Growth capacity in wild tomatoes and relatives correlates with original climate in arid and semi-arid species

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ABSTRACT

Wild tomatoes and relatives (Solanum sect. Lycopersicon, sect. Lycopersicoides and sect. Juglandifolia) constitute a recently derived clade inhabiting a wide range of habitats across latitudinal and altitudinal axes in South America, with important variation in plant morpho-physiological traits. It is not clear to what extent growth capacity and related traits depend on phylogenetic constraints, or are driven by each species' adaptation to the climate of origin. The use of wild tomatoes to improve the adaptation of the domesticated species to variable environmental conditions requires knowledge on which wild species are most suitable for growth capacity improvement. Under common garden conditions, results show that the relative growth rate (RGR) in the tomatoes is better determined by its physiological (net assimilation rate, NAR) rather than morphological (leaf area ratio, LAR) component. Moreover, RGR is correlated with the climate of origin in arid and semi-arid habitat species, and display different biomass allocation strategies depending on the climate, particularly related to the green and senescent leaf fractions. When grown under the same conditions, the domesticated tomato showed important differences in leaf size and leaf mass per area (LMA) as compared to its wild relatives, suggesting modifications related to the domestication process. Several semi-arid species appear as suitable species to improve the domesticated tomato growth capacity under more arid cultivation conditions, as those predicted by climate change.

1. Introduction

The wild tomatoes and relatives (Solanum sect. Lycopersicon, sect. Lycopersicoides and sect. Juglandifolia) constitute a clade of 15–17 species (see Peralta et al., 2008) with monophyletic origin and diverging ca. 6 Mya (Särkinen et al., 2013) to > 7 Mya (Nesbitt and Tanksley, 2002). They inhabit a vast range in latitude (ca. 3500 km) and altitude (ca. 3500 m a.s.l.) in the NW of South America, from highlands and tropical rainforests in the Andes, to the Chilean deserts, and the volcanic island coasts of the Galapagos Islands (reviewed in Peralta et al., 2008). Despite sharing a recent common ancestor, wild tomato species are genetically, ecologically and phenotypically diverse

(Moyle, 2008; Nakazato et al., 2008, 2012; Peralta et al., 2008; Chitwood et al., 2012; Haak et al., 2014; Muir and Thomas-Huebner, 2015; Pease et al., 2016), and some morphological and physiological variation has likely evolved in response to habitat variation (e.g., Rick, 1973; Smith and Peralta, 2002; Bloom et al., 2004; Nakazato et al., 2008, 2010; Easlon and Richards, 2009). Correlations between habitat and traits are consistent with the hypothesis that environmental adaptation contributed to species divergence among wild tomatoes (Nakazato et al., 2010). Furthermore, it has been suggested that climatic rather than soil variables predict the distinct geographic distributions of sister species. In this regard, adaptation along temperature and precipitation gradients has probably played an important role

in diversification of the wild tomatoes (Nakazato et al., 2010).

In spite of the broad variation in the environmental conditions where the wild tomatoes evolved, there is little variation in the plant habit, with all tomato species being herbaceous or sub-shrubs, except the two liana-like species within the section *Juglandifolia* (reviewed in Peralta et al., 2008; Knapp and Peralta, 2016). A comparison of the phylogenetic relationships among wild tomatoes and relatives (Spooner et al., 2005; Peralta et al., 2008) with the environment they inhabit (e.g., Peralta et al., 2008) indicates that climatic niche evolution is labile. Studies correlating climatic, geographic and biological data indicate that differences in the environmental preferences are greatest among sister species pairs, suggesting repeated ecological divergence within each clade (Nakazato et al., 2010). Many morpho-physiological differences among wild tomatoes therefore likely reflect adaptation to different environments, but it is broadly unknown the adaptive significance of this variation.

Functional types and life-forms are often adaptive responses to the climate and rarely phylogenetically conserved, not just among wild tomatoes, but also across many species (e.g., Stebbins, 1952; Levin, 2004; Niinemets and Valladares, 2006; Bennet and Cahill, 2013). However, the recent divergence times, uniform plant habit, and wide range of environments make wild tomatoes and relatives an ideal group to study functional trait variation and evolution. Recently, we have surveyed variation in a number of leaf-level morpho-physiological traits among wild tomato species and relatives, and detected relationship between trait variation and the environment for some key parameters like the leaf mass per area (Muir et al., 2017).

Plant growth capacity is frequently determined by the relative growth rate (*RGR*), which can be split in two major components, the net assimilation rate (*NAR*) and the leaf area ratio (*LAR*), related to physiological and morphological determinants of growth, respectively (e.g., Hunt, 1982; Lambers and Poorter, 1992; Grotkopp et al., 2002; Lambers et al., 2008). In general, across species from different habitats and growth forms, *RGR* tends to be negatively and positively correlated to *NAR* and *LAR*, respectively (e.g., Poorter 1989; Galmés et al., 2005; Lambers et al., 2008). There are no clear trends between *RGR* and climate at a global scale, since the important differences in *RGR* exist across plants with different growth forms. For example, in the comparison of annual and perennial grasses from the same genus, higher *RGR* always corresponds to the annual form (Lambers et al., 2008). Lower *RGR* may also be an adaptation to resource-poor habitats, as compared to counterparts from resource-rich environments (Grime and Hunt, 1975; Chapin, 1980; Poorter and Welschen, 1993), which can be extended to species from less favorable environments, like saline and alpine envirnments (reviewed in Lambers et al., 2008). Both the life form and resource availability could be partially correlated with major environmental factors like temperature and precipitation, which could secondarily result in trends across climate in *RGR*, *NAR* or *LAR* variation. However, within species groups with little variation in the growth form (like tomatoes), relationships between climate and growth parameters could be more evident.

