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Long- and medium-term effects of aridity on the chemical defence of a widespread Brassicaceae in the Mediterranean

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ABSTRACT

Aridity does not only vary along different regions but the frequency of drought is also supposed to increase in the future as a consequence of climate change. Plants may respond to changes in abiotic conditions by adjusting their investment in resources such as chemical defences against herbivores and pathogens. However, knowledge is scarce about how such investments may differ in response to long- or medium-term changes in precipitation. *Biscutella didyma* (Brassicaceae) grows in Israel along a steep precipitation gradient. Four populations along this gradient (arid, semi-arid, Mediterranean, and mesic Mediterranean climate) served as source populations for the current study. In two of these populations, rainfall had been manipulated for ten years, simulating dry, normal, and wet conditions. Seeds from the four populations and the rainfall manipulation treatments were collected and grown under standardised conditions to investigate whether shifts in constitutive defences in relation to the aridity conditions have occurred over long- or medium-term. Young leaves of 10-week old plants were harvested and analysed for their glucosinolate contents, the characteristic defence metabolites of Brassicaceae. Plants originating from the arid region had the lowest glucosinolate concentrations, whereas plants originating from the opposite end of the gradient had the highest, indicating local adaptation in response to long-term conditions. This pattern may be explained by lower or modified enemy pressure, or by limited resource availability in the arid region. The rainfall manipulation over ten years did not affect glucosinolate profiles of the offspring. This may indicate limited potential for rapid evolutionary response but also other factors than drought as the selective agent.

1. Introduction

Plant species often exhibit ecotypic differentiation in life-history traits in response to local environmental conditions which can be based on phenotypic plasticity or are genetically determined (Petrů et al., 2006; Rice et al., 2013; Zhou et al., 2013). For the Mediterranean basin, current climate change scenarios predict increasing temperatures and precipitation declines (Smiatek et al., 2011). Increasing drought impacts the plant quality, since plants must adapt their resource allocation to optimise water uptake (Chaves et al., 2003) and modify various physiological and morphological traits in response to changing climatic conditions (Alberto et al., 2013; Reyer et al., 2013).

Changed resource allocation under drier climates may also affect the investment in chemical defence against enemies. Herbivore and pathogen pressure were found to be reduced in arid environments compared to wetter sites (Coley and Barone, 1996; Brenes-Arguedas et al., 2009), potentially leading to diminished defence investment. Furthermore, concentrations of defensive chemicals may decrease in stressed plants attributable to limited resources (Rhoades, 1979). At the same time, nutrients may become increasingly available in the plant tissue under drought stress, which may render these plants more prone to herbivory as suggested by the plant stress hypothesis (White, 1984). However, evidence for this hypothesis and for effects of drought on allelochemicals has been contradictory (Tariq et al., 2012; Table 1). Alternatively, investment in chemical plant defence may be enhanced with increasing aridity since plant tissue is less replaceable.

Within the Brassicaceae, glucosinolates are the best studied chemical defence compounds (Gershenzon and Müller, 2009). They consist of a β-D-thioglucose group, a sulphonated oxime group and an indolic, aliphatic or aromatic side-chain, depending

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Table 1
Summary of previous work carried out on the effects of water regimes on glucosinolates in various Brassicaceae species.

