranean landraces in breeding programs would allow breeders to select those genotypes with fruit shapes and sizes more similar to the genotype to be improved as gene donors, avoiding the introduction of unwanted, pleiotropic traits from wild species, and reducing the number of backcrosses required to recover the desired fruit morphology and quality.

Despite of the different behaviours described in this section among the studied drought-resilient Mediterranean landraces, several general relationships can be depicted among leaf, whole-plant, and fruit-related parameters. Thus, the Figure 5.2. summarizes the general relationships among the main physiologic and agronomic parameters that resulted from this Thesis.

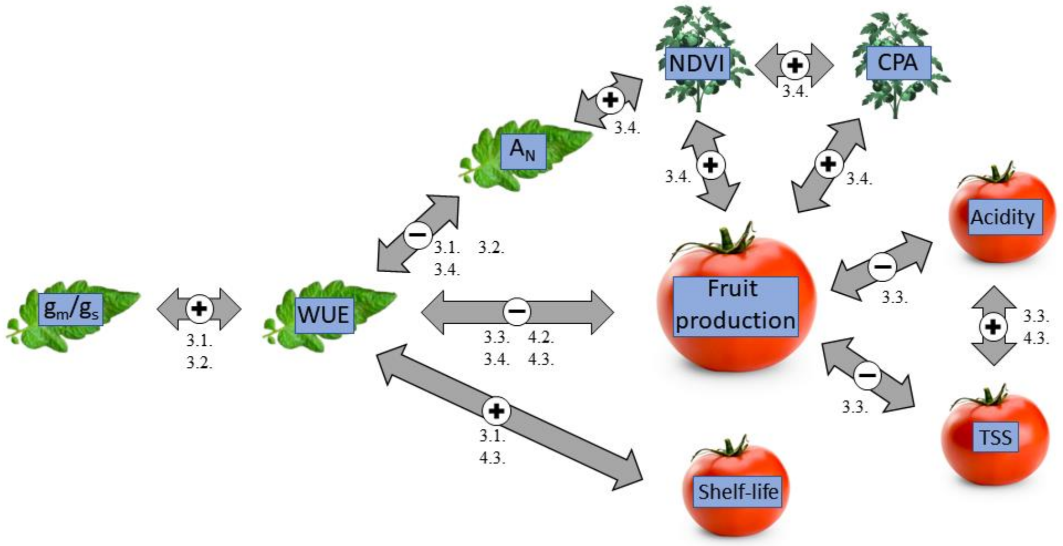


Figure 5.2. Schematic diagram of the relationships among the main physiologic and agronomic parameters, at leaf, whole-plant, and fruit level found in drought-resilient Mediterranean landraces in this Thesis. They are indicated by representing leaf, plant and fruit icons, respectively. Positive (+) symbols inside arrows indicate a positive correlation and negative (-) symbols a negative correlation. The absence of arrows between contiguous parameters mean that no correlation was found. The numbers below arrows indicate the chapter section of this Thesis where the extended discussion of the relationship can be found. For parameters abbreviations, see ‘Symbols and abbreviations’ section in page ‘iii’ of the present Thesis.

5.2. The use of Mediterranean landraces as scion or rootstock to improve tomato drought resilience

The identification of those genes responsible for particular plant and fruit traits for most vegetable crops, and the continuous improvement of gene editing technology in recent decades, have improved and accelerated molecular breeding (reviewed in Hao et al. 2020). However, breeding programs usually require large numbers of lines to evaluate, select, recombine and inbreed to be successful and to genetically fix the desired traits, which is time and resource consuming (Silva Dias, 2014). Alternatively, vegetable grafting has been found as an easy and quick technique to improve crop agronomic performance under different cultivation conditions, allowing to break many genetic and sexual barriers difficult to overcome in breeding programs (King et al., 2010). The high effectiveness of grafting to overcome biotic stresses has popularized its use all over the world (Lee and Oda, 2002; Lee et al., 2010; Louws et al., 2010). For instance, several rootstocks reducing the incidence of biotic stresses as fungal, bacterial or nematode infections in tomato have been found (Keatinge et al., 2014; Louws et al., 2010; Singh et al., 2017).

