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

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ABSTRACT

Although grafting has become an effective tool to enhance many traits in horticultural crops, its role in improving the performance of local landraces is yet to be proven. The aim of this work was to assess the performance of the 'Ramellet' tomato, a landrace from the Balearic Islands, when grafted onto different rootstocks. For this purpose, two 'Ramellet' genotypes were grafted on two commercial ('Beaufort' and 'Maxifort') and a wild (*Solanum pimpinellifolium*) tomato rootstock species, and cultivated in greenhouse under commercial conditions. Plant yield, morphology and photosynthetic traits were measured in all combinations, with non-grafted and self-grafted 'Ramellet' plants used as controls. A significant effect of the rootstock on key parameters related to yield, plant growth and photosynthesis was found in both 'Ramellet' genotypes. Stomatal conductance increased, resulting in a decreased water-use efficiency in both genotypes grafted on the commercial rootstocks. Oppositely, when grafted on *S. pimpinellifolium*, stomatal conductance decreased and water-use efficiency increased in one of the 'Ramellet' genotypes. Remarkably, there was a significant correlation between water-use efficiency, plant growth and yield. Overall, the results highlight the potential of grafting to alter several physiological traits of local landraces and to provide new clues towards advancing our understanding in the underlying determinants of water-use efficiency and plant yield.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most abundantly produced vegetable crops in the world, with its consumption notably rising in the last decades (FAO, 2016). Continuous breeding resulted in improved tomato cultivars with increased productivity and higher resistance to both biotic and abiotic stresses. However, fixing a desired trait in novel cultivars with breeding techniques is not always easy in a short time, especially when tomato wild relatives are used as the source of traits or resistances (Araus et al., 2002; Bai and Lindhout, 2007; Foolad and Panthee, 2012).

Grafting is an alternative and faster method to improve tomato cultivars. It consists in the union of different plant parts, frequently a scion and a rootstock, and involves processes of tissue regeneration (Lee and Oda, 2002). It is a common, extended and automated technique not only in tomato but also in many other horticultural crops (Lee et al., 2010). It has allowed to improve fruit yield (Di Gioia et al., 2010; Flores et al., 2010; Savvas et al., 2011; Turhan et al., 2011), resistance to biotic stress like soil borne diseases (Rivard and Louws, 2008) and viruses like the tomato mosaic virus (ToMV) (Leonardi and Giuffrida, 2006); and also tolerance to abiotic stresses like drought, thermal and salinity among others (Estañ et al., 2005; Penella et al., 2015; Schwarz et al., 2010; Yang et al., 2015). Nevertheless, it is worth to mention that grafting efforts towards yield increase have resulted many cases in a reduction of fruit quality traits (*e.g.,* Di Gioia et al., 2010; Pogonyi et al., 2005; Turhan et al., 2011, but also see Flores et al., 2010) and thus, many efforts are currently focused in recovering or prevent loosing of such traits (Causse et al., 2011; Djidonou et al., 2016; Kyriacou et al., 2017; Tieman et al., 2017). In order to achieve physiological improvements through grafting, hybrids involving different tomato wild relatives and domesticated cultivars have commonly been used as rootstocks, given their more vigorous roots, with particular importance

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for the widespread use of *Solanum habrochaites* S. Knapp & D.M. Spooner in the breeding for rootstocks.

It is known that rootstocks can modify the characteristics of the scion variety (Rouphael et al., 2010). During the graft process, the disruption of the vascular connections affect the hydraulics of the plant and may alter water and nutrient uptake, being regulated by the replaced rootstock (Martínez-Ballesta et al., 2010). Rootstocks can also upset the hormonal balance of the scion. For instance, auxins are determinant for the success of the graft, being involved in the differentiation of the vascular tissue and the hydraulic performance of scion. Hormonal and hydraulic signals regulate the growth of the scion by affecting several physiological parameters, among them those governing the photosynthetic capacity of the plants (Aloni et al., 2010). For instance, both net CO_2 assimilation rate (A_N) and stomatal conductance (g_s) have been reported to increase after grafting a scion onto a vigorous rootstock in tomato (He et al., 2009; Lee et al., 2010; Liu et al., 2011; Penella et al., 2016; Yang et al., 2015), as well as in other crops like watermelon (Yang et al., 2012), apple tree (Liu et al., 2012) and orange tree (Machado et al., 2013). These results indicate that grafting alters the intrinsic water-use efficiency at leaf level (WUE_i, estimated as the ratio of A_N/g_s) (Kumar et al., 2017; Rouphael et al., 2008; Schwarz et al., 2010). Although it has been widely reported that plant growth and production are negatively related to WUE_i, the data sustaining this relationship has predominantly been obtained in non-grafted plants (Antony and Singandhupe, 2004; Cattivelli et al., 2008; Galmés et al., 2011; Rytter, 2005). It would be necessary to investigate if the negative correlation between WUE and plant growth and production is sustained in grafted plants, where genetic limitations are overcome by means of combining two different genotypes in a single individual.

Many tomato grafting experiments have used improved commercial varieties as scion (*e.g.,* Flores et al., 2010; Magán et al., 2008; Santa-Cruz et al., 2002; Venema et al., 2008) and even heirloom varieties (Barrett et al., 2012a, 2012b, 2012c; Masterson et al., 2016; Nicoletto et al., 2013). However, to the best of our knowledge, there are no studies on the role of grafting on tomato landraces. As a main difference, crop landraces are highly heterogeneous and have selective traits better related to adaptation to local cultivation conditions and environment, rather than traits focused on high yield and growth. Despite this, landraces maintain a recognizable set of characteristics (*e.g.,* Casañas et al., 2017; Saxena and Singh, 2006; Zeven, 1998). In this regard, the Mediterranean basin is considered a secondary center of origin for tomato crop (Figàs et al., 2015), mainly due to the high number of landraces that can be found. There, during centuries of local cultivation, many landraces acquired adaptations to particular conditions, such as low water availability or high salinity, which are currently gaining commercial interest.

