



Integrating temperature and nutrition – Environmental impacts on an insect immune system



Stephanie S. Bauerfeind^{a,*}, Klaus Fischer^b

^aDepartment of Immunology, University Medicine of Greifswald, 17489 Greifswald, Germany

^bZoological Institute & Museum, University of Greifswald, Johann-Sebastian-Bach Str. 11/12, 17489 Greifswald, Germany

ARTICLE INFO

Article history:

Received 23 September 2013

Received in revised form 25 January 2014

Accepted 7 March 2014

Available online 15 March 2014

Keywords:

Diet

Food quality

Haemocytes

Lysozyme

Phenoloxidase

Pieris napi

ABSTRACT

Globally increasing temperatures may strongly affect insect herbivore performance. In contrast to direct effects of temperature on herbivores, indirect effects mediated via thermal effects on host-plant quality are only poorly understood, despite having the potential to substantially impact the herbivores' performance. Part of this performance is the organisms' immune system which may be of pivotal importance for local survival. We here use a full-factorial design to explore the direct (larvae were reared at 17 °C or 25 °C) and indirect effects (host plants were reared at 17 °C or 25 °C) of temperature on immune function of the temperate-zone butterfly *Pieris napi*. At the higher rearing temperature haemocyte numbers and prophenoloxidase activity were reduced. Plant temperature, in contrast, did not affect immune competence despite clear effects on insect growth patterns. Overall, thermal and dietary impacts on the insects' immune responses were weak and trait-specific.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Global temperatures have increased at a rate of approximately 0.2 °C per decade in the last 30 years (Hansen et al., 2006) and will continue to rise in coming decades by 1–4 °C until 2100, depending on the emission scenario used (IPCC, 2007). Well documented responses of species to the environmental change already at hand include shifts in temporal and geographic niches (Altermatt, 2011; Hegland et al., 2009; Visser, 2008; Walther et al., 2002; Walther, 2010). Across taxa, the capacities of species to respond to climatic changes through plastic and genetic changes have been less widely studied, but are now widely acknowledged as the basis for in situ adaptation and thus the local persistence of species (Chown et al., 2010; Hofmann and Todgham, 2010; Mitchell et al., 2010; Nyamukondiwa et al., 2011).

Environmental temperatures are known to have strong and pervasive effects on ectotherm life including e.g. developmental and life history traits (e.g. reviewed in Angilletta (2009), Bauerfeind and Fischer (2013a), Fischer et al. (2011)), behavioural traits (Berwaerts and Van Dyck, 2004; Geister and Fischer, 2007), reproductive traits (Fischer et al., 2003), stress responses and immune function (e.g. Hoffmann et al., 2003; Karl et al., 2011).

Insects have a highly developed innate immune system involving humoral and cellular defence mechanisms (Lavine and Strand, 2002). Humoral defences include the production of antimicrobial peptides (including lysozymes that are produced in the insect fat body and play a key role in the defence against gram⁺ bacteria; c.f. Franke and Fischer, 2013), reactive oxygen and nitrogen species, and enzymatic cascades that regulate coagulation or melanisation of the haemolymph (Lavine and Strand, 2002). A key enzyme involved in melanogenesis is phenoloxidase PO (for a review on PO function see González-Santoyo and Córdoba-Aguilar (2011)). If PO is needed for an immune defence, its inactive zymogens (proPO) are converted into active PO (in order to prevent autoimmunological damage; González-Santoyo and Córdoba-Aguilar, 2011). As PO is active for only a short time after an immune challenge, measuring levels of inactive proPO may provide a more accurate measure of immunity (Cerenius et al., 2008). PO is a costly trait whose production and maintenance appear to have fitness costs and can be viewed as an indicator of an individual's condition even more than being an indicator of resistance *per se* (González-Santoyo and Córdoba-Aguilar, 2011). Cellular defences include haemocyte-mediated phagocytosis, nodulation, and encapsulation as well as clot formation in response to wounding (Lavine and Strand, 2002). The humoral and cellular defence systems considerably overlap and are well coordinated with one another (Lavine and Strand, 2002), e.g. after encapsulation, one of the agents killing the foreign organism is the production of toxic quinones and

* Corresponding author. Tel.: +49 (0)3834/865518; fax: +49 (0)3834/865545.

E-mail addresses: stephaniebauerfeind@web.de (S.S. Bauerfeind), klaus.fischer@uni-greifswald.de (K. Fischer).

hydroquinones via the proPO cascade (see Lavine and Strand (2002) and references therein).

Recently, environmental impacts on immune function have been acknowledged to be of potentially pivotal importance for local survival in changing environments (Martin et al., 2010; Polley and Thompson, 2009; Rohr et al., 2011). Environmental temperatures strongly affect overall resistance to a wide variety of parasites and impact on latency periods and the recovery from an infection (see Catalán et al. (2012), Murdock et al. (2012a,b)). Although immunological parameters have been shown to readily respond to thermal variation, the few studies available so far suggest that responses to environmental change are complex and general patterns seem difficult to formulate, yet (for a review see Murdock et al. (2012a, 2013)).

Generally, warmer temperatures seem to increase insect immune performance through increases of haemocyte numbers and the enzymatic activity of phenoloxidase (PO) and lysozymes (Catalán et al., 2012; González-Santoyo and Córdoba-Aguilar, 2011; Lavine and Strand, 2002; Murdock et al., 2012b). Also, infected animals have been shown to prefer warmer microclimates (behavioural fever; Kluger et al., 1998). Furthermore, increases to stressful temperatures reduce insect immune performance which is likely due to a trade-off with molecular stress mechanisms (Karl et al., 2011).