However, not only in tomato but also in other horticultural crops like pepper and aubergine, there are no available commercial rootstocks conferring notorious tolerance to abiotic stresses. Considering that drought and saline stresses are major limitations in agriculture, exploring the use of experimental rootstocks has become a prime (Iacono et al., 1998; López-Marín et al., 2017; Nilsen et al., 2014). Chapter 4.1. of this Thesis presents a compilation of the effects of grafting and the use of different rootstocks to overcome the deleterious effect of abiotic stresses over photosynthetic performance in different species. It shows that the use of specific rootstocks can increase the protection of the reaction center of PSII, while other rootstocks increase the expression of Rubisco-related genes, resulting in improved photosynthetic performance. In general, grafting has the capability to act on different biophysical and biochemical processes in the scion. Despite the huge amount of available information in scientific literature about the scion-rootstock interactions, there are still important gaps to be filled, particularly those regarding the response of grafted plants to water stress. Sánchez-Rodríguez et al. (2012) found that the scion antioxidant response to water deficit was determined by the used scion and not by the rootstock. Moreover, Penella et al. (2017a) highlighted that higher tolerance to both salt and drought stresses in pepper plants grafted onto a non-commercial rootstock and onto two pepper wild species was related to the capacity of those rootstocks to reduce Na^+ allocation to scion leaves, and to their deeper and more vigorous roots. Similarly, Weng (2000) associated the increased photosynthetic rate of tomato grafted onto a wild *Solanum* species (*S. mammosum* L.) under water deficit conditions to the increased water uptake ability.

In the present Thesis, differences in plant growth, physiologic and agronomic traits have been found between non-grafted and plants grafted onto different rootstocks, indicating the potential of grafting to modify scion performance depending on the used rootstock (Table 5.2.). In the two ‘de Ramellet’ landraces and the commercial ‘de Ramellet’ genotype screened in this Thesis, no major differences have been found between non-grafted and self-grafted plants, with the exception of some traits related to scion growth vigour and fruit quality (Chapters 4.2. and 4.3.). The lack of differences between non-grafted and self-grafted vegetables in leaf morphology, leaf gas-exchange and fruit production parameters has been partially explained by the high compatibility between scion and rootstock (Kawaguchi et al., 2008; Penella et al., 2017b). However, the graft effect has been neglected in most reviews regarding its effect in plant growth, fruit production and fruit quality (Kumar et al., 2017; Kyriacou et al., 2017; Rouphael et al., 2010; Singh et al., 2017).

Table 5.2. Significant (YES) and non-significant (NO) differences between non-grafted and self-grafted plants (Self-grafted) and between non-grafted plants and plants grafted onto a rootstock different to the scion (Rootstock) for the main physiologic and agronomic parameters measured in this Thesis after a one-way ANOVA ($P < 0.05$). For parameters abbreviations, see 'Symbols and abbreviations' section in page 'iii' of the present Thesis.

	Parameter	Self-grafted	Rootstock
Leaf morphology and water status	LMA	NO	YES
	Ψ_{PD}	NO	NO
Leaf composition	$\delta^{13}C$	NO	NO
	Leaf N	NO	YES
Plant growth	Scion FW	YES	YES
	Max height	NO	YES
	RSE	NO	YES
	RLA	YES	YES
	Max leaves	NO	YES
Leaf gas-exchange	A_N	NO	YES
	g_s	NO	YES
	WUE_i	NO	YES
	ΦPSII	NO	NO
Agronomic traits	Fruit production	NO	YES
	Fruit weight	NO	YES
	Fruit number	NO	NO
	TSS	YES	YES
	Acidity	NO	NO
	Hardness	YES	YES
	Shelf-life	YES	YES

Therefore, the results in this Thesis endorse that grafting is a very versatile technique if considering that a single scion genotype can be "immediately" improved by grafting onto different rootstocks and vice versa, a single rootstock genotype can be used to improve different scions. This provides a wide range of options to farmers and breeders for improving their crops and to develop parallel scion and rootstock breeding programs, respectively. Particularly, when considering Mediterranean landraces, Casals et al. (2018) showed the success of the commercial rootstock 'Beaufort' (deRuiter Seeds, The Netherlands) to improve fruit production and quality in two genotypes grown under conventional and organic management systems. Similarly, Moreno et al. (2019) observed that a Mediterranean tomato landrace grafted onto different commercial rootstocks increased fruit production and lycopene content, but decreased other fruit quality traits like TSS or acidity. In this Thesis, it has been observed that intrinsic WUE_i of the 'de Ramellet' tomato landrace can be improved with no impairment in fruit production under WW conditions through grafting onto specific rootstocks (Chapter 4.2.). On the one hand, when grafted onto *S. pimpinellifolium*, two 'de Ramellet' landrace scions showed a significant WUE_i increase as compared to non- and self-grafted plants mainly due to a large reduction in g_s with no change in A_N. On the other hand, although the use of commercial rootstocks increased g_s maybe due to their vigorous root system (Oztekin et al., 2009), the increase in A_N was not proportional to that observed in g_s leading to a general decrease in their

WUE_i. Moreover, commercial rootstock g_s enhancement was not translated in an increased fruit production, but almost all commercial rootstock graft combinations had lower fruit production than non- or self-grafted plants.

