

Comparative demography of an epiphytic lichen: support for general life history patterns and solutions to common problems in demographic parameter estimation

Robert K. Shriver · Kerry Cutler · Daniel F. Doak

Received: 9 May 2011 / Accepted: 2 March 2012
© Springer-Verlag 2012

Abstract Lichens are major components in many terrestrial ecosystems, yet their population ecology is at best only poorly understood. Few studies have fully quantified the life history or demographic patterns of any lichen, with particularly little attention to epiphytic species. We conducted a 6-year demographic study of *Vulpicida pinastri*, an epiphytic foliose lichen, in south-central Alaska. After testing multiple size-structured functions to describe patterns in each *V. pinastri* demographic rate, we used the resulting estimates to construct a stochastic demographic model for the species. This model development led us to propose solutions to two general problems in construction of demographic models for many taxa: how to simply but accurately characterize highly skewed growth rates, and how to estimate recruitment rates that are exceptionally difficult to directly observe. Our results show that *V. pinastri* has rapid and variable growth and, for small individuals, low and variable survival, but that these traits are coupled with considerable longevity (e.g., >50 years mean future life span for a 4-cm² thallus) and little

deviation of the stochastic population growth rate from the deterministic expectation. Comparisons of the demographic patterns we found with those of other lichen studies suggest that their relatively simple architecture may allow clearer generalities about growth patterns for lichens than for other taxa, and that the expected pattern of faster growth rates for epiphytic species is substantiated.

Keywords Demography · Life history · Lichens · Life span · Epiphytes

Introduction

The life history of a species is the combination of traits regulating population dynamics and also individual fitness. This set of traits governs both a species' ability to persist in a given environment and many aspects of its ecological dynamics, including population changes, ecosystem role (e.g., biomass accumulation), and community interactions. Development of general theories explaining the life history patterns within and across taxonomic groups has been topic of longstanding interest in ecology (see e.g., Cole 1954; or more recently, Linares et al. 2007; Garcia et al. 2008). Despite this interest, quantitative characterizations of full life histories have concentrated on vertebrates, vascular plants, arthropods (van Straalen 1985; Boggs and Ross 1993), and some commercially important mollusks (e.g., Chen and Liao 2004), with far less attention to most other taxonomic groups (but see, for example, Hughes and Jackson 1985; McFadden 1991; Linares et al. 2007; Rogers 1989). If generalities about life history variations and their ecological drivers are to be adequately tested and refined, a considerably broader range of taxa should be subjected to careful life history analysis, especially those with physiological

Communicated by Miguel Franco.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2301-4) contains supplementary material, which is available to authorized users.

Present Address:

R. K. Shriver (✉)
University Program in Ecology, Duke University,
Durham, NC 27708, USA
e-mail: robert.shriver@duke.edu

K. Cutler · D. F. Doak
Department of Zoology and Physiology,
University of Wyoming, Laramie, WY 82071, USA

structures and constraints differing from those of the common focal groups in population ecology.

Lichens are one of the many under-represented groups in life history studies. Lichens are major members of many communities worldwide, and have been the subject of numerous ecological investigations. Major themes in the ecological literature of lichens include their sensitivity to pollutants (Conti and Cecchetti 2001), patterns of species diversity (Dietrich and Scheidegger 1997; Rosentreter 1995), and their important roles in nutrient and energy flows (Pike 1978; Knops et al. 1996). However, interest in lichen ecology has not extended to any extensive degree to their population ecology, including life history analysis. Survival, growth, and reproductive rates of lichens are the drivers that shape their community and ecosystem roles, but of these, only growth patterns have received any substantial attention (Armstrong and Bradwell 2011; but see Rhoades 1983; Loso and Doak 2006). While many studies have sought to quantify lichen growth rates, the focus of most research has either been biomass accumulation or the use of lichen sizes to date surfaces for geological studies, rather than on understanding their ecological dynamics per se (Benedict 2009; Bradwell and Armstrong 2007; but see Armstrong and Bradwell 2011). Recent work has emphasized the diversity of lichen growth patterns (Armstrong and Bradwell 2011); however, little attention has been given to the selective environments that would produce different life history patterns—in particular for the many species that, like epiphytes, must cope with dynamic substrates with limited durations. In addition, few attempts have been made to measure survival or reproduction or to incorporate multiple rates or temporal variance into a complete life history analysis.

Here, we apply a demographic approach to quantify the life history of a common epiphytic lichen, *V. pinastri*, in south-central Alaska. *V. pinastri* is a foliose lichen of temperate and subarctic forests, and occurs predominantly on the relatively short-lived trunks of *Alnus* shrubs throughout large areas of its range. We used a 6-year demographic study of *V. pinastri* to estimate demographic patterns for this typical epiphytic species. Our analyses focus on two questions. (1) What are the basic demographic patterns exhibited by *V. pinastri*, and what life history characteristics (e.g. lifespan) do these lead to? (2) Does a comparison of the growth patterns of *V. pinastri* with those of other lichens support generalities from life history, especially generalities about life history variation in response to habitat stability or disturbance regime? In particular, we would expect epiphytic species to show demographic patterns commensurate with their often short-lived substrates. In addition to addressing these issues, during the course of our work, we confronted two common problems in the development of many demographic

models—the efficient parameterization of multiple modes of growth and shrinkage, and the inability to directly observe recruitment events—and suggest general solutions to these common demographic stumbling blocks.

Materials and methods

Species biology, study sites, and population sampling

Vulpicida pinastri is a circumboreal epiphyte which occurs across boreal and high-altitude temperate forests of Europe and North America. *V. pinastri* has a compact, foliose growth habit and most individual thalli can be readily distinguished. Three reproductive structures are present on thalli: sexually reproducing apothecia are present but uncommon; luminant yellow powdery soredia, from which the species derives its charming common name “Powdery Sunshine Lichen,” are abundant; and conidia-producing pycnidia are also present (both soredia and pycnidia are asexual reproductive structures). We were not able to distinguish between new thalli arising from sexual versus either mode of asexual reproduction.