In nature, shifts in environmental temperatures as predicted in climate change scenarios will not only exert direct effects on ectotherms, but will simultaneously affect the availability and quality of dietary resources such as host plants of herbivorous species. Thermal conditions during plant growth impact on multiple processes including photosynthesis, respiration, evapo-transpiration, nitrogen mineralisation and availability to the plant, and the production and composition of plant biomass (e.g. Way and Oren, 2010). A recent meta-analysis by Zvereva and Kozlov (2006) revealed that increasing temperatures may only weakly affect plant nitrogen content, C/N ratio or leaf mechanical traits, while other characteristics may be more profoundly affected (e.g. leaf water content, carbohydrates, phenols, terpenoids; Bohinc and Trdan, 2012; Kuokkanen et al., 2001; Veteli et al., 2002). While the effects of thermal conditions on plant growth and metabolism are well known, the consequences thereof for herbivores are less well documented even though the interactions between temperature and nutrition are of a potentially high ecological importance (Bauerfeind and Fischer, 2013a,b; Janković-Tomanić and Lazarević, 2012; Verdú et al., 2010; Wojewodzic et al., 2011). For instance, a high temperature during plant growth resulted in host plants that impeded development and diminished body mass of the herbivorous caterpillars of a Lepidopteran species (Bauerfeind and Fischer, 2013a). Thus, potential negative effects of global warming may be exaggerated by a combination of direct effects on the focal species itself and indirect effects mediated via changes in host plant quality (Cornelissen, 2011; Huey et al., 2012; Kingsolver et al., 2011; Netherer and Schopf, 2010).

Such indirect thermal effects may also affect immune responses in herbivorous species, as both the constitutive and induced immune defence system depend on sufficient and adequate nutrition (Cotter et al., 2011; Ponton et al., 2013; Schmid-Hempel, 2005; Siva-Jothy and Thompson, 2002; Vogelweith et al., 2011). Different immune pathways have been shown to respond differently to dietary quality and are involved in mutual trade-offs (Cotter et al., 2011; Lee et al., 2008; Schmid-Hempel, 2005; Vogelweith et al., 2011). For instance, in caterpillars, lysozyme and phenoloxidase activity were maximised for different dietary protein and carbohydrate intake (Cotter et al., 2011). Therefore, it is important to consider various components of the immune system at a time.

Given these profound effects of environmental conditions on the immune system, the last decade has seen the rise of a discipline

that has been coined 'ecological immunology' and that focusses on the impact of ecological parameters on the complexities and within- and across-species variation of the immune system (e.g. Boughton et al., 2011; Rolff and Siva-Jothy, 2003; Ponton et al., 2011). Within this discipline, sub-fields such as 'nutritional immunology' have emerged (Ponton et al., 2013) that focus on single extrinsic factors. Our study contributes to this field by integrating two environmental factors (temperature and nutrition) and as such crossing sub-field boundaries (see also Triggs and Knell (2012)).

We here use the temperate-zone pierid butterfly *Pieris napi* (Linnaeus, 1758) to investigate interactive effects between larval rearing and plant growth temperature on adult butterfly immune parameters, in order to assess detrimental effects on performance. Our design enables us to simultaneously assess the direct and indirect (mediated via host plant quality) effects of temperature on ectotherm performance (Bauerfeind and Fischer, 2013a). The measured parameters include the activity of phenol- and prophenoloxidase, lysozyme-like activity of the haemolymph and haemocyte numbers. Specifically, we predict (1) direct thermal effects: increasing mean temperatures should result in an increased immune reactivity (Angilletta, 2009; Murdock et al., 2012a, 2012b; Thomas and Blanford, 2003; Triggs and Knell, 2012) and (2) indirect thermal effects: growing plants at a higher temperature is expected to reduce plant quality, negatively affecting herbivore performance (Bauerfeind and Fischer, 2013a; Cornelissen, 2011) and thus reducing immune reactivity.

2. Materials and methods

2.1. Study organism

P. napi is a temperate-zone butterfly that is widely distributed across northern Eurasia (Ebert and Rennwald, 1993) forming a complex of different subspecies (Espeland et al., 2007). The species is bi- to trivoltine in most parts of its range with the first butterflies appearing in April/May and the last ones in September/October in Northern Europe (Ebert and Rennwald, 1993), although populations with only one generation per year occur. The morphology and life history of *P. napi* varies depending on altitude and latitude with more strongly melanised phenotypes occurring at high elevations and latitudes (Tuomaala et al., 2012). The sexes show a pronounced dimorphism with the females being smaller than the males in this highly polyandrous species (Wiklund and Kaitala, 1995). *P. napi* hibernates as pupa. The principal larval host plants are several species of Brassicaceae (such as *Cardamine pratensis* and *Alliaria petiolata*); the species is of limited importance as a pest species in contrast to the closely related *Pieris brassicae* (Ebert and Rennwald, 1993). For this study 19 *P. napi* females were collected near Greifswald, north-eastern Germany.

2.2. Experimental design

Field-caught females were transferred to climate cells at Greifswald University, and were provided with water, sucrose solution (ca. 30 vol.%) and leaves of *A. petiolata* and *Sinapis alba* for egg deposition (25 °C, 60% relative humidity, L:D 20:4). On day 5 after hatching, resulting larvae were individually transferred to translucent plastic pots (250 ml, lined with moist tissue) and randomly divided among two rearing temperatures (17 °C and 25 °C). 17 °C approximates the average mean temperature in June/July in the part of Germany where the experimental population was derived from (German weather service, www.dwd.de), while 25 °C was chosen to cover a thermal range sufficiently high to elicit physiological responses of both plants and butterflies. Thus, it was not intended to mimic predicted climate change here, but to include

Download English Version:

<https://daneshyari.com/en/article/5921631>

Download Persian Version:

<https://daneshyari.com/article/5921631>

[Daneshyari.com](https://daneshyari.com)