

Growth of the Lichen *Rhizocarpon lecanorinum*, with Comments on Aplin-Hill and Lichenometric Curves

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Received February 21, 2004; Accepted March 3, 2004

Abstract

The radial growth rate of a foliose or crustose lichen initially accelerates, then approaches a limiting (asymptotic) rate. In many cases, the thallus margin remains intact and continues radial growth at an unreduced linear rate. A number of lichenometric curves for *Rhizocarpon geographicum* have suggested a different pattern. For most of its lifespan, this species reportedly grows at a rate well below that attained in young thalli. In the present study, a set of growth rate data for *R. lecanorinum* is presented and interpreted with reference to the Aplin-Hill model. This species has a shorter lifespan than *R. geographicum*, and achieves its maximum growth rate more rapidly, possibly owing to a higher ratio of photobiont to mycobiont mass in very young thalli.

Presented at the 4th International Symbiosis Congress, August 17–23, 2003, Halifax, Canada

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The early transition from accelerating to linear radial growth also appears to be correlated in *R. lecanorinum* with precocious apothecium formation. We suggest that trade-offs among growth and reproductive traits have led to diversification of life history strategies within *Rhizocarpon*. No decline was evident in the radial growth rate of larger thalli of *R. lecanorinum*. This finding conflicts with the results of lichenometric studies of *R. geographicum*. However, the major inflection present in many published lichenometric curves is probably a methodological artefact.

Keywords: *Rhizocarpon lecanorinum*, lichen, growth, life history, Aplin-Hill model, lichenometry

1. Introduction

The radial growth rate (mm yr^{-1}) of a circular crustose or foliose lichen accelerates following thallus establishment. As acceleration slows, the growth rate approaches a constant value (Armstrong, 1976; Hill, 1981). In some lichens, growth continues at or near this limiting ('linear', 'asymptotic') rate, even after senescence or experimental removal of the thallus centre (Armstrong, 1979; Armstrong and Smith, 1987). A functional interpretation of these changes was first proposed by Beschel (1961, p. 1046): 'As long as the organic substances produced by a thallus are shared by all its parts, a constant production rate per area will lead to an exponential increase of thallus area and diameter ... [As] a radius is approached past which transport becomes ineffective, the central parts will cease contributing to the marginal growth. Only an outer ring of constant thickness will be responsible for further increase in diameter, and such increase will become linear.' Proceeding from similar assumptions, Proctor (1977) examined growth of the lobate-crustose ('placodioid') lichen *Diploicia canescens*; he showed that the relative growth rate of this species, expressed on an areal basis ($\text{mm}^2 \text{mm}^{-2} \text{yr}^{-1}$), is approximately proportional to the area of an 'annulus of constant width within the growing [thallus] margin.'

In fact, the marginal growth zone of circular thalli lacks sharp limits definable by structural or physiological features. This led Aplin and Hill (1979) to formulate a growth model based on assumptions about the overall production and transport of carbohydrate in such thalli. Specifically, Aplin and Hill (1979, p. 349) postulated: (i) 'photosynthetic production ... is uniform over the whole [thallus] area;' (ii) 'carbohydrate can move in any direction ... to satisfy demands created by utilisation;' (iii) 'the rate and direction of this movement is proportional to and determined by [carbohydrate] concentration gradients.' The equation derived from these assumptions (see Materials and Methods, equation 1) approximates the asymptotic course of radial growth recorded for many lichens (Hill, 1981, 2002).

Lichenometric studies of the long-lived, prothallus-forming, areolate-crustose lichen *Rhizocarpon geographicum* have, for the most part, suggested a different pattern. Plots of maximum thallus size versus substrate age generally imply that the maximum radial growth rate of this species is attained during an early 'great period' of growth, followed by a much longer phase of slower radial growth. That is, for most of its long lifespan, *R. geographicum* reportedly grows at a rate well below that achieved in young thalli (review: Innes, 1985). Aplin and Hill (1979, p. 355; see also Armstrong, 1983, 1988) accordingly suggested that the Aplin-Hill model does not fit this species and that 'the mechanism of growth of crust lichens such as *Rhizocarpon* may be fundamentally different to that of foliose or placodioid lichens.'