All fieldwork was conducted in the Kennicott Valley, in the Wrangell Mountains of Alaska. Eight study sites were haphazardly chosen in mature white spruce (*Picea glauca*)/alder (*Alnus viridis* ssp. *crispa*) forest. All study sites were located within 0.30 km of one another and between 700–730 m elevation. In this habitat, *V. pinastri* primarily occurs on the bark of alders (*A. viridis* ssp. *crispa*), with far smaller numbers on spruce. A spruce bark beetle outbreak occurred in the study area, peaking in 1996 (Matsuoka and Handel 2007) with low levels of continuing tree mortality throughout the study period (D.F.D., personal observation). Tree death further thinned the already sparse spruce canopy, but had little obvious impact on the already dense alders in the subcanopy.

In 2004, four study sites were established. At each site, five alder stems were chosen, and on each, ten lichen thalli were individually marked with a carpentry staple and aluminum tag and subsequently followed until their death or the end of the study in 2009. In 2005, four additional sites were established, for a total of 400 individual lichen thalli. In each year (ranging from 18 May to 13 June), each thallus was relocated and digitally photographed with a scale bar. Thallus surface areas were subsequently estimated using Adobe Photoshop (Adobe Systems, San Jose, CA, USA). Individual thalli were distinguished by growth form and isolation; focal thalli were haphazardly chosen to span the full distances along each alder stem on which *V. pinastri* occurred, and to sample a wide range of thallus sizes.

To quantify establishment of new thalli, we collected two additional datasets. Two $2 \times 15 \text{ cm}^2$ recruitment

plots, established on stems near others with focal thalli, were photographed in each of the eight sites in each year and compared across years to locate new lichens. Unfortunately, this method resulted in very few clearly identifiable new thalli (four over the entire study). As an alternative, we made estimates of recruitment based on predicted population size distributions. For this estimation procedure, we quantified the size distributions of the entire lichen populations on six alder stems collected near our study sites in 2010 (total of 653 thalli). On each stem, we measured the major and minor axes of all lichens occurring from ~ 0 to 200 cm up the stem (the range of heights of nearly all lichens in our study area) and visually estimated the percentage of the elliptical outline of each thallus that was not filled. Measured thalli were assumed to approximate an ellipse and visual estimates of unfilled ellipse area were used to correct deviations from this ideal shape. These visual estimates of thallus area correspond well with those from our digital analysis ($r^2 = 0.947$, $n = 20$ thalli: slope not significantly different from 1).

Estimation of vital rates

We characterized the demography of *V. pinastri* using continuous, size-dependent functions for growth, variance in growth, and survival (Easterling et al. 2000; Morris and Doak 2002). For each vital rate, we fit a series of 8–12 alternative general linear models (GLMs; see ESM), and used AIC comparisons to identify the best-supported model (cf. Doak and Morris 2010; Palmer et al. 2010), including effects of size, year (categorical), and their interactions. Initial graphical exploration of the data indicated that growth was far more linear when using $(\text{thallus area})^{0.5}$ and we thus used the square-root of area as the basic size measure in all GLM analyses. This pattern corresponds to findings suggesting that only the part of a lichen thallus near the periphery can contribute to radial growth (Armstrong and Smith 1998; Aplin and Hill 1979).

Modeling of *V. pinastri* growth was complicated by a problem that plagues many other demographic studies of plants and some animals: while most individuals grow or shrink by modest amounts and are well-approximated by normally distributed errors around an average growth rate (Easterling et al. 2000), a smaller number suffer much more extreme shrinkage (Wikelski and Thom 2000; Salguero-Gomez and Casper 2010) resulting in a highly skewed distribution of growth rates (Fig. 1a, b). In our system, such shrinkage is most often due to mechanical damage to thalli from mammals or falling branches. To account for these two types of growth without adding undue complexity to our models, we estimated growth and shrinkage as a two-part process. First, each thallus has a size- and year-dependent probability, p_n , of undergoing

‘normal growth or shrinkage’ (NGS) and a $(1 - p_n)$ probability of undergoing ‘extreme shrinkage’ (ES). The probabilities of reaching any given size if undergoing NGS or ES are then characterized by their own size- and year-dependent means and variances.

While the use of a two-part growth process is straightforward, it requires a clear and justifiable method of classifying each observed annual growth rate as NGS or ES. Our goal in making this distinction is to separate normally distributed growth and shrinkage rates from more extreme amounts of shrinkage. While this is simple in concept, there was not a sharp break between these two sets of growth rates in our data (Fig. 1a). Therefore, we used the following approach: (1) finding the difference between $(\text{area})_t^{0.5}$ and $(\text{area})_{t+1}^{0.5}$ for all thalli across all years and taking the mean of these values (0.00947) as the average growth rate (while there is a statistically significant effect of starting size on these values, it is extremely weak: $r^2 = 0.02811$, $p < 0.05$), (2) estimating the average squared deviations (variance) around this mean using only the positive differences, (3) using this estimate of the mean and variance of growth differences to find the lower 1 % tail of the corresponding normal cumulative distribution function (CDF) for size differences (-0.26676), and (4) using this lower value to make the cutoff between NGS and ES values. This results in a normally distributed set of NGS values and a skewed set of much rarer ES events (Fig. 1b). We followed Easterling et al. (2000) in assuming normally distributed errors for the mean and variance of NGS, using $(\text{area})_{t+1}^{0.5}$ as our dependent variable and $(\text{area})_t^{0.5}$, area_t , and year as potential explanatory variables. For analyses of mean ES, the ratio of $(\text{area})_{t+1}^{0.5}/(\text{area})_t^{0.5}$ was used as the dependent variable to better achieve normality. Thus, we fit alternative models for five growth processes: the probability of NGS, the mean and variance of NGS, and the mean and variance of ES.

Modeling of survival and p_n used logistic models, while all other growth rates were modeled assuming normally distributed errors. Estimation of recruitment rates was based on predictions from full matrix models and is described below.

