Two Mediterranean annuals feature high within-population trait variability and respond differently to a precipitation gradient

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Abstract

Intraspecific trait variability plays an important role in species adaptation to climate change. However, it still remains unclear how plants in semi-arid environments respond to increasing aridity. We investigated the intraspecific trait variability of two common Mediterranean annuals (\textit{Geropogon hybridus} and \textit{Crupina crupinastrum}) with similar habitat preferences. They were studied along a steep precipitation gradient in Israel similar to the maximum predicted precipitation changes in the eastern Mediterranean basin (i.e. \textasciitilde30\% until 2100). We expected a shift from competitive ability to stress tolerance with decreasing precipitation and tested this expectation by measuring key functional traits (canopy and seed release height, specific leaf area, N- and P-leaf content, seed mass). Further, we evaluated generative bet-hedging strategies by different seed traits. Both species showed different responses along the precipitation gradient. \textit{C. crupinastrum} exhibited only decreased plant height towards aridity, while \textit{G. hybridus} showed strong trends of generative adaptation to aridity. Different seed trait indices suggest increased bet-hedging of \textit{G. hybridus} in arid environments. However, no clear trends along the precipitation gradient were observed in leaf traits (specific leaf area and leaf N-/P-content) in both species. Moreover, variance decomposition revealed that most of the observed trait variation (\textasciitilde50\%) is found within populations. The findings of our study suggest that responses to increased aridity are highly species-specific and local environmental factors may have a stronger effect on intraspecific trait variation than shifts in annual precipitation. We therefore argue that trait-based analyses should focus on precipitation gradients that are comparable to predicted precipitation changes and compare precipitation effects to effects of local environmental factors.

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Keywords: Climate change; Functional ecology; Plant height; Drought stress; Rainfall gradient; Trait–environment relationship; Local adaptation; Phenotypic plasticity

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Introduction

Climate change has been identified as one of the major threats to biodiversity (Sala et al. 2000). Still, our understanding of how plants respond to climate change is scarce (Franks, Weber, & Aitken 2014; Matesanz & Valladares 2014). Plant communities in semi-arid regions, like the Mediterranean, are predicted to be particularly vulnerable to climate change (Wu, Dijkstra, Koch, Penuelas, & Hungate 2011; Golodets et al. 2015; Harrison, Gornish, & Copeland 2015; Knapp et al. 2015), since decreasing precipitation and increasing temperature has led to an ongoing aridity in these regions (Sheffield & Wood 2008; IPCC 2013). In contrast, a recent long-term precipitation manipulation experiment revealed that a decrease of precipitation (~30%) has only a marginal effect on the species composition and biomass production, presumably because species are adapted to a high variability in precipitation (Tiélbörger et al. 2014; Bilton, Metz, & Tiélbörger 2016). These contrasting findings call for a better understanding of how plants respond to decreasing precipitation.

Theory predicts a fundamental trade-off between competitive ability and stress tolerance in plants (Grime 1974, 1977; Westoby 1998). In the Mediterranean region, plants should show adaptations towards competitive ability under mesic conditions and stress tolerance with increasing aridity (Schiffers & Tiélbörger 2006; Liancourt & Tiélbörger 2009). However, these adaptations may be expressed in different niche dimensions and include various vegetative and generative functional traits. The competitive environment under mesic conditions should select for large plant height and rapid growth rates, indicated by high specific leaf area and leaf nitrogen content (Chapin, Autumn, & Pugnaire 1993; Westoby 1998; Cornwell & Ackerly 2009). In contrast, stress tolerance is mediated by low growth rates, i.e. decreasing specific leaf area with aridity (Reich et al. 1999; May, Giladi, Ristow, Ziv, & Jeltsch 2013; Baruch et al. 2017). With respect to generative strategies, a higher dispersal ability is assumed to be beneficial under arid conditions for two reasons. On the one hand, plants under environmental stress may invest in dispersal ability in order to escape from the adverse conditions of the mother-plant site (e.g. Levin, Cohen, & Hastings 1984; Imbert & Ronce 2001). On the other hand, bet-hedging theory predicts that plants increase risk-spreading strategies, like dispersal, under arid conditions, because precipitation becomes increasingly unpredictable (Siewert & Tiélbörger 2010). An increased dispersal ability may be beneficial if the spatial arrangement of suitable habitats changes in time, e.g. through increasing variation of annual precipitation in arid areas (Noy-Meir 1973; Siewert & Tiélbörger 2010). Plants may increase their dispersal ability by a higher amount of seeds that have a lower seed mass (Weiher et al. 1999). Further, species that produce different seed types (seed heterocarpy) may alter the ratio between specific seed types, for instance they may produce a higher proportion of seeds with a well-developed pappus (Imbert & Ronce 2001). In general, seed heterocarpy is regarded as an alternative bet-hedging strategy to cope with spatio-temporal variability (Venables 1985; Imbert 2002). Therefore, it can be expected that species increase seed heteromorphism under unpredictable, arid conditions. Several studies revealed that heterocarpic species show adaptations towards aridity (Ellner & Shmida 1984; Imbert & Ronce 2001; Gemeinholzer, May, Ristow, Batsch, & Lauterbach 2012) and there is some evidence that seed heterocarpy is associated with dry, unpredictable environments (Ellner & Shmida 1984; Imbert 2002). However, studies are missing that compare responses of generative traits between heterocarpic and homocarpic species.

