



Short-term drought and long-term climate legacy affect production of chemical defenses among plant ecotypes



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ABSTRACT

Long and short-term climatic variation affect the ability of plants to simultaneously cope with increasing abiotic stress and biotic interactions. Specifically, ecotypes adapted to different climatic conditions (i.e., long-term legacy) may have to adjust their allocation to chemical defenses against enemies under acute drought (i.e., short-term response). Although several studies have addressed drought effects on chemical defense production, little is known about their intraspecific variation along resource gradients. Studying intraspecific variation is important for understanding how different environments select for defense strategies and how these may be affected directly and indirectly by changing climatic conditions.

We conducted greenhouse experiments with the annual *Biscutella didyma* (Brassicaceae) to test the effects of long-term climatic legacy versus short-term drought stress on the concentrations of defense compounds (glucosinolates). To this aim, four ecotypes originating from a steep aridity gradient were exposed to contrasting water treatments. Concentrations of chemical defenses were measured separately in leaves of young (8 weeks) and old (14 weeks) plants, respectively. For young plants, ecotypes from the wettest climate (long-term legacy) as well as plants receiving high water treatments (short-term response) were better defended. A marginally significant interaction suggested that wetter ecotypes experienced a larger shift in defense production across water treatments. Older plants contained much lower glucosinolate concentrations and showed no differences between ecotypes and water treatments. Our results indicate that younger plants invest more resources into chemical defenses, possibly due to higher vulnerability to tissue loss compared to older plants. We propose that the strong response of wet ecotypes to water availability may be explained by a less pronounced adaptation to drought.

1. Introduction

Plant traits and strategies vary along environmental gradients as a result of abiotic and/or biotic filters that shape plant responses (Reich and Oleksyn, 2004; Johnson and Rasmann, 2011). How abiotic factors, such as water availability, affect traits fundamental to plant fitness and to the ability to cope with biotic stressors, is a key question in ecological research (Chaves et al., 2003; Halpern et al., 2010; Williams et al., 2015). In particular, increasing efforts have been devoted to studying how allocation of resources to plant defense strategies varies within species distributed along environmental gradients. One of the major assumptions regarding such allocations (Resource availability hypothesis, Coley et al., 1985; Sampedro et al., 2011) postulates that plants

living in adverse environments, where replacement of tissues incurs high metabolic costs, will invest more into the production of secondary metabolites (Mailer and Cornish 1987; Haugen et al., 2008; Schreiner et al., 2009). Another prominent hypothesis (plant vigor hypothesis) suggests that bigger and thus more vigorous plants growing in productive environments are highly nutritious and thus preferred by herbivores (Price, 1991) compared to plants growing in low-resource environments (Bouchereau et al., 1996; Gutbrodt et al., 2011; Mewis et al., 2012). However, most empirical tests of these hypotheses were performed employing many plant species across geographic ranges that encompassed different habitats and underlying abiotic conditions. Although this allowed for addressing the role of macroevolutionary processes on plant defense strategies, selection of specific plant defense

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traits could not be unequivocally tested due to confounding effects with species identity. Accordingly, we do not yet know much about whether or not variation in plant defense is caused by long-term evolutionary processes or plastic responses or both, and whether long-term and short-term responses would be in the same direction.

Studies using intraspecific comparisons may uncover how variation in plant traits is constrained by abiotic and biotic factors (Woods et al., 2012; Pratt and Mooney 2013) that are often neglected in large-scale multispecies comparisons (Abdala-Roberts et al., 2016). Plant ecotypes that have evolved under different climates may have adapted their defense strategies to the local biotic and abiotic constraints according to one of the above hypotheses. Such strategies may result from the direct influence of climate on plant traits (i.e., long-term climatic legacy) or from indirect effects. For example, climate may select for different levels of herbivore abundance (Haddad et al., 2001; Pearse and Hipp 2012; Abdala-Roberts et al., 2016) to which plants will respond with increased or decreased defense production. In a recent review, Hahn and Maron (2016) illustrated how the well-known trade-off between growth and defense is not necessarily corroborated for intraspecific comparisons. In high resource environments, plants are exposed to higher herbivore load, but can allocate more resources to both growth and defense due to their larger “energy budget” (Pennings et al., 2009; Pellissier et al., 2014). Conversely, conspecifics constrained by limited resources invest little in both traits. Therefore, positive rather than negative trait correlations may be observed when comparing different populations that occur or have evolved in different environments (van Noordwijk and de Jong, 1986). This suggests that while trade-offs between growth and defense may still be observed, the allocation of resources between these traits within individuals may be highly context-dependent. Thus, the likelihood of observing trade-offs may depend on resource availability, species-specific traits, abiotic and biotic factors and their interaction.

