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Unveiling annual growth chronologies from inter-nodal branch elongations in a fruticose lichen in southern Europe

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ABSTRACT

Techniques for retrospective analysis of size dynamics at annual resolution remain poorly developed in lichens in general, and fruticose lichens in particular. Only a few attempts in very high latitudes suggested that growth might be studied as a chronosequence of inter-nodal branch elongations. Here we evaluated, for the first time, this hypothesis in a dry Mediterranean environment using the lichen *Cladonia rangiformis* as a case study. Mixed models supported a strong positive relationship between humidity measured as precipitation/PET and inter-nodal branch elongations. Importantly, model selection suggested that (i) the number of intermodal elongations were a major determinant of stem elongation, and (ii) a second-order temporal autocorrelation denoted legacies of environmental influences at least over the next 2 y. The strong growth–humidity relationship, along with the potential legacies observed, support the idea that inter-nodal branch elongations could be used to reconstruct growth chronologies at annual resolution in drylands. This finding highlights the high vulnerability of these organisms to rising aridity, and opens a new venue for climate reconstruction and other potential applications in Ecology and Earth Science disciplines.

1. Introduction

Morphology and macroscopic features in lichens can provide valuable information on individual-level responses to climatic fluctuations and other type-disturbances. Among the most conspicuous of such features, morphological structuring tied to aging in crustose and foliose lichens has been intensively studied and applied, for instance, in substrate dating (Webber and Andrews, 1973; Benedict et al., 2009; Joshi et al., 2012). In this sense, lichenometry has been proved to be decisive in evaluating geomorphological processes and the ensuing impacts on land forms and human societies (Winchester and Harrison, 2000; Jomelly et al., 2007). However, the vast majority of studies have used systematic radial measurements in crustose lichens such as *Rhizocarpon* sp. (Armstrong, 2004). In fruticose growth forms, techniques for size reconstruction have been comparatively less studied due to the structural complexity of thalli. Only a few reported attempts in boreal latitudes suggested that growth in these lichens can be studied as a chronosequence of inter-nodal branch elongations (Gorodkov, 1936; Igoshima, 1939; Glinka, 1939; Abdulmanova et al., 2015). Some authors have demonstrated that annual growth of fruticose lichens consist of a three-phase process in which only one is representative of the biomass accretion manifested as branch elongation (Andreev, 1954; Scotter, 1963). In drylands, this approach has been never put forward before although fruticose lichens are pivotal functional constituents of their biological soil crusts covering ample ground areas and having a major role in ecosystem functions and services (see Belnap et al., 2003).

The broad range in growth forms and the simplicity of the standardized techniques in lichenometry suggest that lichens can

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be excellent tools for climate reconstruction and early detection of climate changes on natural ecosystems (Sancho et al., 2007, 2017). This method has been proved successful in arctic-alpine environments where lichen longevity is extraordinary high and growth rates are rather low (Armstrong, 2004). In drylands, lichenometry is gaining more attention over the last two decades and latest findings support evidence that most soil lichens would be experiencing important declines under increased intensity and frequency of dry spells despite their ability to thrive desiccation (Escolar et al., 2012).

Together with other biotypes, soil fruticose lichens are ubiquitous organisms having also a notable contribution to valuable ecosystem services such as protection against erosion, hydrological regulation or carbon fixation (Eldridge et al., 2003; Elbert et al., 2012; Concostrina-Zubiri et al., 2016). Moreover, fruticose lichens are important feeding resources for large mammals and insects in boreal and temperate biomes (Llano, 1956; Backor et al., 2003; Inga, 2007). Like the rest of lichens, fruticose ones are vulnerable to the ongoing climatic changes (Aptroot and van Herk, 2007; Escolar et al., 2012) as poikilohydric organisms highly dependent on air moisture and temperature (see Matos et al., 2015). For instance, *Cladonia* spp. reveal faster growth during moist periods according to demonstrations that net assimilation rates increase with increased moisture content in the thallus (Kershaw and Rouse, 1971). Translated to field observations, other authors have evidenced the high correlation between annual growth rate and precipitation (Kärenlampí, 1971) and the importance of the length of the growing period, which is also contingent upon temperature (Andreev et al., 1954). Consequently, climate change might jeopardize survival and functioning of many fruticose lichens. However, the role played by fruticose lichens in drylands worldwide is less known. More specifically, there are not specific studies in fruticose lichens connecting growth patterns and climate in drylands, and so major uncertainties rise regarding the future of these organisms and the provisioning of the associated services under the ongoing climate changes.