The present study reports and analyzes a set of growth rate data for *R. lecanorinum*, a species of the north temperate and southern boreal zones of North America and Europe. The thallus of *R. lecanorinum*, like that of *R. geographicum*, comprises distinct areoles in a black prothallus. However, these species differ in a number of anatomical, developmental, chemical, and ecological features (Clayden, 1997, 1998). It was therefore of interest to determine whether or not these differences are reflected in the growth characteristics of the two species. The objectives were: (i) to assess the applicability of the Aplin-Hill model to *R. lecanorinum*; (ii) to compare the shape of the radial growth rate curve of this species to that of *R. geographicum* as inferred from published lichenometric studies; (iii) to interpret the growth characteristics of *R. lecanorinum* in developmental and ecological contexts.

2. Materials and Methods

Radial growth was measured in a range of thallus sizes over a one year period. Because growth rates vary from year to year in response to climatic fluctuations, this approach cannot yield a reliable calibration of thallus size and age. It assumes, however, that a set of measurements of different-sized thalli can approximate the variation occurring over the lives of individual thalli. The study was carried out on thalli growing on Ordovician slate in disused, southeast-facing spoil tips near the Penrhyn Quarries at Bethesda, North Wales (53°10'N, 04°04'W, elevation 220 m, UK National Grid Reference 23/629644). Flags of slate bearing nearly circular thalli without marginal contacts were assembled on a large block face with an inclination of about 15°, and left for six months before the study began. Sixty-four thalli were set up for measurement in the following diameter (longest thallus dimension) classes: ≤ 2 mm (16), $>2-5$ mm (15), $>5-10$ mm (9), $>10-20$ mm (15), $>20-30$ mm (7), and >30 mm (2). Most thalli >30 mm in diameter had begun to disintegrate at their

centres and merge at their margins with neighbouring individuals of *R. lecanorinum*.

Radial extension of the prothallus was measured at 4 to 8 points around each thallus. The slates were brought indoors for this purpose and examined at 25 \times magnification, allowing a minimum increment of 0.04 mm to be detected with an eyepiece graticule. Small dots of India ink covered with beads of Araldite® epoxy resin, positioned at least 2 mm from the edge of the prothallus, served as reference marks.

The data were analysed with reference to the growth model of Aplin and Hill (1979; Hill, 1981, 2002). This predicts that the radial growth rate of a circular lichen thallus is a function of its radius (r):

$$dr/dt = \alpha sr/(r + 2s) \quad (1)$$

where α is a rate constant (units: yr⁻¹) postulated to reflect the rate of carbohydrate production, and s is a distance constant (units: mm) accounting for lateral movement of carbohydrate. The full curve of equation 1 is a rectangular hyperbola (Fig. 1). Taking the reciprocal of both sides of the equation yields a straight-line relationship between $1/r$ and $1/r$:

$$1/r = (r + 2s)/\alpha sr = 1/\alpha s + [(2/\alpha) \cdot (1/r)] \quad (2)$$

This could be used, in principle, to assess the goodness of fit of the function to a set of growth rate data. However, reciprocal transformation introduces considerable unevenness ('heteroscedasticity') in the variance of y ($1/r$) at different values of x (r).

Aplin and Hill (1979; Hill, 1981) showed that a linear relationship is also obtainable by integrating equation 1:

$$r_2 - r_1 = \alpha s t - 2s \ln(r_2/r_1) \quad (3)$$

Values for α and s can thus be estimated (again, in principle) from the intercepts of a graph ('Aplin-Hill plot') of $\ln(r_2/r_1)$ against $(r_2 - r_1)$. In this case, however, the non-independence of the variables $\ln(r_2/r_1)$ and $(r_2 - r_1)$ invalidates the use of simple linear regression to fit a line to the transformed data. This was noted by Aplin and Hill (1979), who instead fitted the line using specialized error analysis and numerical optimization. Subsequent investigators have used either a non-statistical approach (e.g. Proctor, 1983) or linear regression (Hill, 2002) to obtain values for α and s from Aplin-Hill plots.