Trait shifts along natural precipitation gradients can be used as a space-for-time approach, in order to predict long-term trait responses to decreasing precipitation (Sandel et al. 2010). On the one hand, trait shifts may indicate ecotypic differentiation along environmental gradients. On the other hand, trait shifts allows to get a mechanistic understanding in which niche dimensions species respond to climate change (Petri, Tiélbörger, Belkin, Sternberg, & Jeltsch 2006). While several empirical studies observed intraspecific trait shifts of plants along precipitation gradients, the majority of these studies investigated only a limited number of populations (n < 5) (e.g. Aronson, Kigel, Shmida, & Klein 1992; Liancourt & Tiélbörger 2009; Ariza & Tiélbörger 2011; Harel, Holzapfel, & Sternberg 2011; Petri et al. 2006) and/or used precipitation gradients that were orders of magnitude more than the predicted precipitation changes (e.g. Volls, Mendlinger, & Ward 2002; Lázaro-Nogal et al. 2015; Dyer, Woodward, & Petersen 2016). Hence, it remains unclear whether trait responses along large-scale precipitation gradients are actually of importance along precipitation gradients corresponding to predicted precipitation changes. Additionally, evidence is growing that a substantial proportion of intraspecific trait variability is actually found within populations (Albert et al. 2010; Messier, McGill, & Lechowicz 2010; Siefert et al. 2015). This high intraspecific trait variability may be even more important than interspecific trait variation to buffer negative effects of climate change, such as drought (Jung et al. 2014). Therefore, a critical assessment of how intraspecific trait variability is distributed across scales, i.e. within-populations and between populations along precipitation gradients may help to reveal the importance of predicted precipitation changes for trait adaptation under climate change.

The aims of the current study are a) to test whether Mediterranean annuals show adaptations ranging from competitive ability to stress tolerance along a precipitation gradient and b) to quantify how much of the observed intraspecific trait variation can actually be attributed to differences in amounts of precipitation. As in other semi-arid regions, Israel is experiencing a decline in annual precipitation with a shortened growing season for the last centuries (IPCC 2013; Ziv, Saaroni, Pargament, Harpaz, & Alpert 2014), which is predicted to continue (IPCC 2013). Our study region in Israel is set at the transition zone between Mediterranean...
and desert ecosystems along a steep precipitation gradient (300 mm–420 mm). Furthermore, the study region is located within the most southern distribution edge of many Mediterranean plants. Thus, Mediterranean species should be particularly vulnerable to reduced precipitation in this region. Our study species are two widespread Mediterranean annuals *Geropogon hybridus* and *Crupina crupinastrum*, having similar environmental preferences but differing in their regeneration strategy (heterocarpic and homocarpic, respectively). We measured key functional traits that are expected to respond to decreasing precipitation and estimated their bet-hedging strategies with different trait indices.