Here we evaluated the climate–growth relationship in *Cladonia rangiformis* Hoffm. thalli by assuming that inter-nodal branch elongations are directly connected to current conditions so fluctuating tightly coupled to climate. Specifically, we aimed to model the relationship between inter-nodal branch elongation and annual climatic humidity (precipitation/evapotranspiration) in a number of thalli collected in a Mediterranean water-limited environment. We hypothesized that annual aridity will affect growth negatively in this lichen species, and thus, inter-nodal branch elongations associated to dry years should be narrower than those representative of wet years. Additionally, inter-nodal branch elongations should also shape size-development patterns as it is typical of other long-living organisms such as woody species. If true, our results will provide a new biometric tool for climate, geomorphology and biotic reconstruction under changing conditions in dry ecosystems.

2. Material and methods

2.1. Study site

The study was set in the Tierra de Pinares county, an extensive territory located in central–north Iberian Peninsula (41°19′N–4°12′W, 841 m a.s.l). All the material in the field was collected in inner sand dunes in an open public pine forest stand nearby the town of Cuéllar (Segovia province, Fig. 1a). Specifically, field sampling was conducted in a protected area where there is no evidence of human influence on thalli and the herbivore pressure is insignificant. In this area, the small lichen cushions form a more or less continuous cover in which neighbor individuals are in physical contact. The climate is continental Mediterranean, characterized by cold winters and hot and dry summers. Mean annual precipitation is 430–470 mm with maximum seasonal spells in May and October. Mean annual temperature is 12 °C and mean minimum temperature is below 0 °C during winter (December–March) and mean maximum temperature is above 30 °C during summer (June–September; averaged climatic data for the last 60 y). Soils are very sandy and unconsolidated, and partially podsolized due to the dune morphology. Thus, the organic layer is extremely poor and acidic and in correspondence, the water retention capacity is extremely low (Gómez-Sanz and García-Viñas, 2011).

Pinus pinaster is the dominant tree species, although other pines (*Pinus sylvestris* L., *Pinus nigra* Arnold) and oaks (*Quercus ilex* L., *Quercus faginea* Lam. and *Quercus pyrenaica* Willd.) are marginally present in the nearby seasonal streams or located in ground depressions. Tree distribution is nonetheless scattered with average densities between 10 and 15 trees per hectare in this area. In open ground areas, a disperse vegetation is composed of dwarf shrubs such as *Helichrysum stoechas* (L.) Moench., *Lavandula stoechas* subsp. *pedunculata* (Mill.) Samp. *ex* Rozeira, and a very-rich annual plant community dominated by species such as *Vulpia bromoides* (L.) Gray, *Rumex acetosella* L. or *Corynephorus canescens* (L.) Beauv which, all together, hardly cover 30 % of the ground surface. In turn, a rich lichen cover dominated by fruticose lichens such as *C. rangiformis* and *Cladonia subrangiformis* Sandst., and foliose lichens such as *Cetraria aculeata*, cover more than 70 % of the ground (Fig. 1b).

Here we used the lichen *C. rangiformis* as a case study because it is the most conspicuous species in our soil lichen community and the most frequent and abundant *Cladonia* species in the Iberian Peninsula ranging from coastal areas up to 2500 m.a.s.l. This species is widely distributed throughout the European continent, from Boreal biomes in the Scandinavian Peninsula to temperate zones in the British Isles and Central Europe, and Mediterranean enclaves in North Africa, Italy and Greece. This species occurs preferentially on bare-sandy soils where it forms sponge-like individuals (Fig. 1c) composed of a complex arrangement of fruticose thalli (Burgaz and Ahti, 2009). This lichen is characterized by the presence of green spots on a grayish–whitish background on the surface of branches. In a Mediterranean continental environment, *C. rangiformis* is active from the end of the winter season to the beginning of the summer season when thalli become inactive and dehydrated due to drought as many other hot-desert lichen species (Kershaw, 1985). After the seasonal drought and before the arriving of the winter season, this lichen species become active again and produces the hymenial discs for sexuality before the arriving of the winter season.