Model construction and analysis

Separate projection matrices were constructed for each of the five annual transitions, with year-specific effects on vital rates when supported by AIC analysis (ESM Table S2). We used a relatively fine division of sizes: 25 classes of 0–2.5 cm in 0.1-cm intervals (where size classes defined as $\text{area}^{1/2}$). This precision approaches that of most implementations of integral projection models, while retaining the advantages of a matrix model formulation in implementation and interpretation. All the a_{ji} matrix elements below the top row (the reproductive elements) were estimated as:

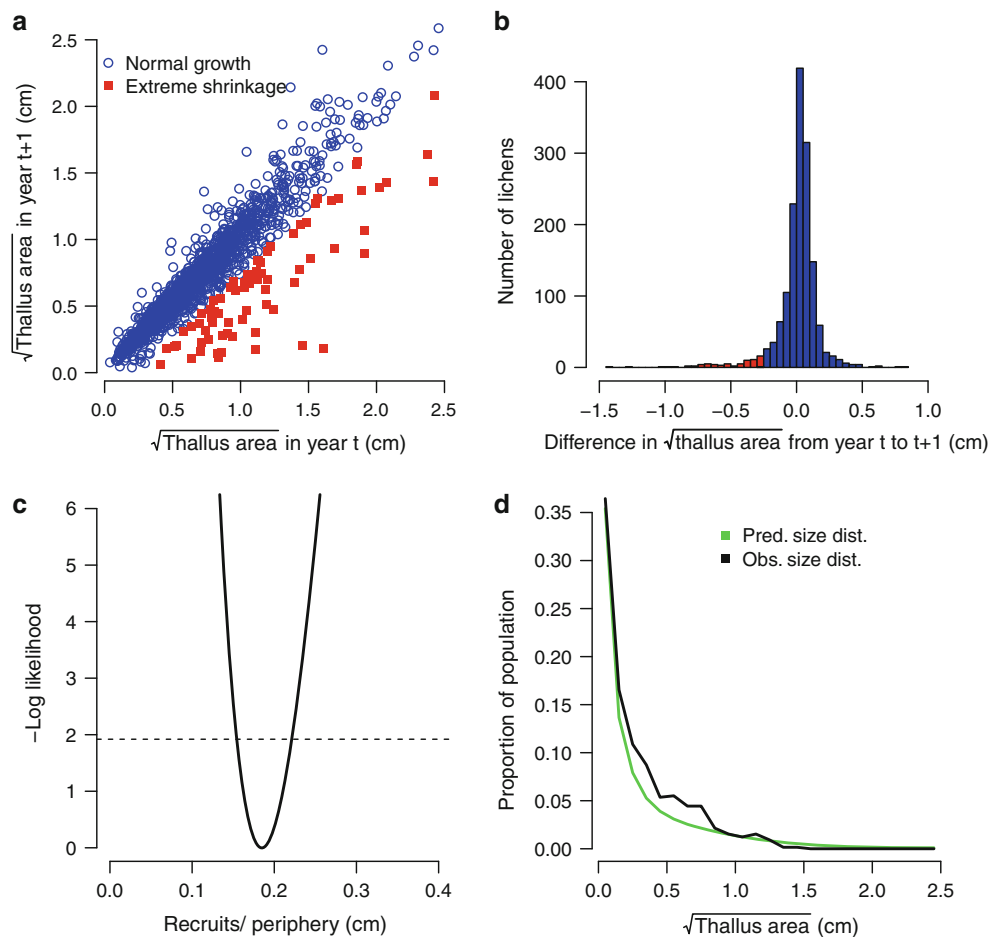


Fig. 1 Fitting of growth and reproductive rates. **a** Plot of $(Area_{t+1})^{1/2}$ versus $(Area_t)^{1/2}$, showing skewed distribution of growth. **b** Histograms of normal growth and shrinkage (blue) and extreme shrinkage (red) values. **c** Likelihood profile for estimates of recruitment rate

using predictions of population stage structure (horizontal dashed line boundaries of 95 % confidence limits). **d** Observed and predicted size distributions from fitting r , the reproductive rate

$$a_{ji} = s_i(p_{n,i}n_{ji} + (1 - p_{n,i})m_{ji})$$

where s_i is the probability of survival for the i th size class, $p_{n,i}$ is the probability of “normal growth or shrinkage” for the i th class, n_{ji} is the probability of normally growing or shrinking from the i th class to the j th class, and m_{ji} is the probability of moving from the i th to the j th class with extreme shrinkage. To estimate n_{ji} and m_{ji} values, we used the mid-point size for class i as the starting size, and a normal CDF to calculate the total probability of falling within the range of sizes in the j th class.

Reproductive elements, a_{li} , could not be directly estimated from our data, but could be estimated based on predictions of a full demographic model. By assuming that the relative reproductive contribution of each size class was proportional to thallus circumference (see ESM for discussion of this assumption and alternatives), we reduced the estimation of reproduction to a single, size-relative

parameter, r . We used an optimization routine to find the values of r resulting in mean matrices that best predicted either $\lambda = 1$ or the observed size structure of the population (see ESM). The estimated r values from these two methods were then inserted into each year-specific matrix, providing a fully-parameterized stochastic model for *V. pinastri*. We used the resulting model to compute long-term stochastic growth rate (λ_S) values, using independent identically distributed (IID) selections of our five annual matrices (10,000 years of growth, discarding the first 1,000 years), and to generate age distributions for thalli of different sizes, as well as the mean total life span conditional on reaching a given size, using the average matrix (Cochran and Ellner 1992). To estimate confidence limits around the λ_S value, we employed a parametric bootstrap procedure based on the means and covariances of parameter estimates for the best predictive model for each vital rate and using a value for r , the reproductive rate, derived from the best fit model.

