



Research article

Population variation in drought-resistance strategies in a desert shrub along an aridity gradient: Interplay between phenotypic plasticity and ecotypic differentiation



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ABSTRACT

Adaptations to drought of deciduous and evergreen species in arid environments are associated with resource-acquisitive (drought avoidance) and resource-conservative (drought tolerance) strategies of water use, respectively. Few studies have addressed whether a single species can exhibit both drought avoidance and drought tolerance strategies along an aridity gradient, and none have evaluated the role of ecotypic differentiation and phenotypic plasticity in shaping such strategies. In the desert shrub *Encelia canescens*, distributed along an aridity gradient in the Atacama Desert, we hypothesized that populations located in sites with lower and more variable rainfall (northern populations) would exhibit patterns of trait means and plasticity reflecting a water-conservative strategy, while populations in less arid and less variable environments (southern populations) would exhibit a water-acquisitive strategy. We also tested the hypothesis that functional variation in trait means and plasticity are not alternative mechanisms of adaptation to the environment. In a common garden experiment using plants from seeds collected from six populations spanning the species distribution range we found that plants from the northern populations were smaller, had fewer leaves, lower photosynthetic rates and had higher plasticity for root:shoot ratios and lower plasticity for leaf shedding, suggesting a resource-conservative strategy compared to plants from the southern populations, which showed a resource-acquisitive strategy. We found no association between variation in trait means and plasticity, which indicates that these are not alternative mechanisms of plant adaptation to environmental variation. Results suggest that *E. canescens* populations have evolved different strategies to cope with drought stress depending on their location along the Atacama Desert's aridity gradient. This gives us a better understanding of the ecological and evolutionary processes that drive phenotypic variation among populations.

1. Introduction

Plant species in arid environments show different adaptations to cope with drought (Larcher, 2003). In particular, desert woody plants show features that can be related to either drought avoidance or drought tolerance (Lambers et al., 2008). Deciduous species, which avoid drought through leaf shedding and physiological dormancy, must take advantage of wet periods; consequently, they have traits to acquire and use water quickly: relatively large leaf areas, high growth rates and high photosynthetic rates. In contrast, evergreen species may tolerate

drought and show traits that secure water uptake from deeper sources (high root:shoot ratio) and decrease water loss (high stomatal control, small leaf area) (Poorter and Marksteijn, 2008; Slot and Poorter, 2007; Ward, 2009). Thus, deciduous and evergreen species show resource-acquisitive and resource-conservative strategies of water use, respectively. Several studies at the interspecific level have reported how traits related to drought avoidance or tolerance vary along aridity gradients (Hallik et al., 2009; Marksteijn and Poorter, 2009; Slot and Poorter, 2007). However, few empirical studies have addressed whether a single species can exhibit both drought avoidance and drought tolerance

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strategies along a water availability gradient (e.g., Brouillette et al., 2014). In other words, there is scant evidence of changes in the relationships among traits (i.e., trait syndromes) along water availability gradients in such a way that contrasting strategies (acquisitive vs. conservative) are observed.

Differences in functional traits related to water use among populations of a single species can result from phenotypic plasticity, ecotypic differentiation or both (Dudley, 1996; Gianoli and Gonzalez-Teuber, 2005; Heschel et al., 2004; Lázaro-Nogal et al., 2015; Ramírez-Valiente et al., 2010). Phenotypic plasticity to water availability is greater in populations with greater temporal heterogeneity in soil moisture (Gianoli, 2004; Gianoli and Gonzalez-Teuber, 2005; Lázaro-Nogal et al., 2015; Liu et al., 2014; Molina-Montenegro et al., 2010), while the magnitude of population differentiation often correlates with environment, that is, increasing differences in selection pressures along environmental gradients may promote increased population differentiation (Akman et al., 2016; Bradburd et al., 2013; Sexton et al., 2014; Shimono et al., 2009; Wang et al., 2013). Phenotypic plasticity and ecotypic differentiation are non-mutually exclusive means of adaptation to environmental variation (Valladares et al., 2014); however, they have been considered as alternative strategies (Hassel et al., 2005; Salamin et al., 2010) and have been compared for their effectiveness in coping with climate change (see Vázquez et al., 2017) and for their contribution to phenotypic divergence in invasive plants (Liao et al., 2016). Little integration of ecotypic differentiation and phenotypic plasticity into the fundamental ecology of plant species, particularly as it relates to resource-use strategy (Reich et al., 1997), has been attempted so far.

Plant phenotypic adjustments to water availability, via plastic responses and/or adaptive population differentiation, involve a suite of physiological, morphological and biomass allocation traits, which do not show consistent trends in their relative importance or extent of variation, rather showing idiosyncratic patterns (Bibee et al., 2011; Gianoli and Gonzalez-Teuber, 2005; Heschel et al., 2004; Lázaro-Nogal et al., 2015; Ramírez-Valiente et al., 2010). Typically, plants deal with reduced soil moisture by showing less, smaller, and thicker leaves, reduced photosynthesis and increased water-use efficiency, which reduces evaporative water losses, and increased biomass allocation to roots, which enhances water uptake; plants are also of smaller size, which reduces overall photosynthetic carbon demand (Lambers et al., 2008; Larcher, 2003; Schulze et al., 2005). Importantly, this phenotypic variation is ecologically significant (Gianoli and Valladares, 2012) and it is often associated with plant performance and fitness in natural and experimental populations (Carlson et al., 2016; Geber and Griffen, 2003; Heschel et al., 2002; Maherali et al., 2010).