**Materials and methods**

**Study region**

Our study region is situated in the Southern Judean Lowlands in Israel (31°24′–31°41′N; 34°46′–24°52′E) (Fig. 1). The region consists of a mosaic of semi-natural vegetation, with grazing by cattle and goats since the Bronze Age, and intense agricultural farming. As a result, the semi-natural vegetation features semi-steppe batha types and grasslands with a high proportion of annual species (>65%) (see Giladi, Ziv, May, & Jeltsch 2011 for a detailed description of the study region). The precipitation decreases drastically along a short stretch of 30 km from approximately 420 mm in the north to about 300 mm in the south, resulting in a 30% decrease that corresponds roughly to maximum predicted precipitation change until 2100 in the Mediterranean basin (IPCC 2013; see Evans 2008; Lelieveld et al. 2012; Saaroni, Ziv, Lempert, Gazit, & Morin 2015 for predicted precipitation changes in Israel). Soil fertility increases with precipitation (May et al. 2013), while diversity of microhabitats, due to shrubs, bare rocks and varying soil depths remains constant along the precipitation gradient (Bergholz et al. 2017). Previous vegetation studies in the region revealed a decrease of species richness and individual plant density towards the arid end of the precipitation gradient (Giladi et al. 2011) accompanied by a decrease of community-weighted mean traits of specific leaf area and plant height (May et al. 2013). These findings indicate a shift from a more competitive environment in the north to more stressful conditions in the south. During the sampling season in 2010–2011, the annual precipitation was approximately 66% of the mean annual precipitation (see Appendix A: Fig. 1).

**Study species**

We selected two annual species that are common in the entire Mediterranean region: *Geropogon hybridus* (L.) Sch.Bip. and *Crupina crupinastrum* (Moris) Vis. Both species belong to the family *Asteraceae* and are primarily found in batha on various soil types. Furthermore, both species occur under very similar environmental conditions in Israel (Table 1). The study region is situated at the Southern margin of their distribution range (see Appendix A: Fig. 2). *C. crupinastrum* is homocarpic and produces one to six similar seeds in each of the one to 16 capitulas produced by an individual. *Geropogon hybridus* is heterocarpic and produces two different seed types. At the central whorls of the capitula seeds with a fully developed pappus are produced (henceforth pappus seeds). Seeds at the outer whorls contain a reduced pappus with three elongated and two rudimentary aristate scales (hence-
Table 1. Comparison of environmental preferences of both species in Israel. The table shows mean and standard errors of key environmental factors, where both species occurred. Number of sampling points: *Geropogon hybridus* n = 350, *Crupina crupinastrum* n = 321. Asterisk (*) indicates that environmental factor significantly differ between species. Data were taken from BioGIS, 2012. Israel Biodiversity Information System (http://www.biogis.huji.ac.il/).

<table>
<thead>
<tr>
<th></th>
<th><em>Geropogon hybridus</em></th>
<th><em>Crupina crupinastrum</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean annual rainfall</td>
<td>520.32 (±9.02)</td>
<td>534.93 (±10.23)</td>
</tr>
<tr>
<td>[mm]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean January temp.</td>
<td>10.20 (±0.09)</td>
<td>10.13 (±0.11)</td>
</tr>
<tr>
<td>[°C]</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altitude [m]</td>
<td>306.51 (±15.33)</td>
<td>348.32 (±17.86)</td>
</tr>
<tr>
<td>Aspect [°]</td>
<td>194.11 (±3.62)</td>
<td>191.72 (±3.43)</td>
</tr>
<tr>
<td>Slope [°]</td>
<td>5.57 (±0.28)</td>
<td>5.56 (±0.31)</td>
</tr>
<tr>
<td>Seasonal temp. range</td>
<td>15.56 (±0.83)</td>
<td>15.22 (±0.85)</td>
</tr>
<tr>
<td>[°C]</td>
<td></td>
<td></td>
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</tbody>
</table>

forth trident seeds), which are much heavier (mean ± SE: 17.65 ± 0.25 mg) than the pappus seeds (9.75 ± 0.13 mg). About 2% of the seeds are of an intermediate type, which were excluded from further analyses. Individuals in our study region produce mainly one flower (up to four) with five to 60 seeds (see Feinbrun-Dothan 1978, for further description of the species).

**Trait measurements**

The trait sampling was conducted in three sampling areas (6 km × 4 km), which were placed along the precipitation gradient from North to South (Fig. 1). In each area, we selected five study sites where both species co-occurred (central sampling area six study sites). Each study site represented an isolated patch (size mean ± SE: 40.1 ± 26 ha, distance between study sites, mean ± SE: 1298 ± 135 m) of semi-natural vegetation in the agricultural landscape, except for the Southern sampling area. Here, we had to sample three populations on one large patch, as the frequency of both species decreased towards South (distances between the study sites within the large patch: 927 m, 1296 m and 1395 m). Since the dispersal ability of Mediterranean annuals is low (Siewert & Tielbörger 2010) and neighboring populations of *G. hybridus* in the study region show a strong genetic differentiation (Müller et al. 2017), these sampling sites were regarded as separate populations.

