The Lichenologist **49**(5): 535–538 (2017)
doi:10.1017/S0024282917000342

Growth of *Rhizocarpon geographicum* in the summit region of Volcan Barú, Panama

The crustose lichens of the genus *Rhizocarpon* are among the most widely distributed species on rock surfaces worldwide (Armstrong 2011, 2016). Thalli of this species are characterized by yellow-green lichenized areolae on the surface of a non-lichenized fungal hypothallus, which forms a dark marginal ring. *Rhizocarpon* species typically grow very slowly and reach a considerable age, characteristics that have been exploited in numerous studies by earth scientists and archaeologists using these lichens as a tool to estimate the time of exposure of stone surfaces in natural systems (e.g. retreating glaciers, Rodbell (1992)) or to date human artefacts (e.g. tombstones or stone walls, Emerman *et al.* (2016)). There are hundreds of studies on growth in *Rhizocarpon* species (McCarthy & Henry 2012), although the large majority of them do not directly measure growth via repeated observations but rather use 'growth curves' that are constructed from independently dated substrata. This practice has evoked substantial criticism (e.g. Osborn *et al.* 2015). In spite of the large number of publications and the occurrence of *Rhizocarpon* species in both hemispheres over a large latitudinal range from the equator to both the Arctic and Antarctic, there are very few reports about this lichen from the tropics (Rodbell 1992; Solomina *et al.* 2007; Jomelli *et al.* 2008). Moreover, none of them determined growth directly, but used the 'growth curves' criticized by Osborn *et al.* (2015) and others. The database is not much better for other crustose lichens. To my knowledge, the only study measuring radial growth in a crustose lichen in the tropics (Zotz 1999) is on an unidentified *Cryptothecia* species (*Arthoniaceae*) growing epiphytically in the moist lowland forest of Barro Colorado Island in Panama and this reported remarkably high radial growth rates of >5 mm y^{-1}.

The limited information on the growth of tropical lichens in general, and *Rhizocarpon geographicum* (L.) DC. in particular, motivated the current study. Twice within three years, I visited the summit region of the Volcán Barú massif in the Republic of Panama. Taking digital photographs of *Rhizocarpon* thalli on large boulders allowed the direct determination of growth without any of the problematic assumptions that typically underlie lichenometry (Osborn *et al.* 2015).

This study was carried out close to the summit of Volcán Barú (Panama, Chiriquí Province, 8°48·5'N, 82°32·5'W, 3475 m a.s.l.) at an altitude of 3350–3450 m a.s.l. between March 2009 and March 2012. The local vegetation can be classified as *páramo* following the discussion of Weber (1958) for the Chirripó massif in neighbouring Costa Rica, where the tree line is also at *c.* 3300 m. The vegetation is a mosaic of patches of stunted treelets (mostly *Comarostaphylis arbutoides* Lindley subsp. *arbutoides*, *Ericaceae*) and open herbaceous vegetation dominated by grasses and ferns (mostly *Elaphoglossum* sp.) with numerous andesite boulders (Sherrod *et al.* 2008). Steeper slopes are covered by scree and are almost devoid of plant cover, as are rock outcrops and the central crater area (see Supplementary Material Figure S2, available online).

There are only some basic climate data for the study area reported by Zotz *et al.* (2014) for a 12-month period during the third year of the present study. These data indicate strong seasonality. Radiation was twice as high in the drier months (January–March) as it was in the wetter remaining part of the year. Temperatures, with an annual mean of 9·1 °C, were somewhat higher during the dry season, with average maxima of 17·5 °C vs. 15·5 °C during the wet season. In contrast, the average minima tended to be slightly lower (5 °C vs. 6 °C) in the dry season. The entire 12-month measurement period was frost-free with a lowest absolute value of 0·2 °C. However, it is known from other field trips to the summit region of Volcán Barú that frost can occur (G. Zotz, personal observation).