Comparative life histories of lichens

To compare our findings with those for other species, we assembled literature data on lichen demographic rates and life history patterns. First, we searched Web of Knowledge and Google Scholar for “lichen” and “demography”, “population”, “population model”, “growth rate”, “survival”, “mortality” or “dispersal,” and found 85 relevant studies. While few studies report survival or recruitment rates (ESM Appendix S1), we found 13 datasets with size-dependent growth rates that we could compare to those for *V. pinastri*. As all these results were presented graphically, we used the image-capture software Data Thief (Tummers 2006) to estimate the data values for our analyses. Lichen growth rates were reported in a number of different ways and we converted all of these to a relative growth rate (Woolhouse 1968): $RGR = \log(A_2) - \log(A_1)/t_2 - t_1$, where A_1 and A_2 are the thallus surface areas at times 1 and 2, respectively, and t_1 and t_2 are the dates of the measurements, in years. If lichen areas were not reported, we estimated them from the diameters or radii, assuming that the thalli were approximately circular. We used a loess fitting function (“loess” in R; R development core team 2011), with a span of 1.5 to create smoothed curves that reasonably described the size–growth relationship for each species and growth for all years in our *V. pinastri* study. We used only the positive growth rates for all species to estimate a size-specific growth curve, omitting individuals that shrank from this analysis.

The lichen studies found ranged from tropical to boreal environments and from arid to mesic habitats. To compare growth rates while controlling for habitat effects, we used the estimated maximum relative growth rate (MRGR) of juvenile lichens for each study shown in Fig. 4, including three separate studies for *Rhizocarpon geographicum* as well as two additional estimates for *Porina epiphylla* (MRGR 1.57) and *Strigula subtilissima* (MRGR 3.57) (Rogers 1989). Because there could be an effect of smallest size of lichen measured, we estimated the minimum relative growth rate for all species at the relatively small radius of 0.5 cm. We regressed $\log(\text{MRGR})$ on average annual temperature and precipitation from WorldClim (v.1.4, <http://www.worldclim.org>; explained in detail by Hijmans et al. 2005), as well as substrate as a categorical variable (see ESM for detail on models tested for MRGR prediction).

Results

Vulpicida pinastri demography

The best predictive models for the probability of normal growth, mean normal growth, and survival all include effects of year and interactions between size and year,

reflecting considerable variation over the five transition periods (Fig. 2; see ESM for model fitting results). The probability of NGS ranged from >95 % in the 2007–2008 transition to <70 % in 2006–2007. Survival rates of small, but not large, thalli showed similarly high variation (Fig. 2b). Variation in the probability of normal growth and the mean of normal growth is highly correlated (Pearson’s $r = 0.82$ for a 1.5-cm thallus), but neither rate covaries substantially with survival rate ($r = -0.076$ and 0.057 for s of 0.25-cm thallus with p_n and mean NGS, respectively). The best models for mean ES and variance of both growth rates show substantial variation with size (Fig. 2d; ESM Fig. S1) but no inter-annual variation.

Estimating r , the recruitment rate, by fitting to a stable population growth rate or by matching the observed size distribution gave broadly comparable estimates. To achieve a mean matrix with $\lambda = 1$, $r = 0.047$ recruits per cm of thallus periphery, while fitting to the observed stage structure yielded a maximum likelihood estimate of $r = 0.185$, with a relatively narrow likelihood profile (Fig. 1c). A mean matrix including this latter value predicts a stable stage distribution (SSD) that closely matches that observed in 2010 (Fig. 1d). Using r from the $\lambda = 1$ criteria produced an estimate of stochastic growth, λ_s , of 1.003, while the SSD r gave a mean matrix $\lambda = 1.036$ and $\lambda_s = 1.037$ (1.0052–1.0621 95 % CI).

To visualize the life history patterns implied by the demographic parameters, we first ran stochastic simulations to estimate survival curves, as well as estimating survival from the mean matrix (Fig. 3a). The results indicate that, while population growth and individual performance are variable from year to year, *V. pinastri* thalli nonetheless have potentially long life spans, with a new thallus having a 10.3 % probability of reaching 20 years of age, and a 4.8 % probability of achieving 50 years. This longevity is reinforced by patterns in conditional total life span and mean age at residence for different size classes (Fig. 3b, c). For example, a thallus of 0.20 cm², a moderately small size, is predicted to be on average 27 years old and has a conditional total average lifespan of 46 years. Note that these predictions do not account for mortality due to substrate death (thalli rapidly die once the alder stem on which they reside has died; D.F.D., personal observation), and thus are likely to overestimate the mean and variance of size-specific lichen ages, especially for larger individuals.

Comparative life histories of lichens

We were able to find only a handful of previous studies that attempted to estimate either recruitment or survival in ways comparable to a standard demographic study (see ESM). For survival, only two studies contained directly