At each study site we randomly chose ten individuals within an area of approximately one hectare and measured plant height (canopy and seed release height), specific leaf area, nitrogen and phosphorous content of leaves following standard sampling protocols (Perez-Harguindeguy et al. 2013). For *C. crupinastrum*, we counted all open flowers and collected all ripe seeds of the first flower and weighted them afterwards. For *G. hybridus*, trait sampling was done in two steps, since leaves were already withered when seeds of the first flower were fully ripe. First, we sampled all traits as described above except of seed mass. Second, we collected all seeds of the first flower and recorded the maximum plant height of ten additional individuals per study site. Seeds were counted and seed types (pappus vs. trident seeds) distinguished. From each individual four seeds of each seed type (if available) were weighed. Sampling was conducted from 01/04/2011 to 30/04/2011 at the end of the raining season.

Mean seed mass of *G. hybridus* was calculated by the sum of both seed type masses (mean seed mass × number of seeds of the specific seed type) divided by the total number of seeds in order to reflect seed mass and proportion differences between both seed types. For analyses of bet-hedging strategies, we calculated the coefficient of variance of seed masses of each individual, which estimates the degree of seed heteromorphism of each individual. For *G. hybridus*, we further calculated the seed mass ratio between both seed types (mean seed mass of pappus seeds/mean seed mass of trident seeds) as a second index for seed heterocarypy (Ellner & Shmida 1984) and the proportion of pappus seeds as a surrogate for dispersal ability (Imbert & Ronce 2001).

**Statistical analyses**

We used linear mixed-effects models in order to reveal effects of the precipitation gradient on functional traits and bet-hedging indices. As response variable we used the traits canopy and seed release height, specific leaf area, nitrogen and phosphorous leaf content, mean seed mass, seed number as well as total seed mass (mean seed mass × seed number). We included the sampling area as categorical fixed effect and the population as random effect to account for the nested study design. Since generative traits (e.g. seed mass, seed number) commonly depend on plant size (Westoby, Falster, Moles, Vesk, & Wright 2002), these models included also seed release height (henceforth plant height) as predictor. In this way, we ensure that possible trends of generative traits are not just a result of varying plant height along the precipitation gradient. All traits were log-transformed prior to analysis (except ‘prop pappus seeds’, which was arcsine-square root transformed) in order to meet statistical assumptions. Significance of the fixed effects was assessed with a F-test via Kenward–Roger approximation (Halekoh & Hojsgaard 2014) as recommended by Bates, Mächler, Bolker, and Walker (2015).

We used variance decomposition to estimate the proportion of observed trait variation along the precipitation gradient between populations of the same sampling area and within populations. For this purpose, we used linear mixed-effects models with hierarchically nested random effects (Messier et al. 2010), which are population nested in the sampling area. Models of generative traits included seed release height as a predictor (see above). Variance components of the random effects were extracted with the R-function `varcomp`. 
All analyses were conducted for both species separately and were carried out with R Version 3.1. and the R-packages lme4, pkbtest and ape.

**Results**

The majority of the investigated traits were correlated to each other, while in most cases the relationships were similar for both species (see Appendix A: Table 1). The most significant correlations included plant height, being positively correlated to generative traits (mean and total seed mass, number of flowers and seeds), and specific leaf area, being negatively correlated with plant height, number of seeds and flowers. Our study species responded differently to the precipitation gradient (Table 2). *Geropogon hybridus* showed significant trends in generative traits along the precipitation gradient. The species produced a higher number of seeds and mean seed mass decreased with aridity (Fig. 2A, B). Moreover, the production of seed types changed along the precipitation gradient. Both the proportion of pappus seeds and the seed mass ratio increased towards the Southern study sites (Fig. 2C, D). Plant height did not change along the precipitation gradient for this species. In contrast, *C. crupinastrum* showed a decrease of plant height towards the South (Fig. 3B). All considered generative traits of this species appeared to be independent of the precipitation gradient (see Appendix A: Fig. 3), though plant height had a positive effect on number of seeds and flowers as well as on mean seed mass (Table 2). Both species showed no trend in total seed mass or number of flowers along the gradient (Table 2). Leaf traits showed no consistent trend along the precipitation gradient, although sampling area had a significant effect on specific leaf area for both species and leaf N-content in *G. hybridus*. In the central sampling area, plants of both species had on average the highest specific leaf areas and the lowest leaf N-contents (Fig. 3C–F).