Among the Mediterranean landraces, the 'Ramellet' tomato cultivar, locally known as '*Tomàtiga de Ramellet*' (TR) is a traditional long shelf-life tomato from the Balearic Islands, with high variability in leaf morphology, agronomic and fruit quality traits (Bota et al., 2014; Ochogavía et al., 2011). It is particularly adapted to drought, acquired through improvement of its WUE_i as compared to other commercial varieties (s et al., 2013, 2011;). Despite this, one of the traits proven to be more variable within TR was g_s (Bota et al., 2014; Galmés et al., 2011; Ochogavía et al., 2011). Because that, this work is especially focused on the physiological performance of conspicuously different TR genotypes in terms of constitutive g_s when grafted onto different rootstocks, in order to understand how WUE_i and yield are affected with grafting, and to which extent this depends on the rootstock. Results may provide essential information in terms of improvement of tomato landraces, especially related to the effect of a rootstock selected to improve WUE_i and yield.

In this study, several fruit yield, leaf morphological and photosynthetic parameters were measured under commercial conditions on grafting combinations from two different TR genotypes (scions) on two commercial rootstocks ('Beaufort' and 'Maxifort') and a wild species rootstock (*Solanum pimpinellifolium* L.), using non-grafted and self-grafted TR plants as controls. As compared to *S. habrochaites*, *S pimpinellifolium* is a wild relative of the tomato crop that has been less explored in terms of tomato improvement, and particularly through grafting. Reasons mainly rely on the high amount of biotic resistance existing in *S. habrochaites*, especially including soil-borne disease (Foolad, 2007; Grandillo et al., 2011). Nevertheless, when considering abiotic stresses tolerance, *S. pimpinellifolium* has root traits, vigor and growth patterns that could be very useful to improve tomato (Asins et al., 2015; Conesa et al., 2017; Martínez-Andújar et al., 2017; Sumugat et al., 2011). The objective was to determine the effect of the interaction between the different TR genotypes and rootstocks for each particular graft combination. It is hypothesized that drought adapted TR genotypes grafted on commercial rootstocks would decrease WUE_i and increase fruit yield when compared to self-grafted and non-grafted plants; while TR plants grafted on the wild species rootstock would decrease fruit production but enhance WUE_i.

2. Material and methods

2.1. Plant material

Two genotypes of *Solanum lycopresicum* 'Ramellet' ('*Tomàtiga de Ramellet*', TR) were used as scion, corresponding to the UIB seed-bank accessions: TR-1 (UIB1-31) and TR-2 (UIB2-70). These genotypes were selected based on previous characterization of genetic diversity, leaf morphology and anatomy, photosynthetic performance, fruit morphometry and shelf-life (Bota et al., 2014; Conesa et al., 2014; s et al., 2013, 2011;). With particular relevance for the aim of the present experiment, TR-1 displayed the lowest values of stomatal conductance (g_s) under well-watered conditions as compared to other TR genotypes (Galmés et al., 2011). Contrarily, preliminary tests identified TR-2 as one of the TR genotypes with higher g_s (data not shown).

Plants of these genotypes were either non-grafted, self-grafted or grafted onto rootstocks of 'Beaufort' and 'Maxifort' (*S. lycopersicum* L. × *S. habrochaites* S. Knapp & D.M. Spooner, De Ruiter Seeds, Bergschenhoek, NL), and onto the wild relative *S. pimpinellifolium* L. (LA0413–TGRC seedbank). As reported by the seed company, 'Beaufort' and 'Maxifort' are recommended for soil and hydroponic crops, as they are very effective against soil borne pathogens and virus (https://seminis.es/producto/beaufort/684 and https://seminis.es/producto/maxifort/681, consulted on 06-06-2017). *S. pimpinellifolium* was selected as a vigorous wild relative rootstock. The different graft combinations were labelled as TR_X-Y, where "$_X$" indicates the rootstock ($_C$ for non-grafted, $_S$ – self-grafted, $_B$ – 'Beaufort', $_M$ – 'Maxifort' and $_P$ for *S. pimpinellifolium*), while "Y" indicates the scion (1 for TR-1 and 2 for TR-2) (Table 1).

Seeds of TR genotypes and rootstocks were germinated on late January 2012 in polystyrene trays filled with peat-based substrate in a greenhouse. The graft was performed 30 days after germination, when plants initiated the third true leaf, using the tube-grafting method (Lee

Table 1
Different combinations of rootstocks and scions used in this study and their abbreviation.

Scion	Rootstock	Abbreviation
TR-1	Non-grafted	TR_C-1
TR-1	TR-1	TR_S-1
TR-1	'Beaufort'	TR_B-1
TR-1	'Maxifort'	TR_M-1
TR-1	*S. pimpinellifolium*	TR_P-1
TR-2	Non-grafted	TR_C-2
TR-2	TR-2	TR_S-2
TR-2	'Beaufort'	TR_B-2
TR-2	'Maxifort'	TR_M-2
TR-2	*S. pimpinellifolium*	TR_P-2