Testing intraspecific trait variation along resource gradients also allows for separating ecotypic differentiation in response to short-term (i.e., sudden drought) from long-term (i.e., mean annual rainfall) climatic effects. For example, ecotypes from variable climates may respond differently to acute climatic variation (short-term) than ecotypes from stable climates (Penuelas et al., 2004; Carvajal et al., 2015). It has been suggested that plants from more variable and unpredictable environments should exhibit larger plasticity in response to environmental variation (Sultan, 1987; Pratt and Mooney, 2013). Acute climatic variation may increase fitness costs associated with herbivore damage either directly by causing a shift in resource allocation to growth (Kleine and Müller 2014; Kozlov et al., 2015) or indirectly through a shift in biotic or abiotic factors that are linked to chemical defense production (Leimu et al., 2012; Tariq et al., 2013). For example, increased glucosinolate production mediated by drought caused a shift in the strength of the interactions between different herbivore guilds (Tariq et al., 2013). Similarly, Gutbrodt et al. (2011) showed that under drought stress concentrations of nitrogen-containing compounds in leaves increase, therefore increasing food quality for herbivores. Indirect effects of short-term climatic variation can have an important role in plant response, but estimating shifts in herbivore and pathogen defense associated to drought can be challenging as the trade-off between growth and defense is context-dependent (Bode and Kessler, 2012). Furthermore, investment in defense against antagonists can vary across life stages and environments (Boege et al., 2007; Barton and Koricheva, 2010; Sampedro et al., 2011). Generally, younger plants are more vulnerable to herbivores and are expected to produce relatively more chemical defenses, however this varies considerably across taxa (Barton and Koricheva, 2010).

Glucosinolates are a class of chemical defenses, produced mainly by Brassicaceae, that are expressed constitutively and are also inducible (Halkier and Gershenzon, 2006; Hopkins et al., 2009). They have been well studied in an ecological context for their role in defense against herbivores and pathogens (Beekwilder et al., 2008; Bidart-Bouzat and

Kliebenstein, 2008) and are thus well suited to address the above questions. Previous studies indicated that glucosinolate concentrations vary in response to acute drought (Milford and Evans 1991; Haugen et al., 2008), however no significant differences were found in plants exposed to a medium-term rainfall manipulation study (Metz et al., 2014).

We carried out two experiments to test how glucosinolate concentrations vary in response to i) long-term aridity, ii) short-term drought and iii) plant age. We predicted that short-term response to artificial drought would have similar effects on glucosinolate production as long-term climate conditions. Secondly, we predicted that plants inhabiting more variable climates would exhibit a larger plasticity in response to artificial drought. We tested these predictions, in two separate experiments, and we predicted that young plants would show a larger response to drought with respect to glucosinolate production than old plants.

2. Methods

2.1. Seed origins

For both our experiments, we used *Biscutella didyma* L. (Brassicaceae), a winter annual species widespread in the Eastern Mediterranean region (Feinbrun-Dothan, 1986). Seeds of 400 individuals in total were collected in 2012 from four sites along a gradient of decreasing rainfall and increasing climate variability in Israel. At each site, sampling was done over an area of approximately 1 ha and sampled individuals were at least 1 m distant from each other. The sites were characterized by equal aspect, slope, elevation and mean annual temperature, but differed in rainfall regime (Tielbörger et al., 2014). They represent mesic-Mediterranean (MM, 780 mm/year rainfall), Mediterranean (M, 540 mm/year rainfall), semi-arid (SA, 270 mm/year rainfall) and arid (A, 90 mm/year rainfall) conditions, respectively. Decreasing mean annual rainfall is coupled with increasingly variable and unpredictable rainfall patterns towards the drier sites (Holzapfel et al., 2006; Siewert and Tielbörger 2010). In order to remove maternal effects from field-collected seeds, plants were grown for one generation in a greenhouse where they received standardized conditions of natural light, regular watering, and temperatures ranging between approx. 15–18 °C (night) and 18–25 °C (day). These conditions had been successfully applied in previous studies and approximated field conditions (e.g. Metz et al., 2014). Our focal species is predominantly selfing, and wrapping individual plants in transparent, light fabric (organza) prevented cross-pollination in the greenhouse. The seeds produced by the first generation of plants in the greenhouse were used for both our experiments conducted in 2014 (experiment 1 - older plants) and 2015 (experiment 2 - younger plants).

2.2. Experimental set up

In both experiments, we used seeds of 13 randomly selected individuals from each origin grown in the greenhouse. Plants were grown under greenhouse conditions similar to those experienced by the mother plants. In order to account for individual genetic differences, 15 seeds of each maternal sibship were planted in one pot per water treatment in both experiments. Following a standard protocol, pots (10 cm x 10 cm x 10 cm) were filled with a mixture of potting soil and sand (1:1) that had been previously enriched with a total of 100 mg Osmocote® slow release fertilizer (14-14-14NPK; Scotts Deutschland GmbH, Nordhorn, Germany). In both experiments, all pots were watered equally to saturation on the first and third day of the experiment to ensure seed germination. After germination was completed (approx. 10 days), seedlings in each pot were thinned to one. Water treatments started after seven days and subsequently pots were irrigated every 2–3 days, i.e., when plants of the lowest water level showed clear signs of water stress (Fig. 1). During the first experiment, conducted in 2014,

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