Here, we have followed Aplin and Hill in using numerical optimization. However, their analysis of the error ascribes error equally to r_1 and r_2 . This would be appropriate if the main source of variation were error in measurement

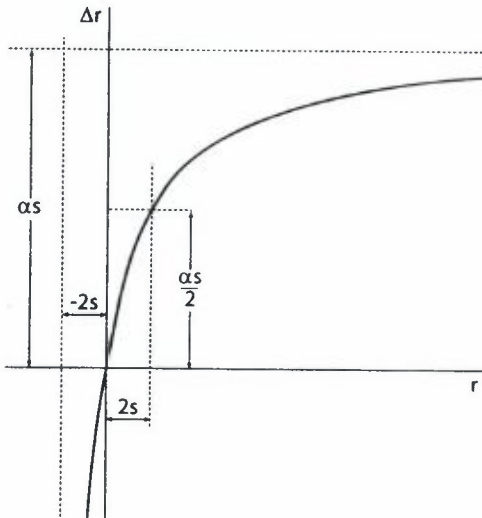


Figure 1. Curve of the Aplin-Hill function, showing the predicted relationship between radial growth rate and thallus size. The maximum (asymptotic) radial growth rate is equal to the product of the rate constant α and the distance constant s . The radial growth rate is half this value at $r = 2s$. The portion of the curve for $r < 0$ has no biological significance.

of two perfectly correlated quantities. However, in this case, the precision with which a thallus can be measured is much higher than the precision with which any ideal model describes the growth of a real thallus; it is therefore more appropriate to treat r_1 as an independent variable (with random values) and r_2 as a dependent variable, determined by r_1 via the Aplin-Hill model with an error term. A full explanation of the curve-fitting method will be presented in a separate paper (in preparation). In brief, it involves direct fitting of the Aplin-Hill model to the original untransformed data. Starting with arbitrary estimates for α and s , we used a two-dimensional Newton's Method to converge on the values of these parameters yielding the regression with the least sum of squared residuals. Bootstrap analysis, with each pair of values omitted in turn, was used to determine 95% confidence limits for α and s .

3. Results

Of the 64 thalli on which measurements were begun, 16 were either partly grazed by slugs or were on rocks overturned (by sheep?) in the course of the study period. These were excluded from the growth calculations. Radial growth in the remaining sample of 48 thalli ranged from 0.15 mm yr^{-1} in a thallus with an initial diameter of 0.9 mm to 0.63 mm yr^{-1} in a 19 mm broad thallus (Fig. 2).