Despite the general trends and responses to grafting described in this Thesis, it has been found that the same rootstock did not have the same effect onto two different scions, even when scions were very similar (Chapter 4.2.). In this sense, the large variability existing among Mediterranean landraces constitutes a handicap to overcome the interactions derived from the used rootstock, and to predict the effect of a specific rootstock on the landrace. In the present Thesis, interaction effects between scion and rootstocks when using a tomato landrace as scion have been found for plant growth, photosynthetic and fruit production traits. Further experiments screening variable genotypes within and among landraces are needed to confirm if it is possible to have a common response for landrace scions to commercial rootstocks, or which are the underlying determinants driving the contrasting behaviours in the scion-rootstock interaction involving landraces.

Aside of providing a desired trait, the only requisite for a successful graft is the rootstock-scion compatibility. When vegetable grafting started to be widely used in horticultural cropping, most of the rootstocks commercially available were not derived from breeding programs selecting for superior combinations, but proceed from pre-existing germplasm collections (King et al., 2010). In this regard, in the recent decades the private sector focused on breeds for genotypes to combine traits. Those are frequently F_1 genotypes involving a wild and a cultivated genotype, which allow easy combination of traits in a single plant, high homogeneity in the generation (i.e., differently from woody species, vegetable rootstocks are obtained from seed-planting), and allow easy protection of the rootstocks against user seed-saving. Hence, vegetable wild relatives, and very recently also landrace germplasm collections, are being explored to obtain tolerant rootstocks to biotic stresses (Colla et al., 2017; Gisbert et al., 2011a; Iwamoto et al., 2007; Lee et al., 2010). Regarding tomato, heirloom genotypes have been experimentally used as rootstocks for tomato scions (Ganiyu et al., 2018) and also for other solanaceous crops like pepper and aubergine (Gisbert et al., 2011b; Rodriguez and Bosland, 2010) to reduce the incidence of biotic stresses.

However, the use of drought-resilient tomato landraces to obtain drought tolerant rootstocks has been neglected, at least in scientific publications. In this Thesis, using a ‘de Ramellet’ landrace as experimental rootstock reduced the impact of WD over plant growth and fruit production (Chapter 4.3.). Moreover, the ‘de Ramellet’ rootstock promoted higher fruit production and fruit number than the commercial rootstock ‘Maxifort’ regardless of the water regime (WW and WD). Therefore, experimental rootstocks have the potential to be used in commercial fields, with similar agronomic performance than commercial rootstocks, and higher potential to increase the resilience to drought stress. Despite the obtained promising results, further experiments are required to confirm which particular genotypes of the ‘de Ramellet’ landrace are the most suitable candidates to be used in the obtention of commercial rootstocks. For instance, the response at different drought stress levels should be tested, decipher if the increased drought resilience is derived only from the root system or if involves a root signal expressed in the scion (e.g., leaf anatomy modifications), as well if such responses are consistent over different scions and cultivation conditions. Overall, this Thesis has shown that landraces agronomic physiologic and agronomic performance can be enhanced by grafting and, moreover, that landraces constitute a notorious germplasm resource to develop drought-resilient rootstocks.

5.3. Selection of the most resilient Mediterranean tomato landraces

Derived from the experiments in this Thesis, a large amount of physiologic and agronomic data has been produced. The main aim of such data was to provide evidences to help disentangling the underlying mechanisms of the crops' resilience under stressful conditions. It also provides tools to help agronomists and breeders to identify useful traits to easily phenotype large tomato collections. However, added to those common aims in basic research, the data in this Thesis can also be used for selecting the most resilient genotypes among the tested. Resilience allows growing with less resources, especially water, but without notorious effects on fruit production. Therefore, this last part of the General Discussion section focuses on a methodology allowing for the selection of the most resilient landraces among the tested ones, representing also a practical case study helping further researchers to deal with selection of resilient genotypes among large germplasm collections.

Crops' response to drought stress and the different strategies to overcome abiotic stress periods has been widely discussed in the published literature. Several approaches have been done to increase the knowledge about drought resilience and/or tolerance, including the effect on plant biomass (Edwards et al., 2016; Eziz et al., 2017; Kellner et al., 2019), radicular growth (Kim et al., 2020; Kulkarni et al., 2017; Wasaya et al., 2018), hormonal signalling (Jan et al., 2019; Verma et al., 2016), osmotic regulation (Blum, 2017), and leaf transpiration control (Bertolino et al., 2019; Kulkarni et al., 2017; Sinclair et al., 2004). That basic research is essential to identify drought tolerance and resilience mechanisms, but in most cases does not allow to determine the most convenient genotypes for farmers (i.e., the most productive under stress conditions). Thus, despite diverse traits related to drought tolerance and resilience have been identified in this Thesis, this section focusses only on fruit production as the key parameter to elucidate the most drought resilient tomato landrace genotypes from a grower's perspective.