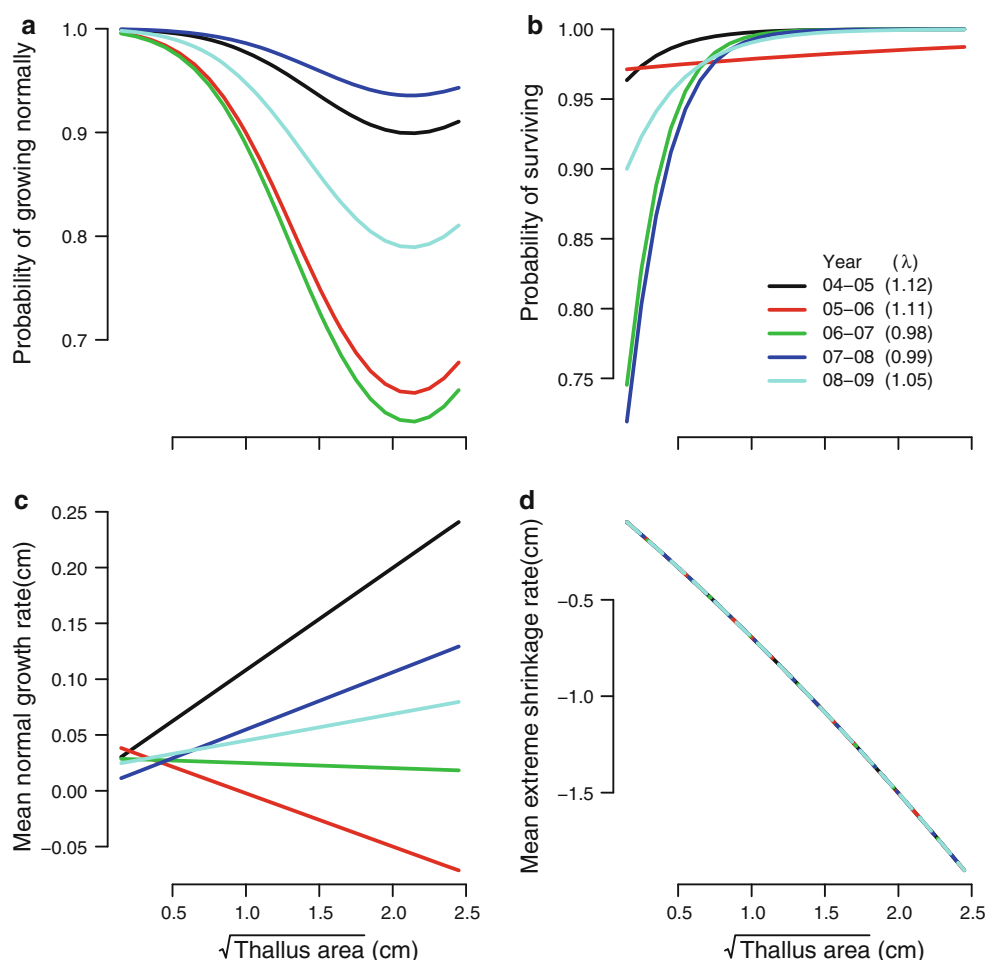


Fig. 2 Size-dependent vital rate functions. *Plots* show best-fit predictions of the **a** probability of normal growth, **b** the probability of survival, **c** mean normal growth, **d** and mean extreme shrinkage.

Year-specific predictions are shown for rates with year effects in the best-supported models. The *legend* shows year-specific population growth rates

comparable rates. Golm et al. (1993) found decreasing survival rates with increasing lichen size, the opposite of our findings for *V. pinastri*, but this study compares only two size classes and their definition of mortality is closer to what we have called extreme shrinkage. Rhoades (1983) found survival rates ranging from 0.75 to 0.878 for six size classes of *Lobaria oregana* (*V. pinastri* survival varies from ~ 0.75 to very close to 1) and a Type 3 survivorship curve similar that of *V. pinastri*.

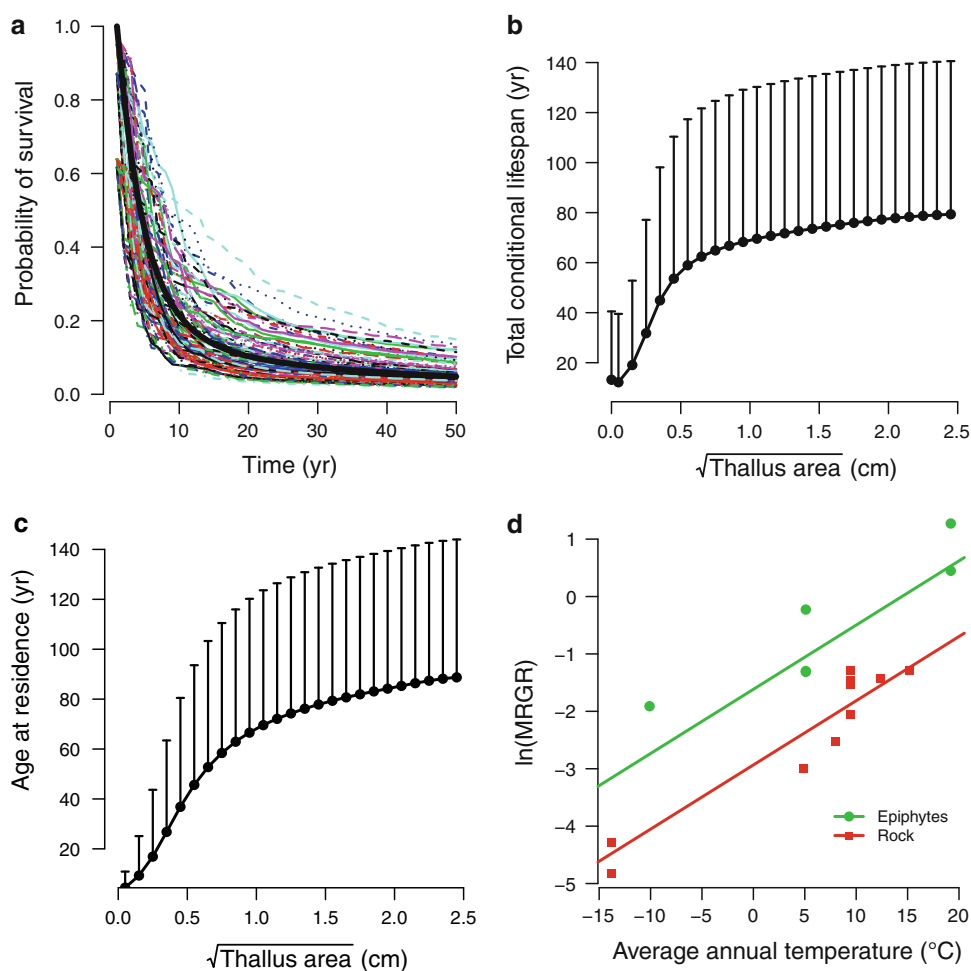
Similarly, recruitment is rarely estimated, and especially not as a per capita rate to which we could compare our rates. We found 23 attempts to address some aspect of reproduction, none of which could be compared to our estimate of successful propagules per unit size. Some of these studies look at the relationship between size of thallus and number of apothecia, rather than number of successful propagules (Ramstad and Hestmark 2001; Jackson et al. 2006). Again, Rhoades (1983) is the most comparable study, finding 0 lobules released from the smallest size class lichen up to 162 lobules released from the largest size

class (thalli >5 g) of lichen, but with no estimates of successful establishment of recruits. Propagule deposition can be measured directly using a sampling method from Armstrong (1987, 1990). However, Armstrong was not directly interested in demography, and thus his methodology does not allow estimates of successful propagule establishment needed for demographic analysis.