2.2. Field sampling of thalli and lichenometry

We collected a total of 42 thalli of *C. rangiformis* following a linear transect of 1000 m east–west across a homogeneous area within the study site. Field collection was carried out in November of 2015 following the premises that (i) individuals (8–10 cm diameter) should be collected one at a time along the transect (not pooled) and, (ii) should be established in open areas out of tree influence. In each thallus we identified and isolated the longest branch ranging from the base to the apical extreme. This process required the help of scissors to separate the lateral branches until reaching the apical part. We also hydrated the material to avoid disruptions in the branches. Once an entire branch in each individual was isolated, it was scanned with a high resolution scanner at 1200 dpi resolution (see some examples in Fig. 1d). We measured every inter-node in each isolated branch using the Image J software (Fig. 1d). We assumed that the apical inter-node represents growth during the year 2015 (the year of the material collecting). Thereafter, a calendar year is progressively assigned to every inter-node

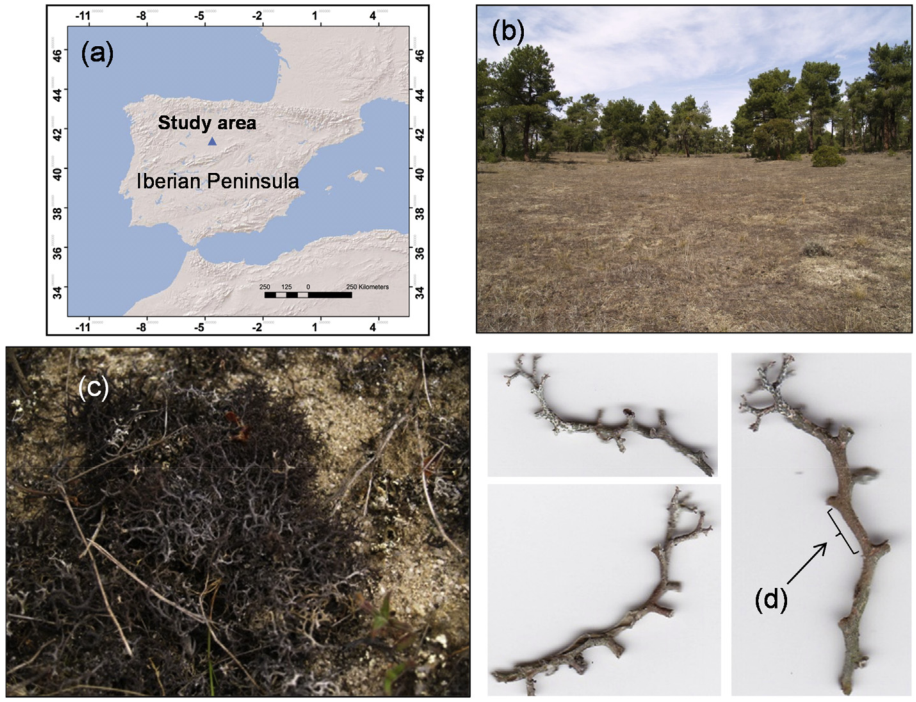

Fig. 1. Study site and details of *C. rangiformis* specimens. Location of the study site in the Iberian Peninsula and physiognomy of the area (a,b), and details of a (c) *Cladonia rangiformis* individual thallus and (d) inter-nodal branch elongations.

downwards to the basal extreme. In order to have a consistent sample size across years we established the beginning of the chronology in 2001.

2.3. Cross-dating

We used a visual cross-dating technique commonly used in dendrochronology (Schweingruber, 1989). For that purpose, we identify pointer years all along the chronology in order to reconstruct a growth pattern common to all thalli. Thus, the initial hypothesis is to assume that the growth of lichens follows a process of annual elongation that ends in a bifurcation from which it starts the elongation of the following year. Each elongation between consecutive dichotomies is thus hypothesized to be representative of annual growth responses of individual thallus. Potential causes underlying the abnormally large or small elongations were sought in the climatic records for this area since 2001: particularly abnormal dry years.