The variance decomposition revealed that most of the observed trait variation remained unexplained by the nested random effects model, indicating that most trait variation (51–98%) existed within populations (Table 3, see also Figs. 2 and 3). Both predictors, sampling area and the population within the sampling area, explained on average similar proportions of trait variations (range 0–41%, Table 3), though it strongly depended on the species and trait under consideration. The population level explained consistently more variation in *C. crupinastrum* compared to *G. hybridus*, whereas the latter consisted more trait variation within the population. As expected, the proportion of the variance explained by the sampling area was in general higher for traits that showed significant trends along the precipitation gradient compared to traits that were not influenced by the sampling area. However, in all models the within-population trait variability was higher than the trait variability between populations and along the precipitation gradient.

**Discussion**

Decreasing precipitation in the Mediterranean basin increases environmental stress for plants. As a result, plant species should show shifts from competitive ability towards stress tolerance along natural precipitation gradients. In this study, we observed that a) two Mediterranean annuals showed contrasting trait responses towards aridity and b) most of the observed trait variation was found within populations.

**Trait responses along the precipitation gradient**

*Geropogon hybridus* responded in generative traits and showed a trade-off between seed mass and seed number (Westoby et al. 2002). Seed mass decreased with aridity, while seed number increased, in agreement with findings at the community level in the same study system (May et al. 2013). Larger seed mass might be an adaptation to a more competitive environment in mesic conditions (Harel et al. 2011). However, Ben-Hur and Kadmon (2015) showed that the competitive hierarchy was not related to seed mass in Mediterranean annuals, which was supported by similar findings from other ecosystem studies (Ben-Hur & Kadmon 2015). An alternative explanation for the observed shifts in seed mass and seed number is that plants under the stressful and unpredictable conditions of arid environments increase their dispersal ability (Siewert & Tiellörger 2010). A higher number of seeds in combination with lower seed mass and higher proportion of pappus seeds should increase the dispersal ability under arid conditions in *G. hybridus*. Similarly, *Catananche lutea*, another heterocarpic annual, increased the dispersal ability towards aridity in the same study region by producing a higher proportion of aerial flower heads at the expense of subterranean flower heads (Gemeinholzer et al. 2012). Moreover, *G. hybridus* showed a higher seed diversification under dry conditions, as the seed mass ratio between pappus and trident seeds increased in the southern sampling areas. While *G. hybridus* increases its dispersal ability with pappus seeds under dry conditions (see above), the heavier trident seeds may guarantee the establishment of at least a few seedlings near the mother plant, which is a suitable site (“mother-plant theory”; Zohary 1937). Hence, *G. hybridus* has a diversified bet-hedging dispersal strategy, which is more developed under dry conditions. Interestingly, the proportion of heterocarpic annuals slightly increased with aridity in our study system (sampling area north = 16.4%, central = 17.6%, south = 18.3%; data taken from Giladi et al. 2011), which goes in line with the intraspecific findings on *G. hybridus* and supports the expectation that seed heterocarpy is associated with unpredictable environments (Imbert 2002). Certainly, seed heterocarpy may increase the fitness in unpredictable environments also through other mechanisms that are not related to dispersal, e.g. contrasting germination behavior between seed types (Venable 1985). However, the seed trait responses of *G. hybridus* indicate an adaptation to deal with
Table 2. Effect of precipitation gradient (sampling area) on functional traits of C. crupinastrum and G. hybridus. The linear mixed-effects models included study site as random effect and sampling area as categorical fixed effect with three levels (north, central, south). Models of generative traits included additionally plant height as covariate. Trend signifies whether traits significantly increase (∎) or decrease (∍) towards north or show no clear trend (∩). Significance of the fixed effects was determined with a F-test via Kenward–Roger approximation. All traits were log-transformed prior to analyses, except of Prop. pappus seeds, which was arcsine root-transformed. Significant effects (p<0.05) of sampling area are bold typed.