Estimates of lichen growth rates are far more common, with over 22 studies reporting size-dependent growth in one manner or another, and comparable growth estimates for 11 species (Fig. 4). Some of these studies were not amenable to comparison due to use of biomass instead of area, non-annual growth rates, or other differences in the format of the presented data, and we did not present all of the studies done on *R. geographicum*, which are numerous due to this species' common use in lichenometry. In a few other cases, only one of multiple datasets for a species was used, and we chose the most complete of these studies. All the comparable studies found similar patterns, with declines in relative growth rate with increasing size

Fig. 3 Life history patterns for *V. pinastri* and comparisons with other lichens.

a Survivorship curves for thalli from 100 stochastic simulations and for the mean matrix (*bold line*). **b** Total life span, conditional on reaching a given size class (labeled with mid-class size), predicted with mean matrix (mean \pm SE). **c** Age of thalli of a given size, predicted with mean matrix (mean \pm SE). **d** Regressions of the log of maximum relative growth rates (MRGR) of epiphytic and saxicolous lichen types with average annual temperature for 16 studies; two points are located at (5, -1.8) and three near (10, -2)



towards a constant RGR value, though with variable absolute rates and slopes. *V. pinastri* has relatively fast maximum juvenile growth compared to two arctic species, *R. geographicum* (Haworth et al. 1986; Bradwell and Armstrong 2007; Armstrong 1983) and *Alectoria minuscula* (Haworth et al. 1986), but slower than *Pseudocyphellaria crocata* (Larsson and Gauslaa 2011), *Buellia canascens* (Aplin and Hill 1979), *Lobaria pulmonaria* (Larsson and Gauslaa 2011), *Lobaria scrobiculata* (Larsson and Gauslaa 2011), *Xanthoparmelia cumberlandii* (Golm et al. 1993), *Parmelia conspersa* (Armstrong 1973), and *Parmelia saxatilis* (Armstrong 1973). Lichens with similar growth rates to *V. pinastri* are *Parmelia glabratula* (Armstrong 1973) and *Parmelia oribicular* (Armstrong 1973). While the consistent deceleration of growth with size and the absence of sharp break points in these growth curves suggest that a fairly general growth rate function could apply to all foliose and crustose lichens, the broad annual growth variation we found in our study also cautions against any assumption of stable annual growth rates. The apparently more stable growth patterns for other species in Fig. 4 is in large part due to small sample sizes or highly averaged data. In contrast to our 158–344 individual

estimates of growth per year (1,543 total), the range of sample sizes we found in the literature was 15–71, with a mean of 40.6 individual annual growth estimates.

As shown in Fig. 4, epiphytic lichens do not always have higher growth rates than saxicolous species. However, the best of the four models of MRGR chosen by AIC, which includes temperature and precipitation effects (adj. $r^2 = 0.9025$; see ESM), shows a positive effect on growth of temperature ($p < 0.001$) and faster growth for epiphytic than for saxicolous species ($p < 0.001$) (Fig. 3d).

Discussion

Our parameterization of a full demographic model for *V. pinastri* adds to the short list of full life history characterizations for lichens. In part, our results confirm generalities about lichen life histories, with remarkably high life spans predicted for a species that is both small (maximum thallus area in our study 6.6 cm^2) and exists on a relatively short-lived substrate. Indeed, longevities for *V. pinastri* are comparable to that of many long-lived plants (Linares et al. 2007; Garcia et al. 2008). However,

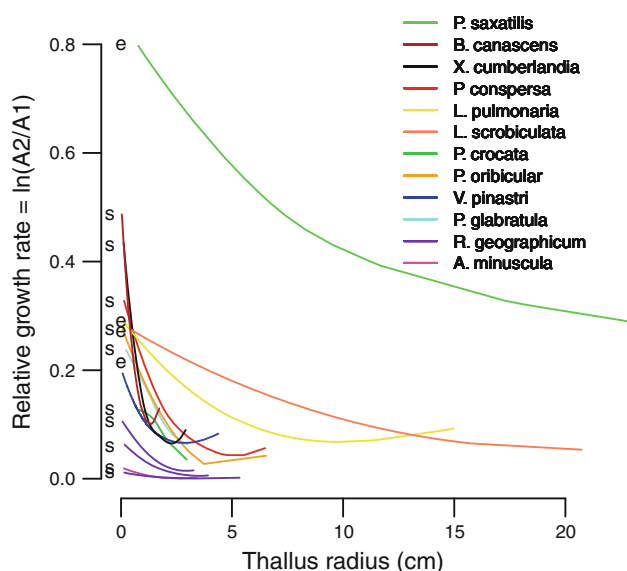


Fig. 4 Smoothed relative growth rates for 12 lichen species (14 studies) as a function of thallus radius. A single line is plotted for all years of our study combined, and further lines for the data from each other species, except *R. geographicum* (data sources: Armstrong 1973, 1984; Haworth et al. 1986; Bradwell and Armstrong 2007; Lättman et al. 2009; Larsson and Gauslaa 2011; Aplin and Hill 1979). Saxicolous (s) lichens and epiphytic (e) lichens are distinguished near the maximum relative growth rates of each species

we also find high variance in demographic performance from year to year, with especially large swings in growth rates of large thalli and survival of small thalli (Fig. 2). While comparable data are difficult to find for a representative range of other species, this vital rate variance implies that individual lichens are not as well-buffered against environmental factors as might be thought, although survival rates of large individuals, often the most demographically important set of vital rates (Franco and Silvertown 2004; Heppell et al. 2000), are relatively invariant (Fig. 2b), conforming to general life history expectations (Pfister 1998). The relatively simple structure of lichen thalli may help explain these patterns. Lichens have no equivalent to an underground storage organ to buffer growth or survival against ephemerally poor conditions. Given the lack of any protected structures or storage organs, high variance in growth rates is perhaps unsurprising, even if uninvestigated in past studies. However, the coupling of high variance in growth with a relatively long life span is still surprising, given patterns seen in other taxa (Garcia et al. 2008). At a population level, the wide variance in annual λ values (Fig. 2) shows that *V. pinastri* has a relatively labile life history. However, the small differences between mean and stochastic population growth rate estimates indicate that *V. pinastri* life history is nonetheless well buffered against environmental variability.

