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The postharvest tomato fruit quality of long shelf-life Mediterranean landraces is substantially influenced by irrigation regimes

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ABSTRACT

Postharvest shelf-life is a critical trait for fleshy fruit and so studies of genotypes with long shelf-life (LSL) phenotypes are of great potential importance, since they can lead to strategies for crop improvement. Examples of such a genotype are the *Delayed Fruit Deterioration* (*DFD*) tomato, and most accessions of the "*Tomàtiga de Ramellet*" (*TdR*) Mediterranean landrace group, some of which have a particularly dramatic LSL phenotype and remain palatable for many months after reaching a fully ripe stage. The *TdR* accessions collectively show a wide variation in shelf-life, although, the basis of this variation is not known. Moreover, little has been reported regarding the relationship between cultivation conditions, fruit shelf-life and specific genetic loci. Here we show that the LSL trait in those landraces is both partially associated with a defined genetic component, in the form of the *alcobaça* (*alc*) mutation, and is profoundly affected by the irrigation regime during cultivation.

1. Introduction

A number of tomato (*Solanum lycopersicum* L.) genotypes have been reported to bear fruit with extended shelf-life after harvesting. This trait can be a consequence of monogenic, non-allelic mutations in ripening regulatory genes, such as *rin* (*ripening-inhibitor*), *nor* (*non-ripening*), *Cnr* (*Colorless non-ripening*), *Nr* (*Never-ripe*), *Gr* (*Green-ripe*), and *alc* (*alcobaça*), (Lobo et al., 1984; Giovannoni, 2004, 2007; Garg et al., 2008; Matas et al., 2009; Benites et al., 2010; Casals et al., 2012). Such ripening mutations are pleiotropic, commonly producing fruit with incomplete ripening, altered pigmentation, impaired or absent climacteric production of ethylene, and a reduced response to exogenous ethylene. However, the severity of the various mutations varies: for example, the *rin* and *nor* mutants are considered non-climacteric and *alc* partially climacteric (Garg et al., 2008; Kosma et al., 2010). Consequently, some of these mutations are of horticultural interest as they can yield fruit with slowed ripening and extended shelf-life, and indeed some of them are widely deployed in breeding programs and present in many commercial cultivars. However, mutations with major effects, such as *rin* and *nor*, can result in fruit with severely perturbed ripening, and consequently with less desirable characteristics, such as lower levels of pigments or sugars, resulting in reduced consumer satisfaction. There is therefore considerable interest in utilizing mutants, such as *alc*, that have more modest effects on ripening, as a well as identifying and deploying alleles of the underlying mutations, as a strategy for shelf-life improvement (Kuzyomenskii, 2007).

An example of a tomato genotype with a particularly notable long shelf-life (LSL) phenotype is the so-called *delayed fruit deterioration* (*dfd*) mutant (Saladié et al., 2007). Unlike non-ripening mutants, such as *rin* and *nor*, fruit from *dfd* exhibit normal, climacteric fruit ripening but little subsequent postharvest deterioration over many months, with minimal water loss or microbial infection (Saladié et al., 2007). These characteristics are also exhibited by the *Penjar* tomatoes of the Eastern Iberian Peninsula (Casals et al., 2012), and by the "*Tomàtiga de Ramellet*" (*TdR*) tomatoes from the Balearic Islands (in the western Mediterranean), (Ochogavía et al.,

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2011). The genetic basis of the LSL trait has not been fully resolved for any of the Mediterranean tomato genotypes, but correlative data indicate a relationship between the LSL phenotype of the *Penjar* tomatoes and the *alc* mutation (Casals et al., 2012).

TdR comprise a mixture of landraces, or a "landrace group" following the definition of Zeven, 1998. All landraces are subject to very similar cultivation-driven or naturally selected determinants, and so, variation in adaptive traits among members of the group reflects environmental and agronomic variables: in this case, difference among growers in the Balearic Islands. Consequently, in this study, we consider *TdR* as a group of landraces (or simply "landraces"), and each particular landrace is considered an "accession", representing a different *TdR* source from the *TdR* seed-collection of the University of the Balearic Islands (UIB).

TdR plants show considerable water stress resistance, which together with the LSL phenotype are thought to reflect historical selection for geographically specific cultivation requirements: the lack of irrigation systems and water availability in the small Mediterranean orchards where the *TdR* has generally been cultivated, and the desirability of fruit in the local diet during the winter (Ochogavía et al., 2011). Water stress resistance appears to be related to higher water use efficiency, and to other adaptations to the Mediterranean climate (Galmés et al., 2011, 2013). However, the relationship among landraces carrying the *alc* mutation, extended fruit shelf-life, and cultivation conditions has not been well characterized.

