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# Fungal and cyanobacterial gene expression in a lichen symbiosis: Effect of temperature and location



Sophie S. STEINHÄUSER<sup>a</sup>, Ólafur S. ANDRÉSSON<sup>a</sup>, Arnar PÁLSSON<sup>a</sup>, Silke WERTH<sup>a,b,\*</sup>

<sup>a</sup>Life and Environmental Sciences, University of Iceland, Sturlugata 7, 101 Reykjavik, Iceland <sup>b</sup>Institute of Plant Sciences, University of Graz, Holteigasse 6, 8010 Graz, Austria

#### ARTICLE INFO

Article history:
Received 4 January 2016
Received in revised form
27 May 2016
Accepted 7 July 2016
Available online 18 July 2016
Corresponding Editor:
Martin Grube

Keywords:
Candidate genes
Environmental stress response
mechanisms
Heat stress
Nostoc
Peltigera membranacea (lichenized
ascomycetes)
Quantitative real-time PCR (qPCR)

#### ABSTRACT

Organisms have evolved different cellular mechanisms to deal with environmental stress, primarily through complex molecular mechanisms including protein refolding and DNA repair. As mutualistic symbioses, lichens offer the possibility of analyzing molecular stress responses in a particularly tight interspecific relationship. We study the widespread cyanolichen Peltigera membranacea, a key player in carbon and nitrogen cycling in terrestrial ecosystems at northern latitudes. We ask whether increased temperature is reflected in mRNA levels of selected damage control genes, and do the response patterns show geographical associations? Using real-time PCR quantification of 38 transcripts, differential expression was demonstrated for nine cyanobacterial and nine fungal stress response genes (plus the fungal symbiosis-related lec2 gene) when the temperature was increased from 5 °C to 15 °C and 25 °C. Principle component analysis (PCA) revealed two gene groups with different response patterns. Whereas a set of cyanobacterial DNA repair genes and the fungal lec2 (PC1 group) showed an expression drop at 15 °C vs. 5 °C, most fungal candidates (PC2 group) showed increased expression at 25 °C vs. 5 °C. PC1 responses also correlated with elevation. The correlated downregulation of lec2 and cyanobacterial DNA repair genes suggests a possible interplay between the symbionts warranting further studies.

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#### Introduction

Climate change and global warming call for studies of how changing environmental conditions affect species survival. Changes in species composition and reduced biodiversity can negatively affect ecosystems and therefore also services they provide for human society (Schröter 2005; Burkle et al. 2013). In the past decades, there have been numerous reports on rapid

climatic changes on global scales, impacting both terrestrial and marine ecosystems (Raven et al. 2005; Diffenbaugh & Field 2013; Penuelas et al. 2013). Increasing temperatures cause major ecosystem changes affecting species on many levels, from metabolism and growth to general species interactions and ecosystem productivity (Penuelas et al. 2013). For a variety of terrestrial organisms (e.g. butterflies, birds, higher plants), increased temperatures have been shown to affect breeding,

E-mail address: silke.werth@uni-graz.at (S. Werth).

<sup>\*</sup> Corresponding author. Institute of Plant Sciences, University of Graz, Holteigasse 6, 8010 Graz, Austria. Tel.: +43 316 380 5645; fax: +43 316 380 9880.

flowering, or the length of the growth season (Parmesan 2006). This can result in asynchronies in the population dynamics of species, uncoupling predator-prey or insect—host interactions and thus even leading to extinctions of local populations (Parmesan 2006). However, climate change is not expected to have the same effect on populations of a species occurring in distinct habitats. For example, a study showed that epiphytic floras are altered more rapidly in open rural areas than in forested areas (Aptroot and van Herk 2007). Therefore, the effect of global warming on a species can be rather complex.

Tolerance of stress associated with changing environmental conditions is an important property allowing organisms to persist in changing environments. Environmental change may e.g. lead to fluctuations, as well as extremes, in temperature, hydrological regime or light conditions, leading to physiological strain for most organisms. There are several strategies enabling the survival of species under pressure due to environmental changes, like migration to favorable habitats or local adaptation (which has a genetic base and acts over long time scales) (Aitken et al. 2008). A third survival strategy is acclimatization, gradual long-term physiological adjustment to the changed local environment (Sork et al. 2010). This is in contrast to short-term physiological adjustment, e.g. to laboratory conditions, which is referred to as 'acclimation'. As one aspect of phenotypic plasticity, acclimatization is based on the capacity of a single genotype to develop variable phenotypes in different environments, manifested in altered biochemistry, physiology, morphology, behavior or life history (Whitman & Agrawal 2009). Acclimatization is an ongoing process, reversible and not passed on to the next generation. Differences in the capacity of species for acclimatization has important implications for their persistence in changing environments and may allow in situ tolerance of changed environmental conditions, thus playing an important role for species to successfully cope with environmental variability (Davis 2005; Aitken et al. 2008; Manel et al. 2010). Thus, migration, genetic adaptation and in situ tolerance of new, stressful conditions (achieved by changes in acclimatization) are key mechanisms for coping with a changing climate.