Comparison of published lichen growth rates and those of *V. pinastri* shows a similar pattern of declining relative

growth with size for all species (Fig. 4), in line with what would be expected from peripheral thallus growth (Armstrong and Smith 1998; Aplin and Hill 1979). In general, this growth pattern conforms with an expectation of decreasing relative growth rate as individual size increases, leading to exponential vegetative growth as seen in plants and many organisms. However, the apparent ubiquity of this trend is still somewhat surprising given past disputes over how lichen growth rates change as thallus size increases (Aplin and Hill 1979; Loso and Doak 2006). Perhaps more interesting is the relationship between substrate type and growth (Fig. 3d). Consistently higher growth rates of epiphytic lichens, compared to saxicolous species in similar climate conditions, suggests that epiphytes may have altered demographic rates that make them better suited to their relatively short-lived substrate. Epiphytes of all taxa must grow and produce offspring within the often short, variable life span of their host substrate, in our case alder stems that rarely live longer than 50 years (unpublished data). In contrast, saxicolous individuals live in a comparatively stable and long-lived substrate, potentially allocating resources to thallus thickening and other structural investments that would be beneficial over a longer period. Previous work on lichens has demonstrated a tradeoff between thallus thickness and dispersal (and thus reproduction) (Johansson et al. 2007), but the degree to which substrate influences this or other life history patterns (e.g., longevity) remains unexplored. More generally, our results for *V. pinastri* and for the comparative growth rates of lichens suggests that epiphytes may represent productive groups with which to test theories of life history evolution in relation to habitat stability, especially since, unlike many substrates, the dynamics of the living bodies of plants may be carefully quantified.

In turning field data into model parameters, we faced two problems that are common to many demographic studies. First, we could not directly observe reproduction and recruitment. The approach of estimating this rate using population level predictions, and, in particular, the predicted and observed stage structure, is promising for other studies. Assuming $\lambda = 1$ is a more common solution to this issue, but this approach is neither easily tested against data in most studies, nor does it allow an actual prediction of population growth rate, as does use of the stage structure comparison. One limitation of this approach in our study is the need to assume that measured size distributions represent the stable stage structure, rather than transient stage structures. This prevented estimation of inter-annual variation in reproductive rates; however, we have no evidence to suggest strong flushes of recruitment (personal observation, D.F.D.). And while we lacked the foresight to collect annual size distributions, the relatively stable survival rates for most thalli of *V. pinastri* suggests there is

limited inter-annual variation. Another problem is that we do not have any clear way to distinguish between two possible size-dependency patterns for reproduction (area or perimeter-dependence). While for our analyses these two assumptions give indistinguishable results (see ESM), for analysis of transient population dynamics following colonization or disturbance there could be important differences.

The proper quantification of growth probabilities is similarly an issue for many demographic studies. The use of continuous state variable functions has increased the efficiency with which growth and shrinkage rates are characterized, but has often relied on assumptions of extremely simple growth patterns (but see Dahlgren et al. 2011). The approach we take here is a modest improvement, but one that greatly increases the realistic characterization of growth by distinguishing between incremental increases and decreases in size and what amounts to the severe bad luck of a minority of thalli. This distinction is likely to exist for many other plants (Salguero-Gomez and Casper 2010) and perhaps some animals (Linares et al. 2007).

Overall, our results suggest that lichens may conform to some life history generalities and confound others. However, the most striking result is that, while lichens are easy subjects for demographic study, there is striking paucity of information with which to evaluate their life history patterns. Lichens, tight symbioses between fungi and green algae and/or cyanobacteria, have very different internal structure and degrees of integration than do most plants or animals, and it is not at all clear whether they are likely to exhibit the same general demographic patterns, given their potentially low abilities to transport photosynthate or other materials within thalli (Armstrong 1979; Honegger 1991) and their multiple modes of sexual and asexual reproduction (Bowler and Rundel 1975). More generally, the vast majority of demographic studies target a narrow range of taxonomic groups, with particularly little attention to sessile marine invertebrates (Linares et al. 2007), non-vascular plants, lichens, or other ecologically dominant groups. This taxonomic bias in turn hampers efforts to formulate and test hypotheses regarding general life history patterns. More encouragingly, our comparison of lichen growth rates for lichens than is likely to exist for plants or many animal taxa, where the complexity of different anatomical structures may well lead to greater diversity of life history patterns. As authors have noted for other taxonomic groups, searching for generalities in life history patterns is important both for tests of life history theory and as a practical tool for conservation planning in the face of limited information (Heppell et al. 2000; Cortés 2002; Linares et al. 2007). Lichens represent an ecologically important, species-rich, and taxonomically variable group for which such comparisons may be particularly powerful.

Acknowledgments This work was supported by NSF DEB 0717049 and 0087078 to D.F. Doak, and by Wyoming NASA Space Grant Consortium (#NN10AO95H) Fellowships to both K. Cutler and R.K. Shriver. We thank M. Franco, R. Salguero-Gómez, and one anonymous reviewer for their helpful comments on the manuscript. All research described complies with the laws of the United States and Alaska.