Species	Conditions	Investigated organ	Effects on glucosinolates[a]	Effects on herbivores	Reference
Alliaria petiolata from three wild populations differing in precipitation, grown under common garden conditions	Well-watered, moderately stressed, and severely stressed plants	Leaves (youngest fully developed leaf)	↓ Decrease in glucosinolate concentrations in plants of severe stress treatment; significant population effect	Specialist *Pieris brassicae* (Lepidoptera) preferred well-watered plants, while generalist *Spodoptera littoralis* (Lepidoptera) preferred severely drought-stressed plants	Gutbrodt et al. (2011)
Arabidopsis thaliana	Well-watered, drought, and water-logged conditions	Phloem sap of leaves	↓ Decrease in 4-methoxyindol-3-ylmethyl glucosinolate under drought stress	Specialist *Brevicoryne brassicae* (Hemiptera) unaffected, while population growth of generalist *Myzus persicae* (Hemiptera) highest on drought stressed plants	Mewis et al. (2012)
Boechera holboellii, *B. stricta*	*B. hoelbollii* from lower, drier elevations, *B. stricta* from higher elevation; under two conditions of water availability (sufficient and low)	Leaves	↑ Increase in total glucosinolate concentrations in *B. hoelbolli* plants (from drier conditions)	Plants under drought conditions are more susceptible to the specialist *Plutella xylostella* (Lepidoptera)	Haugen et al. (2008)
Brassica carinata, lines Holeta-1 and 37-A	Optimal or drought-inducing water supply	Leaves	↑ Increase of 2-propenyl and 3-indolylmethyl glucosinolate in plants with drought-induced water supply; line-specific responses	Not tested	Schreiner et al. (2009)
Brassica napus L. (rapeseed) (genotypes Chine 32, Mali, and Drakkar)	Three drought treatments at three developmental stages	Mature seeds	↑ Increase in total glucosinolate concentrations subsequent to water deprivation, when applied during early stages of development; ↓ Decrease in total glucosinolate concentration when water deficit applied during the reproductive period (in Chine 32); genotype-specific responses	Not tested	Bouchereau et al. (1996)
Brassica napus cv. Wesbrook and *Brassica rapa* cv. Bunyip	Well-watered, reduced water supply throughout growth or only after flowering	Seeds	↑ About two-fold increased glucosinolate concentrations in plants under water stress. No significant difference between the two stress-treatments.	Not tested	Mailer and Cornish (1987)
Brassica napus	Early drought, late drought, or full irrigation	Seeds	↑ Increased glucosinolate concentrations in the drought treatments	Not tested	Jensen et al. (1996)
Brassica oleracea var. *capitata*	Irrigation provided from planting to maturity, during frame development only, during head development only, or no irrigation after plant establishment	Heads	↑ Increased total and individual glucosinolate concentrations in plants not irrigated during head development than in plants receiving irrigation during head development	Not tested	Radovich et al. (2005)
Brassica oleracea var. *italica* (broccoli) Majestic and Legacy	Water stress (80% of water) or control (100% of water)	Florets	↓ Decreased glucosinolate production under water stress, particularly of indole glucosinolates	Not tested	Robbins et al. (2005)
Brassica oleracea var. *italica* 'Calabrese'	Water-logged (>80% water content in soil), well-watered (70–75%), and drought stress conditions (35–40%)	Shoots	↓ Decrease in glucosinolate concentrations (particularly of indole glucosinolates) with increasing drought; glucosinolate-specific responses	No effects on specialist *Brevicoryne brassicae*, while generalist *Myzus persicae* grow largest populations on drought stressed plants	Khan et al. (2010)
Brassica oleracea	Control plants (100% water), low (75%), medium (50%), and high drought stress (25%) for 10 weeks; pulsed water stress treatment	Leaves (fully-expanded young leaf)	↑ Increased total glucosinolate concentrations (particularly of dominant indole glucosinolate glucobrassicin) with increasing drought stress	Fecundity of specialist *Brevicoryne brassicae* higher at intermediate drought stress, while that of the generalist *Myzus persicae* higher at intermediate and low drought stress compared to the other treatments	Tariq et al. (2012)
Brassica oleracea var. *gemmifera* cv. Oliver	Control plants, medium drought, and high drought treatment	Leaves (fully-expanded young leaf)	↑ Increased total glucosinolate concentrations with increasing drought stress; altered sinigrin and progoitrin levels	Highest performance of specialist *Brevicoryne brassicae* and generalist *Myzus persicae* at medium drought stress	Tariq et al. (2013)
Brassica oleracea convar. *botrytis* var. *italica* cultivar Parthenon F1	Irrigated or rain-fed, plants grown in spring and fall	Florets	Significant differences between seasons but not due to water supply	Not tested	Pék et al. (2013)

[a] ↑: increase in glucosinolates with increasing drought; ↓ decrease in glucosinolates with increasing drought.