In the present study, we hypothesized that climate may have shaped different growth strategies among closely related wild tomato species and relatives. Specifically, we examined i) whether growth capacity and biomass allocation differ among wild tomato species originated under contrasting climatic conditions, and ii) which of the underlying determinants of growth is responsible for this variation. Further, we hypothesize that species adapted to the most extreme conditions, in particular those from arid environments, evolved a lower intrinsic *RGR*, as already highlighted as a general trend in plants (Lambers et al., 2008), and that both morphological and physiological adjustments are responsible for such adaptive response. Finally, we have included three domesticated accessions to compare the growth capacity and under-lying components between cultivated and wild tomatoes, in order to distinguish traits favoured during artificial *vs.* natural selection.

For these aims, all plants were cultivated under common garden conditions. We are aware that functional studies performed under these conditions might not parallel natural environmental variation in the wild. However, they are enormously valuable in describing fitness consequences of specific natural trait variation under the same, known environmental conditions, which allows to account for genetically determined trait variation (e.g., Teramura et al., 1981; Martin et al., 2007; Dunbar-Co et al., 2009), also in the tomatoes (Moyle, 2008; Easlon and Richards, 2009). We are also aware that repeating the same experiment under different climatic conditions could lead to different results, responding to different degree of adaptation of each particular species to the experimental conditions. In this regard, the spring-summer Mediterranean climate is optimal for outdoor cultivation of domesticated tomato, allowing the comparison of the crop growth performance with that of the wild species under the same conditions.

2. Material and methods

2.1. Plant material and growth conditions

Nineteen tomato accessions were grown at the University of the Balearic Islands (UIB, Spain). Accessions include the two *Solanum* sect. *Lycopersicoides* species, the two sect. *Juglandifolia* species, 12 sect. *Lycopersicon* accessions (11 species and a variety), and three *S. lycopersicum* cultivated accessions (Table 1). All the wild species accessions were obtained from the Tomato Genetics Resource Center at UC Davis (TGRC; http://tgrc.ucdavis.edu). The domesticated varieties, all with indeterminate growth habit, include two *Ramellet* tomato accessions from the UIB seedbank collection, and a commercial tomato (Table 1).

Seeds were germinated following TGRC indications, and as detailed in Muir et al. (2017). Once most plantlets had at least two true leaves, five plants per accession were harvested to measure the initial leaf, stem and root biomass fractions (see Section 2.2). At the same time, five other plantlets per accession were transplanted to 19 L pots for the remainder of the experiment. Pots contained a 4:1 mixture (v/v) of bog peat-based horticultural substrate (Prohumin-Potting Soil Klasmann-Deilmann, Projar S.A., Valencia, Spain) and perlite (granulometry A13, Projar S.A., Valencia, Spain). Plants were grown outdoors at the UIB experimental field from May to July, under typical Mediterranean climate conditions, with average daily temperature (°C) during the day of 23.9 ± 0.4, 25.4 ± 0.8 and 27.6 ± 0.4, average maximum daily temperature of 25.39 ± 0.4, 26.0 ± 1.2, 29.1 ± 0.4, and average minimum daily temperature of 12.9 ± 0.4, 15.7 ± 0.5, 19.1 ± 0.4, respectively for May, June and July. All plants were irrigated daily to field capacity, and fertilized weekly with 50% Hoagland's solution.

2.2. Biomass measurements and growth-related parameters calculation

We estimated initial size and biomass fractions using the five plantlets per accession harvested at time of transplanting. All leaflets, minus the rachis, were scanned to obtain the leaf area at transplanting (*LA*i) using Image J (Ambrámoff et al., 2004). The biomass was dried in an air-forced oven at 70°C to obtain the total plant biomass at transplanting (*B*$_T$i).

At the end of the experiment period (61 and 78 days after transplanting for the "fast grower" and "slow grower" species, respectively; see Muir et al., 2017 for details), plants of all taxa were harvested at the end of the experiment to obtain total biomass and its fractions. Plant fractions were separated, placed in paper envelopes and dried in an air-forced oven at 70°C to constant weight, to obtain the leaf (*B*$_L$), stem (*B*$_S$) and root (*B*$_R$) biomass fractions. We further separated leaves into green leaves (*B*$_{Lg}$) and senescent leaves (*B*$_{Ls}$); the latter including both leaves with obvious yellow appearance on the harvest date, and abscised leaves. Biomass ratios were calculated by dividing each fraction by the total plant biomass (*B*$_T$): green leaf mass ratio (*LMR*g), senescent leaf mass ratio (*LMR*s), total leaf mass ratio (*LMR*),