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Epiphytic lichen growth in Mediterranean forests: Effects of proximity to the ground and reproductive stage

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Abstract

Reasonable lichen growth rates are required to maintain the important ecosystem functions provided by epiphytic lichen populations. Previously, lichen growth has mainly been quantified in boreal forests. Thus, there is a need for comparable studies from Mediterranean forests. We used reciprocal transplantation to compare relative biomass (RGR) and thallus area (RT_AGR) growth rates of the cephalolichen *Lobaria pulmonaria* and the cyanolichen *Lobarina scrobiculata* ($n = 720$ thalli) in two Mediterranean oak forests. Both juvenile and reproductive thalli were transplanted for 334 days at the base and at breast height of random trees in both forests. We measured functional traits, specific thallus mass (STM) and water holding capacity (WHC), to search for adaptation/acclimation patterns between regions and between local stands. Linear Mixed Models were used to assess the effects of (1) forest, (2) height on the trunk and (3) reproductive stage on RGR, RT_AGR, and functional traits. *Lobaria pulmonaria* grew faster than *L. scrobiculata*, consistent with its more flexible hydration traits. Growth rates in both species were fastest in juveniles at the trunk bases, consistent with trade-offs between (1) growth and reproduction and (2) humidity availability and distance from the ground. In *L. pulmonaria*, STM increased with increasing evaporative demands, consistent with acclimation mechanisms. Fundamental and realized niches differed in *L. scrobiculata*, indicating that high abundance does not necessarily coincide with optimal growth habitat. Both species grew as fast in drier and warmer Mediterranean forests as reported from boreal forests, presumably because local conditions during hydration periods differ less between macroclimate regions than average climatic parameters, and/or because dew formation is frequent, particularly near the ground. Furthermore, STM and WHC of lichens in Mediterranean forests were high, thus partly compensating for the drier conditions. This study improves our understanding of mechanisms underlying epiphytic lichen growth in Mediterranean climates.

Zusammenfassung

Um die wichtigen Ökosystemfunktionen, die von epiphytischen Flechten geleistet werden, zu erhalten, sind angemessene Wachstumsraten erforderlich. Bislang wurde das Flechtenwachstum hauptsächlich in borealen Wäldern untersucht. Es besteht somit ein Bedarf an entsprechenden Studien in mediterranen Wäldern. Wir nutzten reziproke Transplantation, um die relativen Wachstumsraten für Biomasse (RGR) und Thallusfläche (RTAGR) von *Lobaria pulmonaria* und *Lobarina scrobiculata* ($n = 720$ Thalli) in zwei mediterranen Eichenwäldern zu vergleichen. In beiden Wäldern wurden juvenile und reproduktive Thalli nahe der Stammbasis und in Brusthöhe auf zufällig ausgewählte Bäume für 334 Tage transplantiert. Wir maßen funktionale Merkmale, die spezifische Thallus-Masse (STM) und das Wasserspeicherungsvermögen (WHC), um nach Mustern der Adaption bzw.

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Akklimatisierung zu suchen. Lineare gemischte Modelle wurden eingesetzt, um die Einflüsse von (1) Wald, (2) Höhe am Stamm und (3) reproduktivem Status auf RGR, RTAGR und die funktionalen Merkmale zu bestimmen. *L. pulmonaria* wuchs schneller als *L. scrobiculata*, was mit ihrem flexibleren Hydratationsverhalten übereinstimmt. Bei beiden Arten zeigten Juvenile an der Stammbasis die höchsten Wachstumsraten, was mit den Zielkonflikten zwischen Wachstum und Reproduktion und Wasserverfügbarkeit und Entfernung vom Boden übereinstimmt. Bei *L. pulmonaria* nahm die STM mit zunehmenden Evaporationsanforderungen zu, was mit Akklimatisierungsmechanismen erklärt werden kann. Die realisierte Nische von *L. scrobiculata* wich von der fundamentalen Nische ab, was anzeigt, dass hohe Abundanz nicht notwendigerweise mit dem Habitat optimalen Wachstums zusammenfällt. Beide Arten wuchsen in den trockeneren und wärmeren mediterranen Wäldern ebenso schnell wie das aus borealen Wäldern berichtet wird, vermutlich weil sich die lokalen Bedingungen während der Hydratationsperioden zwischen den makroklimatischen Regionen weniger voneinander unterscheiden als die durchschnittlichen Klimaparameter und/oder weil insbesondere in Bodennähe Taubildung häufig ist. Darüber hinaus waren STM und WHC der Flechten in den mediterranen Wäldern hoch, wodurch die trockeneren Bedingungen teilweise ausgeglichen werden konnten.
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Keywords: Functional traits; *Lobaria pulmonaria*; *Lobarina scrobiculata*; *Quercus* forest; Relative growth rate; Spain; Specific thallus mass; Vertical gradient; Water holding capacity