2.4. Statistical analysis

We analyzed growth as function of the number of lichen dichotomies (hereafter age) and humidity, which is assessed following UNEP (1992) as the ratio Annual Precipitation/Potential Evapotranspiration (Thornthwaite, 1948). We fitted linear mixed models to inter-nodal branch elongations assuming a Gaussian distribution of error where individual branches were considered as a random factor and both age and precipitation as covariates in the fixed term. Age was included in the model as a second order polynomial to account for potential non-linear growth patterns throughout lichen formation. The dependent variable (growth) was log-transformed to improve compliance with the assumptions of linear models (homogeneity of variance and normality). We firstly tested in the model the inclusion of a temporal autocorrelation structure since inter-nodal branch elongations are sequential measurements in individual thalli. We thus considered a reference model without autocorrelation structure and a set of models with increasing order of the autocorrelation structure up to 4. We used the Akaike's information criterion corrected for small samples to compare models (AICc, Hurvich and Tsai, 1989). Once the best autocorrelation structure was set, we applied a backward selection of the fixed term starting with a full model including age and aridity. We assumed a difference of 4 units in AICc as a criterion to accept or reject a predictor in the final model (Burham and Anderson, 2004). Statistical analyses were conducted using the *lme* function in the *nlme* package in the R environment (Pinheiro et al., 2013).

3. Results

Mean number of internodes per thalli was 16, with a maximum of 20 and a minimum of 11. The averaged branch elongation chronology showed a few pointer years with extremely short elongations (e.g. 2005, 2009 and 2012), and other showing large elongations (e.g. 2008). The elongation chronology for the oldest specimen collected (1997–2015) showed a notable positive relationship with total annual precipitation (Fig. 2). This growth pattern was found to be consistent all across the measured thallus of *C. rangiformis*. Moreover, this pattern was congruent with the temporal variability in annual aridity (Fig. 3), because those years with reduced growth coincided with intense droughts (particularly 2005), and contrary, the largest elongations coincided with the rainiest years (Fig. 3). The average elongations in 2005 and 2009 were 1.690 and 1.511 mm, respectively. Comparatively, the average elongation in 2008 reached 2.53 mm.

Backward selection supported both aridity and age as strong predictors of inter-nodal branch elongations for the period 2001–2015. Both predictors were related negatively to inter-nodal branch elongations (Fig. 4). Interestingly, selection of the autoregressive structure in the model supported a 2nd order autocorrelation which implies that, at least, environmental and internal influences on inter-nodal branch elongations leave a legacy over the next 2 y. The assumptions of linear models (e.g. homogeneity of

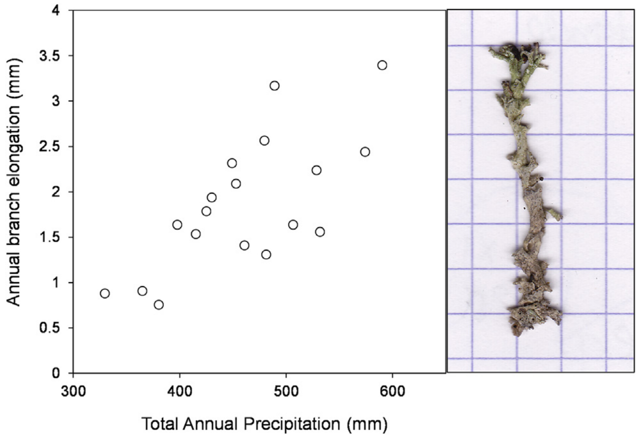

Fig. 2. Branch elongation annual precipitation relationship. Scatter plot showing the relationship between branch elongation and total annual precipitation for the oldest *Cladonia rangiformis* specimen collected.