<table>
<thead>
<tr>
<th>Trait</th>
<th>C. crupinastrum</th>
<th>G. hybridus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trend Sampling area</td>
<td>Plant height</td>
</tr>
<tr>
<td>Seed release height</td>
<td>↗ 17.80 &lt;0.001</td>
<td>3.73 0.052</td>
</tr>
<tr>
<td>Canopy height</td>
<td>↗ 10.85 0.002</td>
<td>2.92 0.090</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>6.93 0.009</td>
<td>5.49 0.019</td>
</tr>
<tr>
<td>Leaf N-content</td>
<td>0.82 0.463</td>
<td>9.65 0.003</td>
</tr>
<tr>
<td>Leaf P-content</td>
<td>0.56 0.585</td>
<td>2.18 0.156</td>
</tr>
<tr>
<td>Total seed mass</td>
<td>0.18 0.840</td>
<td>3.65 0.055</td>
</tr>
<tr>
<td>Numb. flowers</td>
<td>2.77 0.084</td>
<td>3.35 0.066</td>
</tr>
<tr>
<td>Numb. seeds</td>
<td>0.76 0.480</td>
<td>9.13 0.003</td>
</tr>
<tr>
<td>Mean seed mass</td>
<td>0.33 0.721</td>
<td>7.83 0.006</td>
</tr>
<tr>
<td>CV seed mass</td>
<td>0.52 0.601</td>
<td>1.03 0.384</td>
</tr>
<tr>
<td>Prop. pappus seeds</td>
<td>7.43 0.007</td>
<td>16.77 &lt;0.001</td>
</tr>
<tr>
<td>Seed mass ratio</td>
<td>16.77 &lt;0.001</td>
<td>&lt; 0.01 0.985</td>
</tr>
</tbody>
</table>

Fig. 2. Generative traits of Geropogon hybridus along the precipitation gradient with increasing annual precipitation from south to north. Each point represents the mean trait value (±SE) of one study site. (A) mean seed mass, averaged across both seed types (see Materials and methods), (B) number of seeds in the capsula, (C) proportion of pappus seeds, (D) seed mass ratio between the two seed types (mean seed mass pappus seed/mean seed mass trident seed). The statistical analyses included also plant height as covariate (see Table 2).
Fig. 3. Vegetative trait responses of *G. hybridus* (A, C, E) and *C. crupinastrum* (B, D, F) along the precipitation gradient with increasing precipitation amounts towards north. Points indicate the mean trait value of one study site (±SE). Plant height refers to the seed release height.

Table 3. Variance decomposition for each trait and for both species. The table shows the proportion (%) of the trait variation explained by the nested factors sampling area and population. The third column (within) gives the trait variation which remains unexplained, i.e. is found within populations. The analyses were conducted with hierarchically nested linear mixed-effects models. CV$_{tot}$ refers to the coefficient of variation within the whole study region of the untransformed trait. CV$_{pop}$ refers to the average trait variability (coefficient of variation) within populations.

<table>
<thead>
<tr>
<th></th>
<th><em>C. crupinastrum</em></th>
<th><em>G. hybridus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sampling area</td>
<td>Population</td>
</tr>
<tr>
<td>Seed release height</td>
<td>20.10</td>
<td>17.42</td>
</tr>
<tr>
<td>Canopy height</td>
<td>16.74</td>
<td>14.39</td>
</tr>
<tr>
<td>Specific leaf area</td>
<td>28.46</td>
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</tr>
<tr>
<td>Leaf N-content</td>
<td>0.00</td>
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</tr>
<tr>
<td>Leaf P-content</td>
<td>0.00</td>
<td>35.45</td>
</tr>
<tr>
<td>Total seed mass</td>
<td>0.00</td>
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</tr>
<tr>
<td>Numb. flowers</td>
<td>16.35</td>
<td>19.71</td>
</tr>
<tr>
<td>Numb. seeds</td>
<td>11.96</td>
<td>8.06</td>
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<tr>
<td>Mean seed mass</td>
<td>8.98</td>
<td>35.22</td>
</tr>
<tr>
<td>CV seed mass</td>
<td>0.00</td>
<td>1.15</td>
</tr>
<tr>
<td>Prop. pappus seeds</td>
<td>13.12</td>
<td>5.46</td>
</tr>
<tr>
<td>Seed mass ratio</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td><strong>10.26</strong></td>
<td><strong>20.72</strong></td>
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increasing unpredictability due to the spatial and temporal variation in environmental conditions. A recent genetic study revealed genetic differentiation in the same populations of *G. hybridus* along the precipitation gradient (Müller et al. 2017), indicating that precipitation selects for different ecotypes in the study region. Indeed, a common garden experiment revealed that onset of flowering was accelerated with increasing aridity of the source population in *G. hybridus* (Bergholz, unpublished data), which is a common response to aridity (e.g. Hänel & Tielbörg 2015). However, the experiment failed to show significant shifts of generative traits as observed along the precipitation gradient in the field study.