In March 2009, seven large boulders were selected in the open summit vegetation supporting numerous thalli of *Rhizocarpon geographicum* growing on ± plane surfaces. Digital photographs were taken perpendicularly from above with a known reference area. Three years later, in March 2012, another set of photographs was taken of the same surfaces. A total of 36 non-competing thalli, ranging in initial radius from *c.* 1 to *c.* 50 mm, were selected and analyzed by the same person with Adobe® Photoshop® version 6.0 using the 'magic wand' tool. The area of each thallus was re-measured five times with this software, yielding little variation among individual estimates: the mean coefficient of variation (cv) was 0·02 (minimum cv = 0; maximum cv = 0·11). For subsequent analyses the averages of these five area estimates were used.

Lichen thalli are rarely perfectly circular. Thus, the determination of area is more robust than measurements of one or two thallus diameters or radii (McCarthy & Henry 2012), although the latter metric is more commonly used in lichen studies (Armstrong 2016). To facilitate numeric comparisons with these studies, the radius of a perfect circle with an identical area was calculated for each thallus using the formula $r = (\text{thallus area} / \pi)^{0.5}$.

Two analyses were carried out. Firstly, relating area increment to initial thallus area and secondly relating annual radial increment (Δradius) to initial thallus radius. It was assumed that growth rate was constant during the three year growth period. All statistical analyses were performed with R 2.15.0 (R Development Core Team 2014).

Changes in thallus area over time varied with initial size, both in absolute and relative terms. The highest absolute increment of >2000 mm^2 over three years was observed in the largest thallus (initial size *c.* 7600 mm^2) (Fig. 1), while the highest proportional increases were observed in smaller thalli (<20 mm^2) with up to a six-fold increase over three years. Such high proportional increases over three years compare favourably with the results of the carefully executed study by McCarthy & Henry (2012) using a *Rhizocarpon* species from British Colombia, Canada. These authors documented annual increases of >100% in small thalli of <5 mm^2. In general agreement with McCarthy & Henry's (2012) study, areal growth in smaller thalli varied substantially over more than one order of magnitude from 41–598% over three years, whereas larger thalli showed smaller and relatively similar increases of *c.* 30% (Fig. 1). Notably, 4 of the 36 *Rhizocarpon* thalli showed partial dieback and decreased in area. Although we did not include these thalli in our statistical analyses, their inclusion would have hardly affected the numeric outcome of the overall analyses (data not shown).

The analysis of radial changes yielded results consistent with those described above for thallus area, with a significant increase in Δradius with increasing thallus size. The highest radial increments were close to 2 mm y^{-1} in thalli with an initial radius of 30–40 mm (Fig. 2), and the overall average of all thalli was 0·6 mm y^{-1}. Other studies with *Rhizocarpon* species that have included a larger size range of up to 80 mm initial radius (e.g. Iceland (Bradwell & Armstrong 2007); Wales (Armstrong 2016)) consistently report the highest radial increments in thalli of similar size to those of the present study and decreasing Δradius in smaller and larger lichens. Although the present study included only one larger thallus (radius *c.* 50 mm), the much lower Δradius of this particular specimen is suggestive of a similar size-related trend. In absolute terms, the maximum growth rates observed in *Rhizocarpon* thalli at this tropical montane site are considerably higher than those reported for most temperate sites which are typically below 1 mm y^{-1} (Armstrong 2016). Much higher growth rates have been reported from the tropical lowlands in central Panama for another crustose lichen, *Cryptothecia* sp. (*Arthoniaceae*), with radial increases of 5 mm y^{-1}. Interestingly, the only study on the growth of a foliose lichen in the tropics, with *Parmotrema endosulphureum*, reports a very similar radial increment of 4 mm y^{-1} (Zotz & Schleicher 2003). A total of three data points for growth in tropical lichens bears witness to an impressive dearth of information that does not allow any meaningful interpretation of possible elevational or latitudinal trends.

Growth estimates for yellow *Rhizocarpon* from Cordillera Blanca in Peru using a lichenometric approach are considerably lower than the current observations. Rodbell (1992) reports maxima of 0·4 mm y^{-1} and even lower rates are reported by Solomina *et al.* (2007) from the same region: they report a maximum radius of lichens on 100 year-old rocks of just 15 mm. Since radial increments in that study were based on growth curves derived from substratum age estimates, it is unclear whether such differences are related to climate (Cordillera Blanca in Peru is at *c.* 4500 m a.s.l.) or methodology. For a detailed critique of lichenometry see Osborn *et al.* (2015).