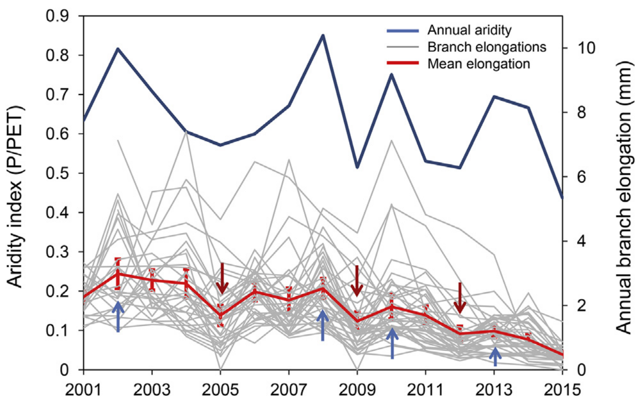

Fig. 3. Growth series. Scatter plot showing inter-annual variability in aridity (precipitation/potential evapotranspiration) and inter-nodal branch elongations in mm of all individual branches studied (in gray) and aggregated mean ± 95 % confident intervals (in red). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

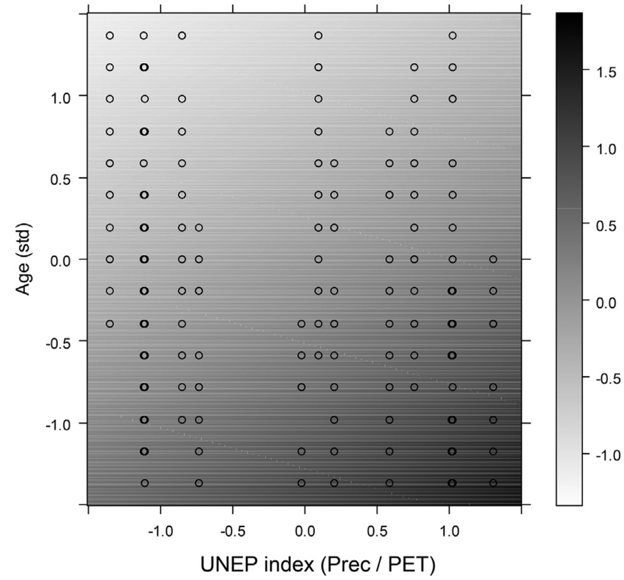

Fig. 4. Growth predictions. Predicted inter-nodal branch elongations as linear function of age (total number of internodes in the individual branch) and humidity (precipitation/PET). The darker the color, the larger the inter-nodal branch elongations.

variance and normality) were fulfilled as shown by the graphical analyses of residuals (Fig. S1). In addition, the model showed a sound goodness of fit with marginal-R^2 of 0.32 and conditional-R^2 of 0.60.

4. Discussion

As hypothesized, our findings on *C. rangiformis* supported the climate–growth hypothesis or more concretely that inter-nodal branch elongations strongly reflected the interannual climatic variability for the time period studied (i.e. 2001–2015, both years included). On the one hand, mixed model estimates supported a positive effect of annual climatic humidity on inter-nodal branch elongations in this fruticose lichen. On the other hand, a 2nd order temporal autocorrelation structure in our elongation data set suggested growth legacies over the next 2 y. Additionally, results also support long-term growth trends associated to lichen development in the form of negative exponential curves. This growth pattern is commonly found in other long-living organisms such as trees and shrubs and is explained on the basis of carbon accretion and respiration dynamics with biomass accumulation (Mencuccini et al., 2005). In crustose and foliose lichens, modeling outputs supported the idea that growth dynamics can be predicted accurately just by considering the lichen geometry and the carbon dioxide diffusion in the thalli: i.e. growth is slow until the radius exceeds the height of the lichen and then accelerates up to an asymptotic value (Seminara et al., 2018). In turn, correlational studies based on growth of *Rhizocarpon geographicum* (L.) DC. showed a hump-shaped model in which growth tend to decline with age in the long run (Benedict, 1967; Bull and Brandon, 1998). It is worth mentioning that fruticose lichens have a three-dimensional structure in which a myriad of blended branches creates a sponge-like organism with an irregular surface in which carbon dioxide diffusion might be progressively limited towards the inner parts of the sponge. Following this reasoning, a negative exponential pattern might be expected in which growth follows the carbon balance dynamics between photosynthesis and respiration.