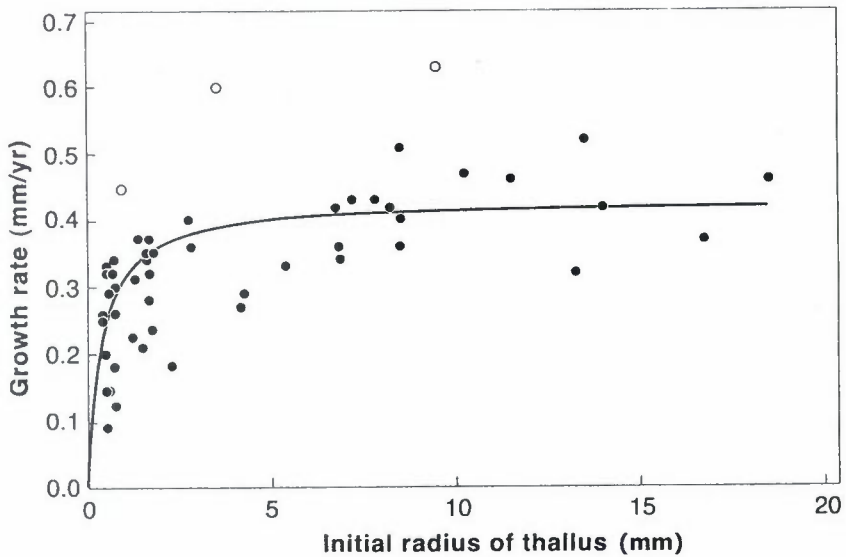


Figure 2. Radial growth of *Rhizocarpon lecanorinum* in relation to thallus size over a one-year measurement period. Open circles indicate a group of three fast-growing thalli which were near-neighbours on a single slate flag. Curve is least squares fit of the Aplin-Hill function to untransformed data.

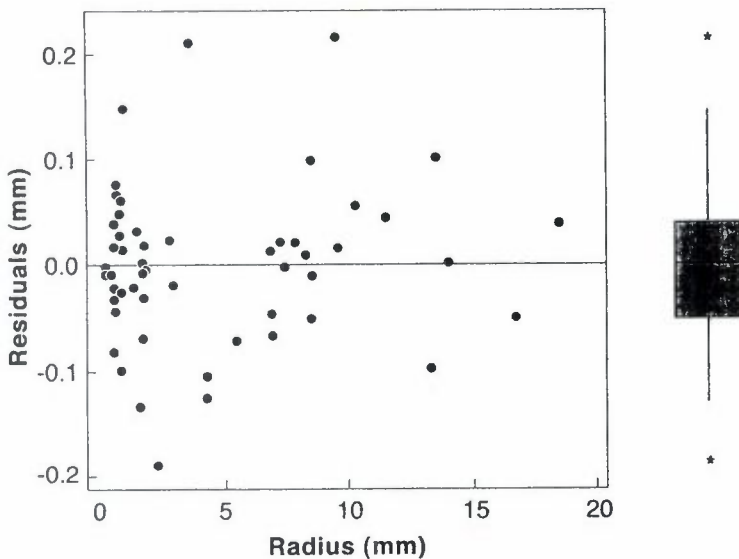


Figure 3. Regression residuals, plotted against radius and with a marginal boxplot. Box from first quartile to third quartile; whiskers to last datum within 1.5 interquartile range (IQR) of box; data more than 1.5 IQR from box flagged as possible outliers.

The radial increments of different thalli of approximately the same size show a wide scatter of values. However, a trend of slower but accelerating growth in small thalli, and faster, more nearly constant growth in larger thalli is evident (Fig. 2). The average increment of the smallest thalli, with initial diameters 0.8–1.5 mm, was nearly two-thirds that of thalli >20 mm in diameter, which had the highest growth rates. The initial phase of rapidly accelerating growth in the smallest thalli is not captured in Fig. 2, as no thalli <0.8 mm diameter were available for measurement.

Through direct fitting of the non-linear Aplin-Hill model to the untransformed data, the functional relationship obtained between the radius and radial growth rate of *R. lecanorinum* thalli is:

$$dr/dt = 0.43r/(r+0.38)$$

This gives the estimates for the two constants

$$s = 0.19 \text{ mm}, \alpha = 2.24 \text{ yr}^{-1}$$

The curve corresponding to this equation is plotted in Fig. 2. There was some concern that three of the data points (indicated with open circles), corresponding to the only thalli measured on one of the slate slabs, seemed to be outliers, possibly representing individuals growing under different conditions. As a precaution, the regression was repeated without these three data. The parameter values changed little ($s = 0.18 \text{ mm}$, $\alpha = 2.25 \text{ yr}^{-1}$), and the fitted curve (not shown) was very similar. It was concluded that these data had little effect on the regression.