References

- Aplin PS, Hill DJ (1979) Growth analysis of circular lichen thalli. *J Theor Biol* 78:347–363
- Armstrong RA (1973) Seasonal growth and growth rate-colony size relationships in six species of saxicolous lichens. *New Phytol* 72:1023–1030
- Armstrong RA (1979) Growth and regeneration of lichen thalli with the central portions artificially removed. *Environ Exp Bot* 19:175–178
- Armstrong RA (1983) Growth curve of the lichen *Rhizocarpon geographicum*. *New Phytol* 94:619–622
- Armstrong RA (1987) Dispersal in a Population of the Lichen *Hypogymnia physodes*. *Environ Exp Bot* 27(3):357–363
- Armstrong RA (1990) Establishment and survival of soredia and fragments of the lichen *Hypogymnia physodes*. *New Phytol* 114(2):239–245
- Armstrong RA, Bradwell T (2011) Growth of lichens: a review. *Symbiosis* 53:1–16
- Armstrong RA, Smith SN (1998) Does radial growth of the lichen *Parmelia conspersa* depend exclusively on growth processes at the lobe tip? *Environ Exp Bot* 39(3):263–269
- Benedict JB (2009) A review of lichenometric dating and its applications to archaeology. *Am Antiq* 74:143–172
- Boggs CL, Ross CL (1993) The effect of adult food limitation on life history traits of *Speyeria mormonia* (Lepidoptera: Nymphalidae). *Ecology* 74:433–441
- Bowler PA, Rundel PW (1975) Reproductive strategies in lichens. *Bot J Linn Soc* 70:325–340
- Bradwell T, Armstrong RA (2007) Growth rates of *Rhizocarpon geographicum* lichens: a review with new data from Iceland. *J Quat Sci* 22:311–320
- Chen B, Liao C (2004) Population models of farmed abalone *Haliotis diversicolor* supertexta exposed to waterborne zinc. *Aquaculture* 242:251–269
- Cochran ME, Ellner S (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecol Monogr* 62:345–364
- Cole LC (1954) Population consequences of life history phenomena. *Q Rev Biol* 29:103–137
- Conti ME, Cecchetti G (2001) Biological monitoring: lichens as bioindicators of air pollution assessment—a review. *Environ Pollut* 114:471–492
- Cortés E (2002) Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conserv Biol* 16:1048–1062
- Dahlgren JP, García MB, Ehrlén J (2011) Nonlinear relationships between vital rates and state variables in demographic models. *Ecology* (in press)
- Dietrich M, Scheidegger C (1997) Frequency, diversity and ecological strategies of epiphytic lichens in the Swiss Central Plateau and the pre-Alps. *Lichenologist* 29:237
- Doak DF, Morris WF (2010) Demographic compensation and tipping points in climate-induced range shifts. *Nature* 467:959–962
- Easterling MR, Ellner SP, Dixon PM (2000) Size-specific sensitivity: applying a new structured population model. *Ecology* 81:694–708

- Franco M, Silvertown J (2004) A comparative demography of plants based upon elasticities of vital rates. *Ecology* 85:531–538
- Garcia MB, Pico FX, Ehrlen J (2008) Life span correlates with population dynamics in perennial herbaceous plants. *Am J Bot* 95(2):258–262
- Golm GT, Hill PS, Wells H (1993) Life expectancy in a Tulsa Cemetery: growth and population structure of the lichen *Xanthoparmelia cumberlandia*. *Am Midl Nat* 129:373–383
- Haworth LA, Calkin PE, Ellis JM (1986) Direct measurement of lichen growth in the Central Brooks Range, Alaska, USA, and its application to lichenometric dating. *Arct Alp Res* 18:289–296
- Heppell SS, Caswell H, Crowder LB (2000) Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81:654–665
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Honegger R (1991) Functional aspects of the lichen symbiosis. *Annu Rev Plant Physiol Plant Mol Biol* 42:553–578
- Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. *Ecol Monogr* 55:141–166
- Jackson HB, St Clair LL, Eggett DL (2006) Size is not a reliable measure of sexual fecundity in two species of lichenized fungi. *Bryologist* 109:157–165
- Johansson P, Rydin H, Thor G (2007) Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. *Ecoscience* 14:81–91
- Knops JMH, Nash TH III, Boucher VL, Schlesinger WH (1996) The influence of epiphytic lichens on the nutrient cycling of an oak woodland. *Ecol Monogr* 66:159–179
- Larsson P, Gauslaa Y (2011) Rapid juvenile development in old forest lichens. *Botany* 89:65–72
- Lättman H, Lindblom L, Mattsson JE et al (2009) Estimating the dispersal capacity of the rare lichen *Cliostomum corrugatum*. *Biol Conserv* 142:1870–1878
- Linares C, Doak DF, Coma R, Díaz D, Zabala M (2007) Life history and viability of a long-lived marine invertebrate: the octocoral *Paramuricea clavata*. *Ecology* 88:918–928
- Loso MG, Doak DF (2006) The biology behind lichenometric dating curves. *Oecologia* 147:223–229
- Matsuoka SM, Handel CM (2007) Nesting ecology of boreal forest birds following a massive outbreak of spruce beetles. *J Wildl Manag* 71:51–63
- McFadden CS (1991) A comparative demographic analysis of clonal reproduction in temperate soft coral. *Ecology* 72:1849–1866
- Morris WF, Doak DF (2002) Quantitative conservation biology: theory and practice of population viability analysis. Sinauer, Sunderland
- Palmer TM, Doak DF, Stanton ML, Bronstein JL, Kiers T, Young TP, Goheen JR, Pringle RM (2010) Synergy of multiple partners, including freeloaders, increases host fitness in a multispecies mutualism. *Proc Nat Acad Sci USA* 107:17234–17239
- Pfister CA (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proc Nat Acad Sci USA* 95:213–218
- Pike LH (1978) The importance of epiphytic lichens in mineral cycling. *Bryologist* 81:247–257
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN: 3-900051-07-0. <http://www.R-project.org>
- Ramstad S, Hestmark G (2001) Population structure and size-dependent reproductive effort in *Umbilicaria spodochoera*. *Mycologia* 93:453–458
- Rhoades FM (1983) Distribution of thalli in a population of the epiphytic lichen *Lobaria oregana* and a model of population dynamics and production. *Bryologist* 86:309–331
- Rogers RW (1989) Colonization, growth and survival strategies of lichens on leaves in a subtropical rainforest. *Aust J Ecol* 14:327–333
- Rosentreter R (1995) Lichen diversity in managed forests of the Pacific Northwest, USA. *Mitt Eidgenöss Forsch* 70:103–124
- Salguero-Gomez R, Casper BB (2010) Keeping plant shrinkage in the demographic loop. *J Ecol* 98:312–323
- Tummers B (2006) DataThief III. <http://datathief.org/>
- van Straalen NM (1985) Comparative demography of forest floor *Collembola* populations. *Oikos* 45:253–265
- Wikelski M, Thom C (2000) Marine iguanas shrink to survive El Niño. *Nature* 403:37–38
- Woolhouse HW (1968) The measurement of growth rates in lichens. *Lichenologist* 4:32–33