One of the most important mechanisms behind in situ tolerance is the environmentally induced alteration of gene expression, resulting in changes in physiology enabling species to tolerate altered abiotic conditions. At the molecular level, both prokaryotes and eukaryotes have evolved multiple methods to sense and respond to changes in their abiotic environment and develop in situ tolerance, most notably environmental stress-response (ESR) mechanisms that include pathways commonly activated under environmental stress such as drought or heat (Apte et al. 1998; Plesofsky-Vig & Brambl 1998; Young 2001; Enjalbert et al. 2006; Gasch 2007; Zahrl et al. 2007; Sato et al. 2008; Che et al. 2013; di Pasqua et al. 2013). Stress-responsive regulatory and damage repair pathways are important for enhancing survival (Wang et al. 2015). Common stress-response regulation pathways such as the Hog1 mitogen-activated protein kinase pathway and the TATAbinding protein mediated pathway induce the transcriptional upregulation of ESR related genes such as heat shock protein (Hsp) or DNA repair genes (Wang et al. 2015). In addition to protein refolding and denaturation systems, DNA damage repair pathways such as the global SOS response system play an important role in repairing stress-related DNA damages (Sargentini & Smith 1986; Voloshin et al. 2003; Nagashima et al. 2006; Cheng et al. 2012; Odsbu & Skarstad 2014).

To determine how species react to environmental changes, it is interesting to include the level of species interactions since species generally do not live in isolation, but with other species. One of the most remarkable interactions between different species is mutualism. In terrestrial ecosystems, mutualistic plant- or fungal-bacterial symbioses are widely distributed (McCowen et al. 1986; Timmusk & Wagner 1999; Yahr et al. 2004; Antonyuk & Evseeva 2006; Albright et al. 2010; del Campo et al. 2013). Symbiosis partners can communicate and strongly influence each other at the molecular level as shown for the plant-bacterial symbiosis of wheat and the rhizobacterium Azospirillum brasilense and for Arabidopsis thaliana and its rhizobacterial symbiont Paenibacillus polymyxa (Timmusk & Wagner 1999; Antonyuk & Evseeva 2006). Lichens are an important form of mutualistic interaction, dominating in over 12 % of all terrestrial ecosystems, (Honegger 2012). Lichens are characterized by the symbiotic association of a filamentous fungus (mycobiont) with one or several photoautotrophic organisms (photobionts), which can be green algae or cyanobacteria (Lutzoni & Miadlikowska 2009; Honegger 2012). Lichens can be very sensitive to changes in their environment such as air pollution (Hawksworth & Rose 1970; Nimis 2002). Using the bioclimatic envelope approach, studies have predicted major future range shifts for lichenforming fungi in response to climate change (Ellis et al. 2007a; Ellis et al. 2007b). However, the molecular background of how lichen populations might react to large-scale climatic changes such as global warming remains to be investigated in more detail. One strategy through which lichens might be able to tolerate climatic changes is the modulation of gene expression, allowing individuals to cope with environmental extremes and stress. In non-lichenized fungi, there have been several studies on gene expression under environmental stress (Gasch 2007), but only few recent studies have investigated gene expression in lichen-forming fungi and their photobionts (Joneson et al. 2011; Athukorala & Piercey-Normore 2015). In the desert lichen Endocarpon pusillum, expression of fungal genes involved in osmoregulation, metabolism and protein repair has been investigated in response to drought (Wang et al. 2015). However, no studies have yet been performed in order to identify and characterize expression of ESR genes in both the lichen-forming fungus and its cyanobacterial photobionts with increased temperature.

The membranaceous dog lichen, Peltigera membranacea, is a key player in carbon and nitrogen cycling in terrestrial ecosystems at northern latitudes due to its high abundance and its symbiosis with nitrogen-fixing Nostoc cyanobacteria (Miadlikowska & Lutzoni 2004). In this study, we investigated the mRNA levels of selected ESR genes of both mycobiont and photobiont of *P. membranacea* to answer the question whether temperature increases of 10 °C or 20 °C cause stress responses, reflected in altered mRNA levels in both symbionts (question 1). The term 'gene expression' is used for the quantity of mRNA relative to a reference gene, measured by quantitative PCR. In addition to examining the gene expression of ESR candidates, expression of two fungal lectin genes (lec1 and lec2) was investigated as lectin genes are thought to play a role in the symbiotic

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