FUNGAL BIOLOGY REVIEWS 32 (2018) 143–155

ELSEVIER

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journal homepage: www.elsevier.com/locate/fbr

Review

Some like it hot, some not – Tropical and arctic mushrooms

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ARTICLE INFO

Article history:
Received 23 January 2018
Received in revised form
24 April 2018
Accepted 25 April 2018

Keywords:
Arctic
Ectomycorrhiza
Host diversity
Morphological and physiological adaptation
Phenotypic and genotypic plasticity
Saprotrophic
Secondary metabolites
Stress tolerance
Tropical lowland rainforest

ABSTRACT

Fungi are of pivotal importance for terrestrial ecosystems. They occur globally and show extremely high species diversities. In this review, we compiled information about the adaptability of pileate basidiomycetes by illustrating their habits in contrasting biomes, the arctic regions and tropical lowland rainforests. Mushrooms are faced with differing stress factors and levels in the two ecozones. They fight such challenges by using, by and large, similar physiological and morphological toolkits. They make them fit for extreme environmental conditions, by expressing traits according to biome characteristics. This way, fungal assemblages are formed and pheno- and genotypic plasticity is capitalised. Still, many questions remain open and need further clarification, such as trade-offs between thermal protection and predator defence, prevailing dispersal modes in the main ecozones, interactions with animals and the mechanisms that create genetic plasticity.

1. Introduction

Ectomycorrhizal and saprobic fungi occur in almost all climate belts and are essential drivers of ecosystem processes (Allen, 1991; Cooke and Rayner, 1984). Saprotrophic basidiomycetes are with more than 80,000 species (Hawksworth and Lücking, 2017) eminently important as decomposers and recyclers of organic material (Dighton and Boddy, 1989; Swift, 1982). The ectomycorrhizal guild as a symbiotic group relies with varying specificity on woody plants as hosts for carbon supply (photosynthate). Carbon is traded mainly for nitrogen and phosphorus extracted from soil-borne, predominantly organic sources in (mineral) nitrogen-limited habitats (Smith and Read, 2008). There are estimates that speak of 20,000 ectomycorrhizal species (van der Heijden *et al.*, 2015), of which ca. 60 % are basidiomycetes, the rest mainly ascomycetes (Tedersoo *et al.*, 2010). In this review, we focus on pileate basidiomycetes.

Like any other organismal group, mushrooms are first of all challenged by climate conditions, particularly thermal and

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https://doi.org/10.1016/j.fbr.2018.04.001

hydrological extremes (Gostinčar *et al.*, 2010). In addition, soil properties play a major role in the habitability of environments (Voroney, 2007). Mushrooms need to disperse and reproduce. To reach a suitable substrate or host, mushrooms not only use wind as dispersal agent, but a number of vectors (arthropods, molluscs, mammals and more), or transport by percolating water (Halbwachs and Bässler, 2015). Biome-related conditions may have significant impacts on dispersal and reproductive modes (Lawrey, 1980; Peay and Bruns, 2014). Moreover, disease and predation are likely to show different patterns in different biomes.

These circumstances raise questions about mushroom diversity, abundance and life strategies in distinct biomes. Biotic and abiotic differences imply adaptations and/or marked pheno- and genotypic plasticity, i.e. stress tolerance. To illustrate the complex factors implicated, we are going to look into two extremely contrasting ecozones, tropical lowland rainforests and alpine/boreal/(sub-)arctic tundras, in the following "arctic" for short (Fig. 1).

We will first compare general geographical and ecological characteristics of the two biomes, followed by a description of fungal responses to environmental stress. Finally, we identify knowledge gaps and suggest further lines of research.

2. Terrae cognitae: general characteristics of tropical and arctic biomes

The extremely different climatic conditions in arctic and tropical ecozones are best illustrated by the climate charts after Walter and Lieth (1967). These diagrammes show the relationship and interplay between seasonal variations of temperature and precipitation. In Fig. 2, two examples from contrasting biomes are shown.

However, there is obviously more to consider than temperature and precipitation when appreciating these biomes. To highlight the diverse environmental conditions for fungal growth, we compare climatic, edaphic and biotic characteristics in Table 1. One should be careful not to regard all biomes tagged with "tropical rainforest" or "arctic" as more or less identical. Antarctic ecosystems exhibit biotic characteristics starkly differing from the Arctic, namely in terms of ectomycorrhizal host absence (Cox *et al.*, 2016; Newsham *et al.*, 2009). One should also note that environmental conditions can significantly differ within arctic biomes (Crawford, 1997). Lowland tropical rainforests in, for instance, neotropical and African areas have significantly distinct plant and animal assemblages (Corlett and Primack, 2011).

Arctic zones are characterised by cyclical disturbance and stress (Crawford, 1997), such as extreme seasonality including ice storms. In tropical lowland rainforests, environmental stress is considerably lower (Whitmore and Burslem, 1998).

Many differences between the contrasting ecozones imply adaptive responses of all organisms occurring in these habitats including fungi.

3. Latitudinal contrasts: environmental conditions in rainforests of the tropics versus arctic biomes

Here, we assess the impact of each environmental factor on mushrooms as listed above (lettering follows Table 1).

a, b) Excessive **temperatures**, be they low or high, pose threats to mushrooms as ectothermic organisms. This mainly applies to the cellular level with its intricate metabolism and membrane architecture (Cooke and Whipps, 1993; Jennings, 1993). Are temperatures too low, the chemical, and under extreme conditions (rupture due to ice crystals), the physical integrity of membranes is distorted, thus impeding their functions. Moreover, the cell solute becomes more viscous and its ion concentration increases, leading to protein inactivation. Excessively high temperatures also cause protein degradation (Deacon, 2006; Smith, 1993), though this threat is more relevant in arid tropical biomes, and not in wet to moist tropical forests.

Fig. 1 – Rainforest (Costa Rica), arctic tundra with reindeer (Varanger north coast, Norway).