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

Kolja Bergholz[a,*], Felix May[b,c], Michael Ristow[a], Itamar Giladi[d,e], Yaron Ziv[d], Florian Jeltsch[a,f]

[a] *Department of Plant Ecology and Nature Conservation, Institute of Biology and Biochemistry, University Potsdam, Am Mühlenberg 3, 14476 Potsdam, Germany*
[b] *German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany*
[c] *Institute of Computer Science, Martin Luther University Halle-Wittenberg, 06099 Halle (Saale), Germany*
[d] *Department of Life Sciences, Ben Gurion University of the Negev, Beer Sheva 84105, Israel*
[e] *Mitrani Department of Desert Ecology, Jacob Blaustein Institutes for Desert Research, Ben-Gurion University of the Negev, Sede Boqer Campus, 84990, Israel*
[f] *Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany*

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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 (*Geropogon hybridus* and *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. −30% 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. *C. crupinastrum* exhibited only decreased plant height towards aridity, while *G. hybridus* showed strong trends of generative adaptation to aridity. Different seed trait indices suggest increased bet-hedging of *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 ($\gg$50%) 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.

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

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*Corresponding author.
E-mail address: bergholz@uni-potsdam.de (K. Bergholz).

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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 (Tielbörger et al. 2014; Bilton, Metz, & Tielbörger 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 & Tielbörger 2006; Liancourt & Tielbörger 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 & Tielbörger 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 & Tielbörger 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 (Venable 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 (Petrů, Tielbörger, 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 & Tielbörger 2009; Ariza & Tielbörger 2011; Harel, Holzapfel, & Sternberg 2011; Petrů et al. 2006) and/or used precipitation gradients that were orders of magnitude more than the predicted precipitation changes (e.g. Volis, 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