Residuals of the regression (using all data) are shown in Fig. 3. As can be seen from the boxplot, the distribution of residuals appears slightly heavy-tailed. This may be evidence of a slight deviation from the Aplin-Hill model, or a sign that the error distribution deviates from normality. However, no really strong trend appears in the residuals, so that the regression appears to explain the data adequately.

Bootstrapping was used to obtain 95% confidence intervals. As the bootstrap distributions are asymmetric, the confidence intervals are not centred on the point estimates. The confidence intervals are rather wide; more data (or less variable data) would be needed to obtain narrower intervals.

95% CI for s : [0.112, 0.297] mm

95% CI for α : [1.55, 3.50] yr^{-1}

It should be noted that these intervals are not independent; high values of s correspond to low values of α , and vice versa.

4. Discussion

Size- and age-related variation, and lichenometric curves

The results of this study indicate that the trend of size-related variation in the radial growth rate of *R. lecanorinum* is similar to that of foliose and placodioid lichens. The wide scatter of values for thalli of a given size is typical of lichen growth plots; it cannot be attributed simply to measurement error (Hill, 1981). Here, the scatter might reflect differences in the structure and vigour of the thalli assembled for measurement. Environmentally induced differences in areole density among thalli could be one source of growth rate variation. The width of the marginal prothallus is a related variable shown by Armstrong and Bradwell (2001) to contribute to growth variability in *R. geographicum*. Genetic variation might also underlie some of the data scatter. However, the capacity for fusion among *R. lecanorinum* thalli at the study site is suggestive of clonal population structure (Clayden, 1997).

Rhizocarpon lecanorinum has a relatively short lifespan. The largest discrete thalli observed in this study (c. 40 mm in diameter, with disintegrating centres) were probably <60 years old, based on Fig. 2 and allowing for slower radial growth in minute thalli. In contrast, *R. geographicum* can attain diameters >200 mm and ages >450 years in Britain (Winchester, 1988). Maximum ages >5,000 years have been reported for this species in arctic regions (Innes, 1985). The rarity of large thalli of *R. lecanorinum* is due in part to its tendency to form dense colonies, coupled with its capacity for interthalline fusion (Clayden, 1997). In contrast, *R. geographicum* often forms mosaics consisting of sharply delimited individuals evidently belonging to different vegetative compatibility groups (Rayner, 1991; Clayden, 1997; Dyer et al., 2001).

Although the number of data points is small, there appears to be no significant decline in the growth rate of larger thalli of *R. lecanorinum*. This finding conflicts with the results of most lichenometric studies of *R. geographicum*. Lichenometric curves relate thallus size (not growth rate) to thallus or substrate age, and are calibrated with reference to the largest thalli occurring on dated substrates. However, the gradient of a lichenometric (size/age) curve at any point should, in theory, be equal to the growth rate of the lichen at that point. Growth rate curves may thus be derived from lichenometric curves. When this is done for the most common type of lichenometric curve (Fig. 4a), the resulting growth rate curve (Fig. 4b) is of a form rarely, if ever, obtained when radial growth is measured directly.

In the few cases (e.g. Armstrong, 1983; Proctor, 1983) where the radial growth of *R. geographicum* has been measured directly, it has been found to vary in a manner similar to that reported here for *R. lecanorinum*, i.e. evidence for a