In view of the ideas discussed above, we expected that, for a woody plant species distributed along an aridity gradient, populations located in sites with lower and more variable rainfall would show patterns of trait means and plasticity reflecting a water-conservative (“evergreen-like”) strategy, while populations in less arid and less variable environments would show patterns of trait means and plasticity reflecting a water-acquisitive (“deciduous-like”) strategy. Furthermore, we expected to find at the species level that phenotypic plasticity and ecotypic differentiation would show either a positive association, resulting from similar selective pressures acting locally, or no association, reflecting the idiosyncratic nature of adaptations discussed above, but not a negative correlation, which would suggest that they are alternative mechanisms of adaptation.

Here, we tested these hypotheses using as study species the native sunflower *Encelia canescens* Lam. (Asteraceae), a drought-deciduous shrub distributed along ca. 600 km of latitudinal range in the Atacama Desert (Northern Chile), where aridity and rainfall variability markedly increase from south to north (Carvajal et al., 2015; Rundel et al., 1991; Squeo et al., 1994). Specifically, to determine whole-plant, morphological and physiological responses of *E. canescens* to experimental drought we used a common garden with plants from six populations.

Table 1

Location and climatic characteristics of *E. canescens* populations sampled per region. Climate data (Mean annual precipitation, MAP; Mean annual temperature, MAT) were obtained from the WorldClim database (<http://www.worldclim.org/>). CHA: Chañaral, CAL: Caldera, PAJ: Caleta Pajonales, CHO: Los Choros, ROM: Romeral, and PAL: Puerto Aldea. De Martonne aridity index (DMAI) was calculated as $MAP/(MAT + 10)$; thus, the lower the index value, the greater the aridity. Values of coefficients of variation (CV) in MAP were calculated as $(\text{Standard deviation}/MAP) \times 100$. Data for CV were obtained from three different sources: ¹The Chilean Meteorological Agency (www.meteochile.cl) for the period 1986–2011, ²CEAZA-Met weather station (www.ceazamet.cl) for the period 1956–2011. ³Weather station from Fray Jorge National Park for the period 1988–2012.

Region	Population	Location	MAP (mm)	MAT (°C)	DMAI	CV (%)
North	CHA	26°18'28" S – 70°26'23" W	18	17.2	0.6	¹ 214.29
North	CAL	26°58'05" S – 70°46'10" W	31	15.3	1.2	¹ 196.93
North	PAJ	27°46'57" S – 71°01'36" W	38	16.0	1.5	¹ 145.27
South	CHO	29°17'53" S – 71°17'33" W	64	16.2	2.4	¹ 129.29
South	ROM	29°43'48" S – 71°19'24" W	80	15.3	3.2	² 82.91
South	PAL	30°18'27" S – 71°35'26" W	106	16.2	4.0	³ 75.09

These populations span almost the entire distribution range of the study species (Appendix S1) and can be grouped into two regions (north and south) with three populations each. *E. canescens* is a suitable study model as earlier work with three populations of this species reported population differentiation and phenotypic plasticity to drought in several functional traits (Carvajal et al., 2015).

2. Material and methods

2.1. Seed collection and population characteristics

Encelia canescens seeds (pubescent achenes, Olivares and Squeo, 1999) were collected in December 2010 from six coastal sites in the Atacama Desert, from 26° to 30°S: Chañaral (CHA), Caldera (CAL), Caleta Pajonales (PAJ), Los Choros (CHO), Romeral (ROM) and Puerto Aldea (ALD) (Appendix S1, Table 1). In each population, we randomly selected 30 shrubs and collected three to five flower heads with mature seeds per shrub. The first three populations are located in the Northern region, while the other three populations lie within the Southern region of the Coastal Atacama Desert. Mean annual precipitation in these populations ranges between 18 and 106 mm, whereas mean annual temperature is fairly stable, fluctuating between 15 and 17 °C (Table 1). For each site we calculated both the De Martonne's aridity index (De Martonne, 1926) ($DMAI = MAP/[MAT + 10]$), where MAP and MAT represent mean annual precipitation and mean annual temperature, respectively, and the coefficient of variation in precipitation ($CV = SD/MAP$), where SD is the standard deviation of the precipitation. The former indicated that all populations belong to a hyper-arid desert, and all of them showed significant interannual variability in precipitation; nonetheless, aridity and CV increased from south to north (Table 1). Furthermore, because MAP = 50 mm is the threshold value that separates xeric scrub (MAP ≥ 50 mm) and semi-desertic scrub (MAP < 50 mm) in Chilean vegetation formations (Moreira-Muñoz, 2011), we grouped populations CHA, CAL and PAJ within the north region (MAP < 50 mm) and populations CHO, ROM and ALD into the south region (Table 1). In fact, populations in the north region were significantly more arid ($F_{1,4} = 15.74$, $P = 0.017$; ANOVA) and variable ($F_{1,4} = 11.25$, $P = 0.029$) than those in the south region.

2.2. Common garden experiment

To assess the degree to which among-population phenotypic

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