An important aspect to consider when comparing diverse genotypes is the impact of management practices on their behaviour. Selection processes have also considered the optimal adaptation to the cultivation practices commonly performed, either for specific tomato varieties or in particular regions, associated to local culture. However, the most appropriate way to compare different genotypes is to grow them under the same environmental conditions and with the same management practices, despite this may suppose a deviation to optimal cultivation conditions, variable depending on the genotype (Easlon and Richards, 2009; Johansen et al., 2019; Moyle, 2008). Thus, due to the large diversity in the tomato collection tested in this Thesis, the common management system performed considered the lowest intervention possible to minimize genotypes modulation due to cultural practices, and to strengthen the observation of their genetic intrinsic capabilities. Plants had no conduction system and were not pruned. As said, despite this could be sub-optimal for specific genotypes, the fruit production obtained under WW conditions is the closest value to the maximum "genetic" fruit production capacity of these genotypes under summer Mediterranean open-field conditions, allowing for a reliable comparison among genotypes.

Another constraint when testing wide diversity of genotypes is that production *per-se*, as an absolute value, is frequently not comparable and cannot be used as a proper measure of resilience. This might not be a problem when selecting among inbreeds, introgression lines, etc. derived from very similar genotypes. Contrarily, landrace collections usually display large variability, being it much more difficult to compare. Two aspects must be considered here. First, the resilience under stress conditions, understood as a resistance to change, is better explained with a proportional value to the behaviour under non-stressing conditions rather than an absolute production value. In this sense, a resilience factor for production was calculated to facilitate the identification of genotypes that better maintained their fruit production under the WD treatment as compared to the control, WW, as follows:

$$\text{Resilience factor} = \frac{\text{WD Fruit production x 100}}{\text{WW Fruit production}}$$

Selecting genotypes based only on the resilience factor can also lead to wrong conclusions. As a mode of example, a genotype with a fruit production of 10000 g plant^{-1} under WW and 8000 g plant^{-1} under WD conditions and another producing 5000 g plant^{-1} under WW and 4000 g plant^{-1} under WD conditions, would have the same resilience factor, 80%. However, the former is doubling the fruit production of the latter, which is relevant for a grower. Therefore, the second consideration is that too different landraces or varieties may intrinsically have very different productions and thus, their performance under stress conditions may also be a reflection of that. Consequently, there is a need to do a categorization of the considered genotypes in order to avoid misinterpretation of the ranking for resilience, allowing for the selection of the most resilient genotype within each category. In the example above, it is very unlikely that such two genotypes, with 50% difference in fruit production under WW conditions, have the same genetic background. In this sense, these large differences in fruit production may be related to the fact that they correspond to very different tomato varieties, which are sometimes not clearly recognized within large landrace collections. Hence, when comparing between a cherry and a beefsteak tomato genotype, the resilience factor may have poor interest for a grower, who may decide on which kind of tomato wants to grow depending on commercial interests.

The categorization of the genotypes performed in this Thesis does not consider origin *per-se*, either geographical or related to the collection source, but uses a double category in a hierarchical form. First, all genotypes were classified based on fruit type considering the four categories in Chapter 3.3. as follows: processing type (PRO), big-sized type (BIG), long shelf-life type (LSL) and cherry type (CHE). Second, within each of the fruit type categories, genotypes were categorized based on their production under control, WW treatment, making a variable number of categories depending on the variation existing among the tested genotypes within each of the fruit type groups. To do so, a hierarchical cluster was performed and, based on the obtained clusters and on the genotypes' distribution, different production ranges were defined within each fruit type.

The Figure 5.3 represents the variability within each fruit type category and the different production ranges identified with the hierarchical clustering. Despite the fruit production under WW conditions was not normally distributed within each fruit type, Figure 5.3. allows to visually check that the hierarchical clustering proportionally distributed the genotypes among the production ranges, with some exceptions (such as the high production ranges in LSL type). It is worth denoting that the latter categorization excludes the "modern" cultivars considered in Chapter 3.3., which are only used here for comparative purposes and are considered in a single category due to the low number of modern genotypes included in the study (i.e., only used as controls). Since Table 5.3. summarizes the data discussed in detail in Chapter 3.3., the present section, focused on genotype selection based on resilience, will not discuss on the composition of the collection regarding production.