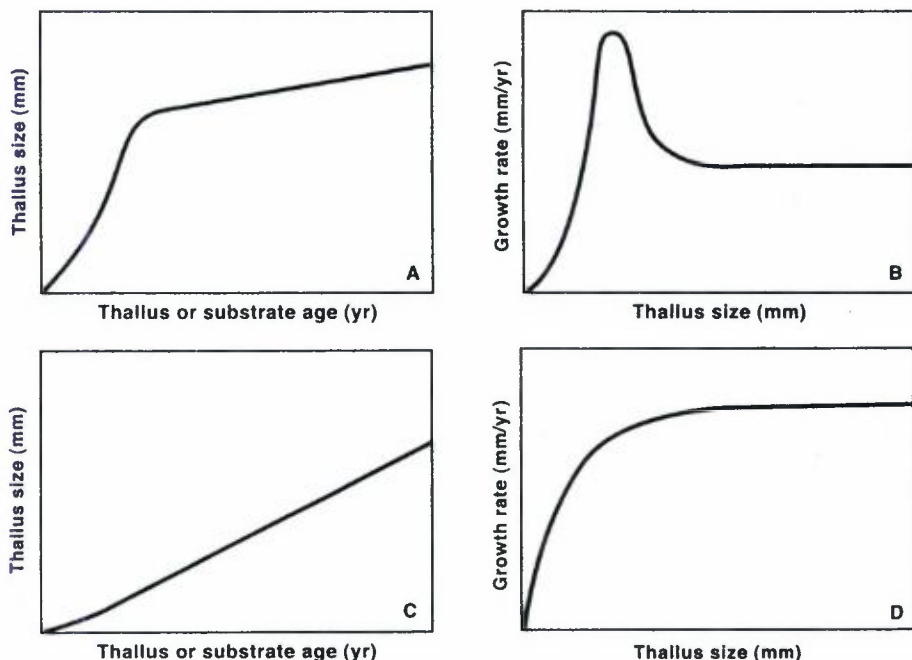


Figure 4. Schematic curves of lichen growth. A. The most common form of lichenometric curve, implying a 'great period' of growth in younger thalli (e.g. Innes, 1983; Winchester, 1984; McCarthy and Smith, 1995; Bull and Brandon, 1998). B. The growth rate curve corresponding to A (numerous examples in Beschel [1958]). C, D. Lichenometric curve and supporting growth rate curve derived from directly measured thalli (e.g. Aplin and Hill, 1979; Proctor, 1983). Note: The lag-period before colonization is not shown in the lichenometric curves.

decline in the growth rate of larger thalli is weak or lacking. The lichenometric curve (Fig. 4c) corresponding to this growth rate curve-form (Fig. 4d) does not show the prominent second inflection commonly present in lichenometric curves constructed by indirect methods (Fig. 4a). That inflection, corresponding to the end of the putative 'great period' of growth, implies a distinct downturn in the radial growth rate. It has been reported from lichenometric studies not only of *R. geographicum* and other crustose lichens, but also various foliose, including relatively short-lived, species (e.g. Beschel, 1958; Winchester, 1984; McCarthy and Smith, 1995).

These observations suggest that the major inflection present in most lichenometric curves could be a methodological artefact. One possible explanation for this anomaly, at least in *Rhizocarpon*, has been suggested by Asta and Letrouit-Galinou (1995). These authors reported that, in an alpine population of *R. geographicum*, fusions like those occurring among individuals of *R. lecanorinum* (see Clayden, 1997) were frequent among small thalli, but

rare among larger ones. The developmental and genetic basis of that observation has not been investigated. However, such age-related differences in the capacity for inter-thalline fusion could lead to overestimates of the ages and radial growth rates of younger thalli. That is because, on rock surfaces with relatively short periods of exposure, the largest, seemingly oldest thalli would sometimes, perhaps often, be composites of younger individuals. Still, it seems unlikely that fusions of small thalli, where they do occur, would have been consistently overlooked in lichenometric studies.

A radical reinterpretation of lichenometric curves has emerged from a recent study of thallus size-frequency distributions in populations of *R. geographicum* and *Pseudephebe pubescens* (Loso and Doak, 2003). That work suggests that demographic characteristics alone, in particular mortality rates of a few percent per year in thalli growing at a constant rate, can give rise to the semblance of a 'great period' of growth. It is unnecessary to posit a decrease in the rate of radial growth of larger thalli to produce this pattern (i.e., as depicted in Fig. 4a). Loso and Doak (2003) infer that mortality influences the probability of finding larger thalli. (To 'mortality' should perhaps be added any loss of thallus integrity that would make it difficult to recognize or measure the potentially largest, oldest thalli.) While large intact thalli become increasingly rare in the population, it also becomes increasingly unlikely that the largest intact thalli found are as old as the longest-exposed substrate surfaces. Thus, the ages of the largest thalli on older substrates will tend to be overestimated, and their radial growth rates underestimated. This being the case, a growth rate curve could not be validly derived from a lichenometric curve, except perhaps for younger thalli.