In contrast to the generative responses of *G. hybridus*, *C. cruciinastrum* showed predominantly a decrease in plant height under drier conditions. This pattern reflects the decreasing productivity coupled with lower competition for light (May et al. 2013). Furthermore, the shorter growing season under dry conditions leads to an acceleration of phenology (Hänel & Tielbörg 2015). As a result, plants invest less time in vegetative growth and therefore reach smaller plant height at the end of the growing season.

Surprisingly, none of the species showed a clear trend of leaf traits along the precipitation gradient, as predicted by theory (Westoby 1998) and observed at the community level (May et al. 2013). Similarly, Albert et al. (2010) revealed that intraspecific responses of leaf traits along environmental gradients were highly species-specific, partly hump-shaped and idiosyncratic. Although studies showed that precipitation affects intraspecific responses of leaf traits in semi-arid environments (Ramírez-Valiente, Sánchez-Gómez, Aranda, & Valladares 2010; Carlson, Adams, & Holsinger 2016; Baruch et al. 2017), these studies analyzed evergreen woody plants, whose leaves have to endure long dry seasons. In contrast, leaves of annuals in our study region withered at the end of the rainy season. As a result, these species may not show stress tolerance in foliar leaf traits towards aridity.

**Trait variation across scales**

The variance decomposition analysis revealed a high proportion of within-population variability (51–98%) within populations. Both species under study showed a typical within-population trait variability for annuals in the study region (see Appendix A: Fig. 4). In comparison to woody plant communities (Bastias et al. 2017) and subalpine grasslands (Albert et al. 2010), we observed a similar within-population trait variability in leaf traits and plant height. However, our analyses revealed further that both sampling area and population level explained only a limited (to negligible) amount of trait variation. Hence, sources of intraspecific trait variability within populations seem to be more important than differences in precipitation amounts or other factors that differ between populations. Our study system is characterized by a high degree of small-scale spatial environmental heterogeneity due to the presence of shrubs and perennial grass tussocks, bare rocks and varying soil depths (Giladi et al. 2011; Bergholz et al. 2017). These structures modulate water and light availability for annual plants (Luzuriaga, Sanchez, Maestre, & Escudero 2012; Segoli, Ungar, Giladi, Arnon, & Shachak 2012). As a result, varying environmental conditions should favor different phenotypes and therefore maintain a large variation of genotypes within a population (Ravenscroft, Fridley, & Grime 2014). For instance, the higher water availability of deep-soil hollows should favor large individuals with high growth rates, i.e. high specific leaf area. In contrast, dry slopes should select for small individuals. Therefore, small-scale heterogeneity may, in particular, be important for buffering negative effects of climate change, as it fosters populations having individuals with different traits (Fridley, Grime, Askew, Moser, & Stevens 2011; Ravenscroft et al. 2014). Moreover, the study system features a substantial variation of precipitation amounts between years (CV ~0.35). This temporal variability may additionally maintain diversity in genotypes within populations, with genotypes that are adapted to different water availability, e.g. dry and wet years. Our study was conducted in a particularly dry year, in which the most northern sites received precipitation equaling that at the most Southern site in an average year. Surprisingly, the reproductive output, measured as total seed mass and number of flowers, remained constant along the precipitation gradient. This pattern may reflect the high adaptability of populations at the margin of their distribution, indicating that even in a particular dry year the most southern populations are able to successfully reproduce. Therefore, future decrease in average precipitation may not have a large effect on species performance, since species in this region are adapted to large differences in precipitation and small-scale heterogeneity (Tielbörg et al. 2014). However, it should be noted that this study did not investigate other important measures to predict survival chance under climate change, such as survival until maturity and population sizes.

**Conclusions**

Our study revealed that species with similar ecological preferences may respond differently to decreasing precipitation, which impedes the prediction of general intraspecific trait responses under climate change (Cochrane, Yates, Hoyle, & Nicotra 2015). Moreover, variance decomposition showed that at the scale under study, precipitation explains only a limited amount of trait variation. Therefore, we encourage researchers to quantify and compare the effects of precipitation gradients that correspond to predicted precipitation gradients and evaluate local environmental factors on key functional traits in order to better understand how predicted climate change influences species performance and distribution.
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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2017.11.001.

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