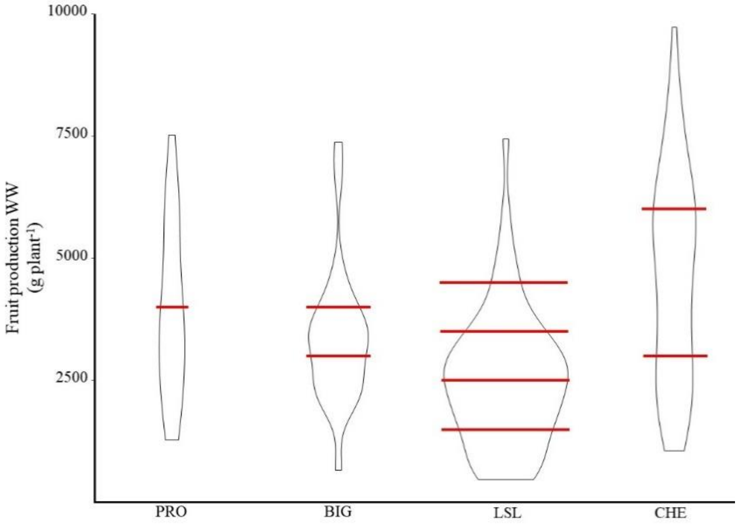


Figure 5.3. Violin plots representing the variability in fruit production under well-watered conditions (WW) within processing (PRO), big-sized (BIG), long shelf-life (LSL) and cherry (CHE) type fruits. Violin plots areas are scaled proportionally to the number of observations. The red bars in each violin plot determine different production ranges within each fruit type.

Table 5.3. Fruit production variability (maximum – minimum) among the studied genotypes in this Thesis under well-watered (WW) and water deficit (WD) conditions and their resilience factor depending on their fruit type, genotype type and the production range under WW. *n* column indicates the number of genotypes included in a production range. For fruit type, PRO means processing, BIG big-sized, LSL long-shelf life and CHE cherry type. Modern genotypes were only included here for comparative purposes with landraces Numbers in brackets near the maximum and minimum fruit production values in WW and WD fruit production columns denote the position of that fruit production within each fruit type when ranking the fruit production under WW conditions (being "1" the most productive). Numbers in square brackets in resilience factor column indicates the interquartile range (IQR) for each production range for landraces and for modern genotypes.

Fruit type	Genotype type	Production range	*n*	WW Fruit production	WD Fruit production	Resilience factor
		g plant^{-1}		g plant^{-1}	g plant^{-1}	%
PRO	Landrace	> 4000	7	7521.3 (1) – 4253.5 (7)	4530.0 (5) – 2411.6 (7)	60 [24]
		< 4000	12	3955.6 (8) – 1292.7 (19)	4628.0 (13) – 1261.5 (18)	84 [25]
	Modern		10	8495.8 – 1640	4652 – 866	89 [49]
BIG	Landrace	> 4000	6	7366.5 (1) – 4039.0 (6)	3774.6 (1) – 1203.3 (6)	53 [14]
		4000 – 3000	9	3740.2 (7) – 3160.8 (15)	2722.0 (12) – 1151.3 (15)	58 [15]
		< 3000	10	2736.6 (16) – 666 (25)	3051.3 (21) – 572.8 (23)	84 [13]
	Modern		4	7127.8 – 3327	4665.3 – 1547.8	66 [21]
LSL	Landrace	> 4500	5	7444.8 (1) – 4704.8 (5)	5165.7 (2) – 1516.0 (3)	57 [20]
		4500 – 3500	7	4426.0 (6) – 3551.2 (12)	4291.5 (9) – 1306.7 (8)	76 [37]
		3500 – 2500	21	3467.3 (13) – 2512.8 (33)	3615.8 (28) – 255 (30)	76 [36]
		2500 – 1500	16	2410 (34) – 1544.6 (49)	3094.5 (46) – 684.3 (48)	86 [39]
		< 1500	14	1277.5 (50) – 499.2 (63)	1965.8 (52) – 325 (58)	104 [62]
	Modern		2	8890.8 – 8830.6	6694.6 – 4247.3	62 [14]
CHE	Landrace	> 6000	14	9729.0 (1) – 6058.6 (14)	5375.3 (14) – 2518.0 (4)	59 [32]
		6000 – 3000	15	5598.2 (15) – 3275.0 (29)	4741.0 (16) – 1590.4 (22)	74 [22]
		< 3000	12	2871.5 (30) – 1062.5 (42)	3312.8 (31) – 876.6 (38)	97 [46]
	Modern		1	2377	618.5	26

The comprehensive categorization and calculation of resilience factors showed in Table 5.3. allows to perform a few comparisons defining the collection. First, within each fruit type, the highest production ranges have the lowest resilience factor and vice versa, confirming the need to categorize fruit production. This tendency can also be observed in Figure 5.4. where, regardless of the fruit type, those genotypes with higher resilience factor have lower fruit production under WW conditions. However, due to the large scattering, it is possible to identify very resilient genotypes in the highest fruit production ranges (see Table 5.4.).