Interpretations of the form of the growth curve of *R. geographicum* and other lichens, based on lichenometric curves, may thus require major revision. More generally, the 'great period' of growth as defined by Beschel (1950), and as understood in most lichenometric studies, is probably an artefact. Fortunately, this finding (if confirmed) should not invalidate the practical application of most published lichenometric curves. Even if they prove not to accurately depict the relationship between thallus size and thallus age, they may nonetheless predict the size of the largest lichen likely to be found on a substrate of a given age. The error involved in the latter determination is likely to be comparable between precisely dated surfaces and surfaces of unknown age. It remains a challenge, as noted by Loso and Doak (2003), to quantify the magnitude of that error.

Applicability of the Aplin-Hill function

The variability of radial growth recorded here for *R. lecanorinum* does not

signify that the Aplin-Hill model fails to fit the data. Rather, it indicates that tighter controls on possible sources of growth rate variation other than thallus size are required to better test its applicability. Similar difficulties were encountered by Armstrong (1983) and Proctor (1983) in their attempts to fit Aplin-Hill curves to growth data for *R. geographicum*. Proctor (1983) estimated the rate and growth constants from visually, not statistically, fitted curves. However, in both studies, as here, the trend of the plots of r against r was generally consistent with the curve of the Aplin-Hill function.

The values for s (0.19 mm) and α (2.24 yr⁻¹) estimated for *R. lecanorinum* are substantially lower and higher, respectively, than the corresponding values ($s = 1.94$ mm; $\alpha = 0.27$ yr⁻¹) reported for *R. geographicum* (Hill, 1981), based on growth data later published by Proctor (1983). Standardization of the statistical approach used to obtain these estimates will make comparisons more reliable. However, some preliminary inferences can be drawn here. In the context of the Aplin-Hill model, these estimates imply: (i) that the effective distance of carbohydrate transport (related to s) is much smaller in *R. lecanorinum* than in *R. geographicum*, and (ii) that *R. lecanorinum* has a much higher maximum relative growth rate (proportional to the rate constant α (see Hill, 1981) in its juvenile stages. These rough estimates must be treated with caution. However, they are in keeping with differences in the growth plots of these two species, and also with contrasts in their developmental morphology (see below).

The data for *R. lecanorinum* do not support the suggestion by Aplin and Hill (1979) and Armstrong (1983, 1988) that there are fundamental differences in the shape of the growth curves of *Rhizocarpon*-like and foliose/placoidoid lichens. On the contrary, the essentially similar asymptotic curves of these growth forms could result from: (i) a stable limit being reached in the number of hyphal cells in an active state of elongation at the thallus margin, the elongation per cell declining gradually to zero at a certain distance (proportional to s ?) from the margin; and (ii) saturation, in these hyphae, of the enzymes involved in the synthesis of structural material. The operation of a saturation-like effect is indicated by the finding of Armstrong and Smith (1996) that regular addition of ribitol and other polyols to intact thalli of *Rhizocarpon* and *Xanthoparmelia* has no significant effect on their radial growth rates.