In conclusion, I report the direct measurements of thallus growth of *Rhizocarpon geographicum* in the summit region of Volcan Barú, which is only the second report on radial growth of crustose lichens in the tropics (cf. Zotz 1999) and only one of three reports for tropical lichens in general (cf. Zotz & Schleicher 2003). With all due caution, the available data suggest that crustose lichens show relatively high growth rates

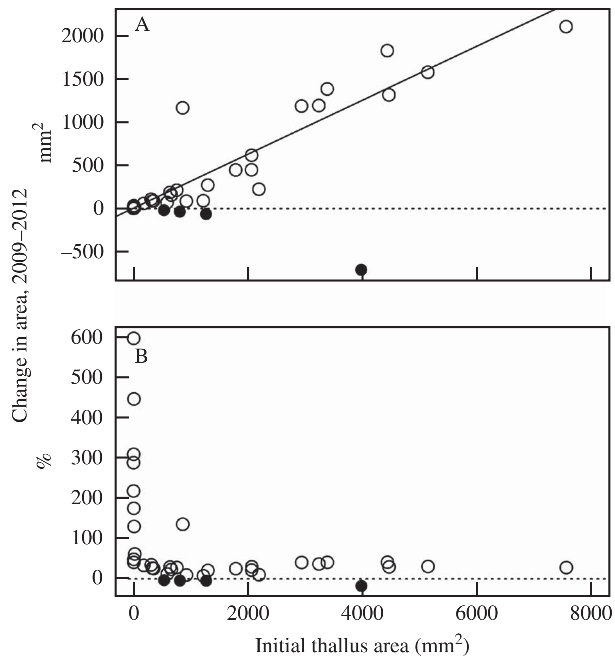

FIG. 1. Relationships between initial thallus area and A, three-year areal increment, and B, three-year proportional increase in *Rhizocarpon geographicum* from the summit region of Volcan Barú, Panama ($n = 36$). ○ = thalli with positive growth; ● = thalli with partial dieback (these were not included in the linear regression analysis) ($y = 6{\cdot}1 + 0{\cdot}31\ x$, $r^2 = 0{\cdot}86$, $P < 0{\cdot}001$).

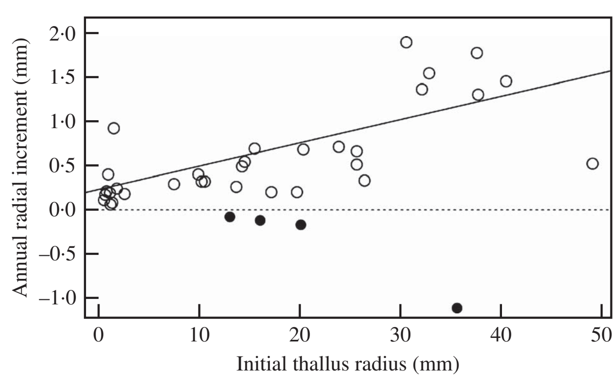

FIG. 2. Relationship between initial thallus radius and annual radial increment in *Rhizocarpon geographicum* from the summit region of Volcan Barú, Panama ($n = 36$). ○ = thalli with positive growth; ● = thalli with partial dieback (these were not included in the linear regression analysis) ($y = 0{\cdot}23 + 0{\cdot}03\ x$, $r^2 = 0{\cdot}31$, $P < 0{\cdot}001$).

in the tropics, but much more work is needed to substantiate or refute this tentative claim.

I dedicate this paper to the late Otto Lange for sparking my interest in lichens and for supporting me continuously during my scientific career. Funds from the Terrestrial-Environmental Sciences Program of the Smithsonian Tropical Research Institute, Panama financed the field trips. Study permits were granted by the Panamanian authorities (ANAM). Helena Einzmann, Glenda Mendieta and Katrin Wagner (all Oldenburg) assisted in the field, Burkhard Büdel (Kaiserslautern) identified the study species, and Brigitte Rieger (Oldenburg) determined the areas of the lichen thalli.

Supplementary Material

For supplementary material accompanying this paper visit https://doi.org/10.1017/S0024282917000342

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