The existence of annual growth pulses in fruticose lichens had been already showed in the classical studies of Gorodkov (1936) and subsequently Igoshina (1939) and Glinka (1939). They found that branching of the podetium generally occurred once each year with variations in the direction between years probably to better explore the space and to maximize photosynthesis and respiration. Later on, studies of Pegau (1968) and Helle et al. (1983) applied the inter-nodal branch elongation pattern in *Cladonia* to date lichens and assess average growth data at the podetium level. Since then, studies in Boreal biomes are scarce and to our known inexistent in the Mediterranean and other dry biomes of the world. In turn, a large body of literature dealing with relations between annual growth and external factors such as climate in foliose and crustose lichens has been extensively developed (Benedict, 1990, 1991; Lange, 1990; Armstrong, 1983, 2004, 2015). In general, a tied relationship between humidity and growth is recognized as a consequence of the poikilohydric character of these organisms. Our results using *Cladonia*, strongly support humidity as an important external forcing of growth at annual time scale resolution as well. Worth also to note that the average inter-nodal branch elongations associated to the dry years 2005 and 2009 were significantly lower (1.690 and 1.511 mm, respectively) than growth in wet years. For instance, branch elongation in the wettest year of the studied period, 2008, reached 2530 mm in average which is almost 40 % higher growth than that of dry years. These growth rates, nonetheless, are lower than those obtained in Boreal biomes where

Cladonia can even reach 4.5–5 mm yr^{-1} in average (see Pegau, 1968; Helle et al., 1983) showing the limitations this lichen found in Mediterranean-type habitats. Importantly, a full hydration of lichens in Mediterranean ecosystems should be hold only during rainy days, which might explain why humidity assessed using precipitation and temperature fit that well in our case study.

Lichens in general are highly resilient organisms to prolonged dry periods in which thalli maintain as dehydrated structures. Although metabolic mechanisms underpinning dehydratation in response to drought are poorly understood yet, the extremophile character of these organisms is broadly recognized (Kranner et al., 2008). Nonetheless, our results supported a significant 2nd order temporal autocorrelation at annual time scale resolution, which introduces new considerations to be accounted for when evaluating climatic vulnerabilities. In this sense, recovery from dehydration after a dry period would demand a quota of resources for activation that might be proportional to the time of inactivation and/or the frequency of times the lichen have to become inactive. Studies in drylands suggest that changes in the regimes of rainfall and non-rainfall water inputs can significantly affect the carbon balance in lichens of biological soil crusts thus exposing them to increased vulnerability under climate change (Ladrón de Guevara et al., 2014). This aspect of lichen growth is critical although it has been largely neglected in the literature. Further efforts should be paid on how growth legacies reflect potential vulnerabilities on lichen performance and fitness under warming scenarios with increased intensity and frequency of dry spells.

Soil lichens play a decisive role in the preservation of ecosystem functions and services (Eldridge and Greene, 1994; Bowker et al., 2008; Maestre et al., 2011). Lichens contribute to the maintenance of biological soil crust (West, 1990), soil bacteria's growth (Akpinar et al., 2009), nitrogen fixation (Veluchi et al., 2006) and the capture by some species of atmospheric humidity, increasing the hydraulic availability in its surroundings (Castillo-Monroy and Maestre, 2011). Even more, specific pairwise interactions between lichens and vascular plants, especially ephemerals, are also critical in dryland dynamics and services (Romao and Escudero, 2005; Escudero et al., 2015). Therefore, a better knowledge of the various aspects of lichen biology, such as what is shown in this article, is essential for the maintenance of these organisms under warming conditions due to climate change (Maestre et al., 2015). Potential applications of these results are two-fold. On the one hand, confirmation of the inter-nodal branch elongation as an accurate estimate of annual growth can be critical to evaluate direct and indirect vulnerabilities of these key organisms under climate change. On the other hand, inter-nodal branch elongations can be used to identify and dating accurately geomorphological processes and events at annual time scale resolution. This would be similar to the toolbox and methodologies used on tree ring widths by dendroecologists in this and other similar areas in the Mediterranean. For instance, dune dynamics and erosion could be described on the basis of population dynamics and growth of this and other similar fruticose lichens which are usually dominant species on bare-exposed soils in Mediterranean ecosystems.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funbio.2019.08.008.

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