Introduction

Epiphytic lichens often represent a highly diverse biodiversity component in forests and play important functional roles in ecosystem functioning (reviewed by Ellis 2012). Previously, lichens were considered slow-growing (Grime 1979), but recent studies reported fast growth (e.g. Gaio-Oliveira, Dahlman, Máguas & Palmqvist 2004; Larsson, Solhaug & Gauslaa 2012, 2014; Bidussi, Gauslaa & Solhaug 2013). However, epiphytic lichen growth is mainly quantified in boreal and temperate climates (e.g. Hilmo 2002; Antoine & McCune 2004; Larsson et al. 2012; Shriver, Cutler & Doak 2012) but rarely in Mediterranean climates (see Gaio-Oliveira et al. 2004) with summer drought (Valladares, Camarero, Pulido & Gil-Pelgrín 2004). Interestingly, these dry and sunny areas share various epiphytic lichens with temperate and boreal regions. To improve our understanding of lichen functioning across contrasting ecosystems and environmental conditions, there is a need to quantify growth rates and functional traits also in Mediterranean forests.

One reason to identify growth-regulating factors is that reproduction and fitness shaping population viability partly depend on growth (e.g. Martínez et al. 2012; Shriver et al. 2012). Although environmental factors determine lichen growth (e.g. Palmqvist 2000; Bidussi et al. 2013), internal factors such as reproductive effort also influence lichen growth by a trade-off between growth and reproduction (e.g. Gauslaa 2006). Lichens grow three-dimensionally: Area expansion enhances the interception surface for light, water, and nutrients; while dry mass gain per area unit e.g. improves water holding capacity (Larsson et al. 2012; Merinero, Hilmo & Gauslaa 2014). The specific thallus mass (STM = dry mass per area) is an important functional trait controlled by light exposure (Snelgar & Green 1981; Larsson et al. 2012) and/or nutrient availability (Asplund, Sandling & Wardle 2012). STM changes when area and dry mass do not increase concurrently, meaning that these processes are regulated differently. Photosynthetic carbon gain shapes dry mass investments (Palmqvist 2000; Larsson et al. 2012), while fungal hyphae expansion drives area growth (Gaio-Oliveira et al. 2004; Larsson et al. 2012). STM is a driver of the water holding capacity (WHC); thick (Gauslaa & Coxson 2011) and large (Merinero, Hilmo et al. 2014) thalli retain more water. STM, and thus WHC, increase with increasing evaporative demands (e.g. Hilmo 2002; Gauslaa & Coxson 2011; Larsson et al. 2012; Merinero, Hilmo et al. 2014). Comparisons of WHC (and STM) in epiphytic lichens between open, dry Mediterranean sites (Valladares et al. 2004) and wet boreal sites including closed rain forests (e.g. Coxson & Stevenson 2007; Larsson et al. 2012) may thus give clues to understand links between site-specific hydration sources and lichen adaptation/acclimation traits.

The vertical distribution of lichens on tree trunks is influenced by e.g. solar radiation and humidity (reviewed by Ellis 2012). Air humidity increases with proximity to the ground, whereas light and wind exposure enhancing evaporation often increase with height (Geiger 1950). In Mediterranean sites, moisture availability is usually a limiting factor causing vertical gradients of lichens on tree trunks (Burgaz, Fuertes & Escudero 1994). The height on the trunk affects lichen performance, evidenced by height-dependent gradients in thallus size in lichen populations (e.g. Martínez et al. 2012).

We studied the cephalolichen *Lobaria pulmonaria* L. (Hoffm.) and the cyanolichen *Lobarina scrobiculata* (Scop.) Nyl. ex Cromb. They are widely distributed globally, but declining and red-listed in many European countries, including Spain (Martínez et al. 2003). In our study area, they inhabited two Mediterranean oak forests spaced by 7 km, although in contrasting proportions. We established reciprocal transplants to compare relative growth rates between species and between sites. In boreal canopies, both species acclimate to higher evaporative demand at greater heights by increasing their WHC (Merinero, Hilmo et al. 2014). To search for height-dependent growth and acclimation, we

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