Second, when not considering the highest production range, the maximum fruit production under WD within each production range was similar or even higher than that under WW, highlighting two important facts. On the one hand, some genotypes behaved similar or even better under WD as compared to WW conditions. The identification of that kind of genotypes is not surprising, since Guida et al. (2017) also found two LSL Italian landraces with similar fruit production under full irrigation and rain-fed conditions. On the other hand, the genotypes with the highest fruit production under WD were not the most productive under WW, even within the lower production ranges (as can be observed in the numbers in brackets in Table 5.3.).

Third, LSL landraces constitute the most variable of the tested groups, as up to 5 different production ranges resulted from the hierarchic clustering. This could be a reflection of a high number of considered genotypes as compared to other groups. However, the number of genotypes is not so different from CHE, which resulted only three production ranges. Thus, one of the reasons behind it might rely on the larger number of geographical regions and cultural aspects considered. For CHE, most genotypes came from Italian regions. In turn, LSL genotypes came from Western Mediterranean, including the Balearic Islands, the Valencian Country, Catalonia, Southern-Italian Peninsula, and Sicily. Interestingly, and despite the LSL collection was largely constituted by Balearic landraces, genotypes from the Valencian Country, Catalonia and Italian regions can be found in all the production ranges identified in Table 5.3. Thus, the large dispersion in LSL genotypes is not only observed when considering all genotypes as a single group, but also when considering the different geographical origins.

During the classification process, a few genotypes with a resilience factor higher than 100 have been found. As they must be analysed carefully, and different steps have been followed to depurate the data. First, genotypes with too low replicates and very low fruit production under WW conditions have not considered in this analysis, since these results could be derived from a bad field adaptation or response to Mediterranean summer open-field conditions, biasing the classification. Second, those genotypes with enough replicates but with very high resilience factors have been discarded or analysed in detail comparing their fruit production with that obtained in similar genotypes under both water regimes. As for the first step, a bad adaptation to WW conditions could hinder the use of the resilience factor to select the most resilient genotypes. Finally, after the depuration work, it is possible to identify those genotypes not reducing or even slightly increasing their fruit production under WD conditions.

The final step is then to select the most resilient genotypes within each of the groups considered in the collection. To do so, and following the hierarchical classification explained above, the Table 5.4. identifies the 13 most resilient genotypes found in this Thesis within each production range and for each fruit type. It is worth to mention that no significant differences were observed in fruit production between WW and WD treatments in any of the selected genotypes (after a one-way ANOVA, *P* > 0.05), confirming their high resilience to drought.

Table 5.4. Selection of the most resilient genotypes in terms of fruit production for each of the fruit type groups and production range categories in Table 5.3. See that table for abbreviations. Particular genotype codes are indicated according to the stablished code in Chapter 3.3. of this Thesis. Values of fruit production under well-watered (WW) and water deficit (WD) conditions and the resilience factor are indicated for each genotype.

Fruit type	Production range	Genotype code	WW	WD	Resilience factor
			Fruit production	Fruit production	
	g plant^{-1}		g plant^{-1}	g plant^{-1}	%
PRO	> 4000	PRO-L4	5596.8 ± 1270.8	4530.0 ± 723.4	81
	< 4000	PRO-L2	3060.8 ± 1073.0	4628.0 ± 578.2	151
BIG	> 4000	BIG-L8	4314.0 ± 1365.2	2901.0 ± 302.8	67
	4000 – 3000	BIG-L16	3420.5 ± 1366.5	2722.0 ±533.5	80
	< 3000	BIG-L13	2182.8 ± 661.4	3015.3 ± 1032.0	138
LSL	> 4500	LSL-L24	5936.7 ± 926.5	5165.7 ± 1075.5	87
	4500 – 3500	LSL-L54	3938.3 ± 1853.7	4291.5 ± 558.3	109
	3500 – 2500	LSL-L47	2663.2 ± 541.2	3615.8 ± 721.4	136
	2500 – 1500	LSL-L51	1672.5 ± 721.3	3094.5 ± 652.7	185
	< 1500	LSL-L60	1206.0 ± 337.3	1965.8 ± 858.3	163
CHE	> 6000	CHE-L23	6058.6 ± 605.8	5375.3 ± 737.6	89
	6000 – 3000	CHE-L19	4423.3 ± 421.4	3986.8 ± 348.9	90
	< 3000	CHE-L41	1758.0 ± 977.7	2309.3 ± 528.7	131

The selected genotypes are highlighted in green in the Figure 5.4. This figure shows how the selection method presented in this section ensures the selection of those genotypes maximizing the fruit production under WW conditions for their resilience factor.