Fruit shelf-life is a consequence of maintaining fruit integrity during ripening and subsequent post-ripe stages, which in turn is dependent on numerous metabolic modifications of the structural polymers of the cell wall, middle lamella and cuticle (Ruiz-May and Rose, 2013). These modifications collectively affect cell-to-cell adhesion, wall and cuticle biomechanical properties, as well as other factors such as fruit transpirational water loss (Brummell and Harpster, 2001; Bargel and Neinhuis, 2005; Dominguez et al., 2011; Seymour et al., 2013). While the molecular processes underlying some of these ripening and post-ripening related events have been elucidated, together with some of the associated endogenous regulatory machinery, far less is known about the mechanistic basis of any environmental variables associated with fruit cultivation that influence shelf-life. However, it does appear that water availability may be an important factor. For example, it has been reported that in some tomato cultivars, higher water availability during cultivation results in larger fruit (e.g., Kirda et al., 2004; Patane and Cosentino, 2010; Patane et al., 2011), which in turn can lead to higher rates of fruit degradation (e.g., Ehret et al., 2008). It has also been shown in tomato that stress conditions during cultivation have benefits in fruit resistance to pathogens, through the expression of metabolites and enzymes with anti-microbial activity, and the exudation of waxy components of the cuticle (Charles et al., 2008, 2009).

TdR tomatoes grown in the Balearic Islands represent potentially valuable landraces in which to study the relationship between water availability, LSL and key genetic loci. *TdR* accessions differ in fruit size and shape attributes, alleles at micro satellite and SNP markers (Conesa et al., unpublished data), and in adaptive traits under water stress conditions (Galmés et al., 2011, 2013). Given the diversity in plant and fruit traits observed in the collection of *TdR* landrace accessions at UIB, we were interested in exploring the diversity in shelf-life among those accessions, and the effect of irrigation. The experiments described here were designed to test whether the LSL phenotype associated with *TdR* tomatoes is correlated with plant water availability during cultivation and whether the *alc* mutation, which has long been related to LSL, is sufficient to confer this phenotype in *TdR* landraces.

2. Materials and methods

2.1. Plant material and treatments

The data presented in this paper resulted from three different experiments performed on *Tomàtiga de Ramellet* (*TdR*) accessions in Mallorca (Balearic Islands, Spain).

The aim of experiment 1 was to test for shelf-life variation among different *TdR* lines. A total of 45 different *TdR* accessions from the University of the Balearic Islands (UIB) seed-collection were selected and distinguished from each other based on diversity in fruit size and shape, plant and leaf morphology (Ochogavía et al., 2011), and on molecular markers distributed throughout the genome (Conesa et al., unpublished data). The selected accessions were planted simultaneously in the experimental field of the UIB, and in a field in Manacor (Mallorca, Spain), in the spring of 2008.

Soil textural analyses were performed using the methods described in Burt, 2004 and soils were classified following the USDA method (Soil Survey Staff, 2010). In the UIB field, the soil was man-made, uniform (i.e., unstructured) and fast draining, with an approximate 0.9 m depth of clay loam-like texture (34% clay, 30% silt and 36% sand), and a calculated maximum plant water availability of 0.13 cm^3 water/cm^3 soil. The soil hydraulic properties were determined based on Saxton et al., 1986 with Soil Water Characteristics software (version 6.02.74) available at the USDA website (http://hydrolab.arsusda.gov/soilwater/Index.htm). Irrigation was supplied through drip lines with the dose controlled to maintain 6–12% of soil water content (SWC), monitored by weekly gravimetrical measurements (Galmés et al., 2011). In the Manacor field the soil was approximately 2 m deep, structured and with a silty clay texture (40% clay, 42% silt and 18% sand), and a calculated maximum plant water availability of 0.15 cm^3 water/cm^3 soil. Irrigation was supplied through drip lines with the dose maintaining SWC values from 18% to 23%, as determined by gravimetric measurements.

The aim of experiment 2 was to test the effect of water stress on *TdR* fruit shelf-life. Due to the greater degree of control and monitoring of plant physiological status in this experiment, as well as the identification of two clear groups among *TdR* accessions based on the results of experiment 1, the number of accessions was reduced for experiment 2, while maintaining maximum variation and including three accessions for each of the two groups. Thus, six *TdR* accessions were selected from the UIB seed-collection to represent the wide variability in fruit and plant morphology and the genetic diversity existing in the Balearic Islands (Galmés et al., 2011). The water stress experiment was performed in the experimental field at UIB in the spring-summer of 2009, with two treatments: well watered (WW), maintained at 100% of potential evapotranspiration (PET) to adjust the SWC from 25% to 30%; and water stress (WS), in which irrigation was reduced to about 20% of PET in order to maintain the SWC from 7% to 10%. Irrigation was supplied through a drip system for both treatments. The SWC and stomatal conductance (g_s) were monitored throughout the experiment to ensure homogeneity in the application of the treatments. The SWC was monitored weekly as in experiment 1 and g_s was measured in all plants, every 1–2 days, with a leaf porometer (Decagon Devices, Pullman, WA, USA; Galmés et al., 2011).

Finally, the aim of the experiment 3 was to test, under cultivation conditions typical for commercial production of *TdR*, the effect of irrigation dose on fruit weight losses during postharvest storage. Thus, a single *TdR* accession (UIB0138), showing similar fruit storage behavior irrespective of water availability during cultivation, was tested with five different water regimes or treatments: 0%, 25%, 50%, 75% and 100% of the PET. This experiment was conducted in the field in Manacor during the spring-summer of 2010. Gravimetric measurements of SWC showed values from 18% to 23% of the field capacity for the 100% PET treatment.