Developmental context

Although the growth rates of *R. lecanorinum* recorded here are within the range of values reported for *R. geographicum*, the maximum rate is achieved more rapidly in *R. lecanorinum*. Comparison of Fig. 2 with equivalent plots for

R. geographicum (Armstrong, 1983; Proctor, 1983) indicates that this contrast is independent of the differences in absolute growth rates among populations. Developmental differences between the two species probably underlie this contrast. In *R. geographicum*, ascospore germination gives rise to a prothallus on which the first areole is formed (Asta and Letrouit-Galinou, 1995). In *R. lecanorinum*, the first areole arises directly from contact between ascospore germ hyphae and the photobiont. The prothallus is formed secondarily following enlargement of this areole (Clayden, 1998). Thus, the photobiont forms a greater proportion of the mass of very young thalli of *R. lecanorinum* than of *R. geographicum*. On this line of reasoning, the ratio of photobiont to mycobiont mass in the early developmental stages of lichens should be correlated with their relative growth rates.

Rapid attainment of the limiting growth rate by *R. lecanorinum* also appears to be correlated with precocious formation of apothecia (Clayden, 1998). It has been suggested (Beschel, 1961; Topham, 1977; Hill, 1981) that the timing of these growth and reproductive changes in lichen thalli are synchronized, perhaps reflecting competition for carbohydrate resources. Apothecia are initiated not only earlier in *R. lecanorinum* than in *R. geographicum*, but also much closer to the thallus margin (Clayden, 1998). Thus, *R. lecanorinum* thalli have scarcely any marginal non-reproductive zone. It is likely, therefore, that the marginal zone contributing to radial growth of the prothallus is considerably wider in *R. geographicum*. This difference is consistent with the contrasting values of the Aplin-Hill distance constant (s) estimated for the two species.

Ecological context

Growing on intensely illuminated, nutrient-poor, rapidly drying rock surfaces, yellow *Rhizocarpon* species exemplify the ecological strategy of stress tolerance. Strategy theory (Grime, 1979; Rogers, 1990; During, 1992) suggests that a species like *R. lecanorinum*, with its high relative growth rate and telescoped life cycle, should behave as a ruderal in relation to other lichens. In the triangular ordination model of Grime (1979), as scaled for lichens by Rogers (1990), this species would indeed fall near the ruderal apex. Crustose lichens such as *Buellia aethalea*, *B. ocellata*, *Lecanora intricata*, and *R. reductum*, which are frequent associates of *R. lecanorinum* (Clayden, 1998), appear to have comparable sets of life history traits. Such traits imply adaptation to disturbance (destruction of biomass) occurring at an intensity greater than that experienced by species with longer lifespans, later reproduction, and greater maintenance of thallus integrity.

The comparative frequency and severity of disturbances to which *R. lecanorinum* and *R. geographicum* are exposed cannot be adequately gauged at present. *Rhizocarpum lecanorinum* typically colonizes freshly exposed rock surfaces (Degelius, 1940; Runemark, 1956; Clayden, 1997, 1998). These are often near ground level and subject to seepage from surrounding vegetation, dust inputs (Runemark, 1956; Wirth, 1972) and grazing by slugs. Although *R. geographicum* is also a colonist of bare rock surfaces and shows niche overlap with *R. lecanorinum*, it tends to occur in windier, drier sites (Wirth, 1972). It may also be more resistant than *R. lecanorinum* to parasitism by other lichen-forming fungi (Clayden, 1997).

Ruderal strategies are prominent in leaf-inhabiting (Rogers, 1989) and soil-inhabiting lichens (Topham, 1977) for which the average interval of habitat destruction is very short. However, this study indicates that, even among longer-lived saxicolous crustose lichens, strategies have become diversified in response to the major selective forces inferred by Grime (1979). By extension, the joint analysis of species' growth rates, longevity, and reproductive characteristics should yield insights into the evolutionary and ecological dynamics of saxicolous lichen communities.

Acknowledgments

We thank David J. Hill, Alan Samostie and Daniel P. McCarthy for helpful comments on an earlier version of this paper. We are also indebted to Michael G. Loso for drawing our attention to his research on the demographic context of lichenometric curves. Financial support to SRC was provided by a Natural Sciences and Engineering Research Council (Canada) Postgraduate Scholarship and by an Overseas Research Student Award from the Committee of Vice-Chancellors and Principals of the Universities of the United Kingdom.

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