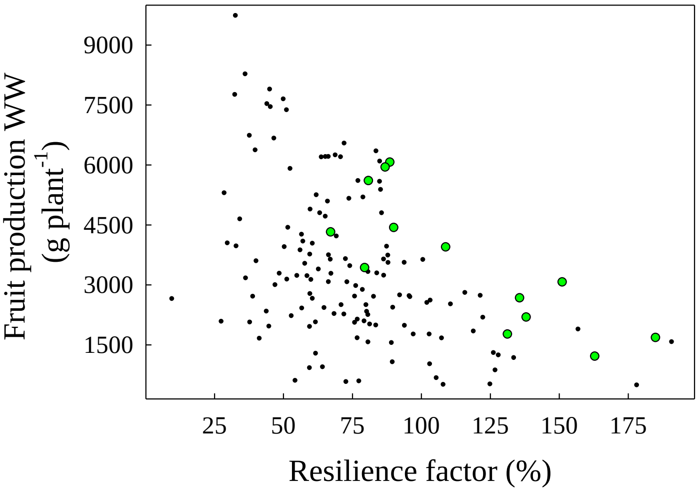


Figure 5.4. Relationship between resilience factor (%) and fruit production under well-watered (WW) conditions (g plant^{-1}). Data are means (*n* = 3-4). Black dots refer to well-watered (WW) landraces, and green dots refer to the 13 selected genotypes in Table 5.4.

It is worth mentioning that production (and its derived resilience factor) is not the only trait that can be used to seek for resilience. Thus, for particular researchers and breeders other traits may be even more important than fruit production, like fruit total soluble solids or a total soluble solids to acid ratio, which has been considered as a key parameter in fruit quality (Bertin and Génard, 2018; Causse et al., 2011). Despite both total soluble solids and acidity content in fruits were measured in this Thesis (see Chapters 3 and 4), the lack of a clear criteria about the best quality trait or ratio to consider for resilience, and the extremely large variation among the scored genotypes within each of the fruit type groups, makes the discussion of lower interest as compared to that for production. Further, despite higher sugar content seems to be desired for breeders, especially related to processing tomato varieties (Lahoz et al., 2016; Thakur et al., 1996), it is also known that particular varieties like the Balearic LSL landraces are particularly acid. In this sense, the lack of acidity makes them of lower quality for Balearic consumers. Nevertheless, this analysis could also be performed with the dataset associated to this Thesis[1].

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[1] Dataset can be consulted online as associated data to the published article: “Tomato landraces as a source to minimize yield losses and improve fruit quality under water deficit conditions”. DOI associated to the article: 10.1016/j.agwat.2019.105722; DOI associated to the dataset: 10.17632/4ftwm74w5z.1

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Chapter 6

Conclusions

From the results presented in Chapters 3 and 4 and the General Discussion, the following conclusions have been drawn to respond to the General Objectives and Specific Objectives in this Thesis:

General Objective 1: ***To study the physiologic and agronomic variability among Mediterranean tomato landraces and their response to water deficit***

Conclusion 1: High variability in leaf parameters, fruit production and fruit quality have been found among Mediterranean tomato landraces, corresponding with a large variability in their physiologic and agronomic performance under water deficit.

Conclusion 2: Mediterranean LSL tomato landraces demonstrated to constitute a reliable alternative to wild species as a source of genotypes to improve drought stress tolerance. The large variation in fruit morphology, fruit quality traits and flavour within and among LSL landraces makes this group an attractive source to breed for future tomato cultivars with a genetic background conferring, separately or together, extended shelf-life and drought tolerance.

Specific objective 1: *To search for the underlying mechanisms determining the variability in the photosynthetic performance among Mediterranean landraces.*

Conclusion 3: A large variability was found among Mediterranean tomato landraces for photosynthetic traits under non-stressing conditions, even when grouping the genotypes depending on their origin. For most of the examined parameters, the intra-group variability was higher than that observed among groups, including parameters as water-use efficiency. Therefore, no photosynthetic traits' specificity can be attributed to particular tomato groups, with no clear differences among landraces and with further groups or modern accessions.

Conclusion 4: Under well-watered Mediterranean climate open-field conditions, Mediterranean landraces' photosynthesis was limited by diffusive parameters (stomatal conductance, mesophyll conductance and the combination of both) rather than by biochemical parameters. Therefore, future research devoted to increase landraces' photosynthetic rate under these environmental conditions should focus on minimizing or overcoming these diffusive limitations.

