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Population differentiation related to climate of origin affects the intensity of plant–herbivore interactions in a clonal grass

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Abstract

With ongoing climate change, it is likely that shifts in species distribution ranges will lead to changes in the type and intensity of plant–herbivore interactions. Plants currently exposed to lower levels of herbivory could have less developed defensive mechanisms and therefore could suffer in case of increased herbivore pressure.

We performed a common garden experiment using clones of *Festuca rubra* originating from four populations experiencing contrasting temperature and precipitation regimes. Clones of identical genotype were subjected to both the control and the herbivory treatment using larvae of the nymphalid butterfly *Coenonympha pamphilus*, a generalist herbivore feeding on several grass species. Various measures of constitutive and induced defence as well as growth response to herbivory were assessed, compared between populations of different climatic origin and related to herbivore performance (larval survival).

The four *F. rubra* populations significantly differed in constitutive defence (content of Si and total phenols), nutritional quality (content of C) and inducibility of defence (change in total phenols), but not in growth response to herbivory. Herbivores survived better on populations from colder climate and better survival was generally related to lower Si content and lower initial plant size.

We demonstrated population differentiation in both constitutive and induced defence against insect herbivory, which directly affected survival of a generalist herbivore. Our findings confirmed the expectation that plants from higher elevations are more prone to herbivory. Moreover, differences in various aspects of plant defence between populations from the same altitude stresses the need of considering multiple factors when assessing the effect of climate on plant–herbivore interactions.

Zusammenfassung

Angesichts des fortschreitenden Klimawandels ist es wahrscheinlich, dass Verschiebungen in den Verbreitungsgebieten der Arten zu Veränderungen in der Art und Intensität der Interaktionen zwischen Pflanzen und Herbivoren führen werden. Pflanzen, die derzeit einem niedrigeren Herbivorie-Niveau ausgesetzt sind, könnten weniger entwickelte Abwehrmechanismen aufweisen und könnten daher im Falle eines erhöhten Pflanzenfresserdrucks leiden.

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Wir führten ein gemeinsames Gartenexperiment unter Verwendung von Klonen von Festuca rubra durch, die aus vier Populationen mit unterschiedlichen Temperatur- und Niederschlagsregimen stammen. Klone mit indentischem Genotyp wurden sowohl der Kontrol- als auch der Herbivorenbehandlung unter Verwendung von Larven des Nymphalidenfalters Coenonympha pamphilus, einem generalistischen Pflanzenfresser, der sich auf verschiedene Grasarten ernährt, unterzogen. Verschiedene Messungen der konstitutiven und induzierten Abwehr sowie der Wachstumsreaktion auf Herbivorie wurden untersucht, verglichen zwischen Populationen unterschiedlicher klimatischer Herkunft und in Zusammenhang mit der Leistung von Herbivoren (Larvenüberleben) gebracht.

Die vier F. rubra-Populationen unterschieden sich signifikant in der konstitutiven Verteidigung (Gehalt an Si und Gesamtphenolen), Ernährungsqualität (C-Gehalt) und Induzierbarkeit der Abwehr (Veränderung der Gesamtphenole), jedoch nicht in der Wachstumsreaktion auf Herbivorie. Herbivoren überlebten besser bei Populationen aus kälterem Klima und ein besseres Überleben war im Allgemeinen mit einem niedrigeren Si-Gehalt und einer geringeren anfänglichen Pflanzengröße verbunden.

Wir demonstrierten eine Populationsdifferenzierung sowohl in der konstitutiven als auch in der induzierten Abwehr gegen Insekten Herbivoren, die das Überleben generalistischen Herbivoren direkt beeinflussten. Unsere Ergebnisse bestätigten die Erwartung, dass Pflanzen aus höheren Lagen anfälliger für Herbivorie sind. Darüber hinaus betonen Unterschiede in verschiedenen Aspekten der Pflanzenabwehr zwischen Populationen aus der gleichen Höhe die Notwendigkeit, bei der Beurteilung des Klimaeinflusses auf Pflanzen - Herbivoren - Interaktionen mehrere Faktoren zu berücksichtigen.

Keywords: Adaptation; Alpine grassland; Elevational gradient; *Festuca rubra*; Insect herbivory; Lepidoptera; Phenotype

Introduction

Climate change can lead to major shifts in community composition and thus can alter interactions between resident species (Tylianakis, Didham, Bascompte, & Wardle 2008). It has been well documented that with changes in temperature and precipitation, species' ranges shift to higher latitudes and altitudes (Parmesan 1996; Konvička, Maradová, Beneš, Fric, & Kepka 2003; Pauli et al. 2012; Parmesan & Hanley 2015). Since plants are sessile organisms and cannot disperse upwards as quickly as animals, it is likely that plant populations will be exposed to increased levels of herbivory (O'Connor 2009; Rasmann, Pellissier, Defossez, Jactel, & Kunstler 2014).

The highest species and functional diversity of herbivores can be found in insects (Speight, Hunter, & Watt 2008), which at the same time are suggested to be extremely sensitive to changing climatic conditions (Bale et al. 2002). Insect herbivores are also likely to have the strongest effects on plant population dynamics (Schoonhoven, Loon, & Dicke 2005; Rasmann et al. 2014). Among plants, grasses are the most widespread species (grasslands comprise between 30 and 40% of terrestrial ecosystems), which are essential for ecosystem functioning, and provide forage for both cultivated and wild animals (Gibson 2009). Although grasses are considered to primarily employ tolerance instead of defence in mitigating damage caused by herbivory (Karban & Baldwin 1997; Gibson 2009), a number of mechanisms have been identified that can act as their anti-herbivore defence (Vicari & Bazely 1993). The most prominent is enhanced silicon uptake, which directly decreases tissue digestibility and also causes abrasion of herbivore mouthparts (Massey & Hartley 2009; Huitu et al. 2014; Hartley & DeGabriel 2016). Grasses are also able to synthesize secondary metabolites such as phenols, which may serve as insect deterrents or toxins (Djurdjevic, Mitrovic, Pavlovic, Perisic, & Macukanovic-Jocic 2005; Gibson 2009; Frew, Powell, Sallam, Allsopp, & Johnson 2016). In their effect on herbivore performance, defensive components of plant tissues often interact with their nutritional quality (Awmack & Leather 2002). Nutritional quality of a plant is often expressed as both the content of nitrogen and carbon and their ratio (Gibson 2009). While nitrogen content corresponds to the amount of proteins vital for insect growth or fecundity, carbon is a proxy for energy sources – carbohydrates, represented by indigestible structural compounds, e.g. cellulose, lignin, or soluble carbohydrates (Schoonhoven et al. 2005). On the other hand the high relative amount of soluble carbohydrates could negatively affect the availability of other sources leading to increased intake of food by the herbivore (Awmack & Leather 2002).

Various direct and indirect defences and inducibility of these defences have been shown to be adaptive, i.e. plants exposed to higher levels of herbivory tend to develop better defensive mechanisms (Schoonhoven et al. 2005; Fornoni 2011; Hartley & DeGabriel 2016; Pellissier et al. 2016). However, relatively few studies have investigated intraspecific population differentiation in multiple aspects of plant defence (Wason & Hunter 2014), and even fewer did so along environmental gradients (Dostálek et al. 2016; Rokaya, Dostálek, & Münzbergová 2016). Moreover, much of our knowledge of plant–herbivore interactions is based on results from experiments applying mechanical damage to the plants, which often fail to induce plant responses, essential for complex biotic interactions (Kalberer, Turlings, & Rahier 2001;