Specific objective 2: *To compare the response to water deficit among Mediterranean landraces and modern genotypes.*

Conclusion 5: Water deficit lead to a general decrease in fruit production and an increase in fruit quality. However, the reduction was not uniform, being dependant on the genotype's fruit type and cultivar group.

Conclusion 6: Despite some modern genotypes showed outstanding behaviour under summer Mediterranean open-field conditions, most of them had a fruit production similar or even lower than Mediterranean landraces and had larger reductions of fruit production percentage under water deficit conditions.

Conclusion 7: F_1 hybrids obtained from landraces showed promising results under drought stress conditions, highlighting the potential of Mediterranean landraces of tomato to be included in breeding programs to increase drought resilience and maintain fruit production and quality.

Specific objective 3: *To investigate the use of phenotyping measurements to monitor the effect of water deficit over physiologic and agronomic tomato performance*

Conclusion 8: Leaf physiologic and fruit quality parameters were better predicted by vegetation indices such as the normalized difference vegetation index, the green normalized difference vegetation index, and the simple ratio; while fruit production was closely related to canopy projected area.

Conclusion 9: Use of phenotyping tools as leaf carbon isotope composition allowed to determine the maximum fruit production of a genotype regardless of the treatment.

Conclusion 10: Correlations between remote sensing and leaf-level physiologic and agronomic measurements depended on the screened genotype group and its response to water deficit. Beyond fruit production, multispectral indices were also correlated with fruit quality, stressing the potential of remote sensing measurements to efficiently manage tomato crop under stress conditions.

Specific objective 4: *To identify the most resilient genotypes to water deficit studied in this Thesis*

Conclusion 11: A methodology to identify the most resilient tomato landraces to water deficit is described in the present Thesis, considering fruit production. According to fruit type groups and the production range under well-watered conditions, 13 Mediterranean tomato landraces have been identified as the most resilient to water deficit, covering the whole variation range in the collection.

General objective 2: ***To analyse the response of Mediterranean tomato landraces to grafting in physiologic and agronomic terms***

Conclusion 12: No graft incompatibilities have been found between Mediterranean tomato landraces and the most used commercial, and even experimental rootstocks, indicating the suitability of grafting to enhance Mediterranean landraces' performance.

Conclusion 13: Mediterranean tomato landraces responded differently when grafted on the same rootstock, but overall, some rootstocks were identified to increase water-use efficiency with no impairment in fruit production.

Specific objective 5: *To determine the capability of grafting to modify the photosynthetic performance and alleviate abiotic stress effects.*

Conclusion 14: Grafting *per se* (comparing non-grafted and self-grafted plants) did not modify net CO_2 assimilation rate, stomatal conductance, or intrinsic water-use efficiency along a large number of vegetable and woody crops. However, the use of specific rootstocks can efficiently improve intrinsic water-use efficiency.

Conclusion 15: Grafting onto specific rootstocks appears as an efficient technique to lessen the effects of abiotic stresses over photosynthetic performance and can contribute to increase crops' resilience to the future climate change conditions.

Specific objective 6: *To determine the efficiency of grafting to enhance the agronomic performance of Mediterranean drought-adapted landraces' when using commercial and experimental rootstocks.*

Conclusion 16: The use of different rootstocks, either commercial or experimental, altered key photosynthetic parameters of the 'de Ramellet' Mediterranean drought-adapted landrace. Using *Solanum pimpinellifolium* as rootstock increased scion intrinsic water-use efficiency and did not decrease fruit production, being a potential rootstock to be used for water consumption reduction.

Conclusion 17: Commercial rootstocks did not increase tomato fruit production in Mediterranean landraces under well-watered conditions but diminished the impact of water deficit in fruit production as compared to non-grafted plants.

Conclusion 18: The effect of the rootstock was variable depending on the 'de Ramellet' genotype used as scion, being for some parameters a genotype dependent interaction between scion and rootstock.

Specific objective 7: *To study the suitability of drought-adapted landraces to obtain drought-resilient rootstocks.*

Conclusion 19: Similar and even improved performance in agronomic terms was observed in the ‘de Ramellet’ genotype used as rootstock as compared to a commercial rootstock, regardless of the water treatment. In fact, the ‘de Ramellet’ landrace used as rootstock appeared as the most suitable rootstock in terms of maximizing fruit production under water deficit conditions. Such results highlight the suitability of the Mediterranean landraces as promising genotypes to be used as, or to breed for novel rootstocks to increase drought stress resilience.