Symbiosis, 38 (2005) 47–57
Balaban, Philadelphia/Rehovot

Growth Curves of Four Crustose Lichens

R.A. ARMSTRONG
Vision Sciences, Aston University, Birmingham B4 7ET, United Kingdom, Tel. +44-121-359-3611, Fax. +44-121-333-4220, Email. R.A.Armstrong@aston.ac.uk

Received December 2, 2003; Accepted April 15, 2004

Abstract

The growth curves of four common species of crustose lichens, viz., *Buellia aethalea* (Ach.) Th. Fr., *Lecidea tumida* Massal., *Rhizocarpon geographicum* (L.) DC., and *Rhizocarpon reductum* Th. Fr. were studied at a site in south Gwynedd, north Wales, UK. Radial growth rates (RGR, mm 1.5 yr^{-1}) were greatest in thalli of *R. reductum* and least in *R. geographicum*. Variation in RGR between thalli was greater in *B. aethalea* and *L. tumida* than in the species of *Rhizocarpon*. The relationship between growth rate and thallus diameter was not asymptotic; RGR increasing in smaller thalli to a maximum and then declining in larger diameter thalli. A polynomial curve was fitted to the data; the growth curves being fitted best by a second-order (quadratic) curve, the best fit to this model being shown by *B. aethalea*. A significant linear regression with a negative slope was also fitted to the growth of the larger thalli of each species. The data suggest that the growth curves of the four crustose lichens differ significantly from the asymptotic curves of foliose lichen species. A phase of declining RGR in larger thalli appears to be characteristic of crustose lichens and is consistent with data from lichenometric studies.

Keywords: Lichen, crustose species, radial growth rate (RGR), growth curve, hypothallus, areolae

0334-5114/2005/$05.50

1. Introduction

The radial growth rate (RGR) of many foliose and some placodiod lichens increases with size in smaller thalli and later approaches asymptotically to a constant growth rate in larger thalli (Armstrong, 1974a; Hale, 1974; Proctor, 1977). These growth curves have been explained by simple models in which either the relative growth rate ($mm^2\ mm^{-2}\ yr^{-1}$) is assumed to be proportional to an area of thallus in an annulus of constant width within the growing margin (Trinci, 1971; Proctor, 1977; Armstrong, 1979) or that the rate of RGR is assumed to be a positive function of thallus radius (Aplin and Hill, 1979; Childress and Keller, 1980). The best fit to the data is provided by the Aplin and Hill model (Aplin and Hill, 1979; Hill, 1981) which has two constants: 1) a distance constant 's' which relates to the efficiency of carbohydrate use for growth and the distance over which substances are translocated within the thallus or lobe and 2) a rate constant 'a' which relates to the rate of photosynthetic production and the efficiency of carbohydrate use for area increase (Hill, 1981).

Two sources of evidence suggest that the growth curves of crustose species may differ from those of foliose species. First, the growth curve of *Rhizocarpon* species derived from lichenometric studies, i.e., where RGR is inferred from a graph of the diameter of the largest thallus versus substratum age, indicate the presence of various growth phases including establishment, juvenile, maturation, and senescence phases (Porter, 1981). Most lichenometric studies, however, suggest an initial 'lag' phase leading to a phase of accelerating growth up to a maximum (the 'great' period) followed by a phase of declining growth (Beschel, 1973; Mottershead and White, 1972; Miller, 1973; Bull and Brandon, 1998). Second, a few studies (Armstrong, 1983; Haworth et al., 1986; Mathews, 1994) have attempted to determine the growth curve of crustose species by direct measurement.

A study of 39 thalli of *Rhizocarpon geographicum* (Armstrong, 1983) suggested that the growth curve was not asymptotic, RGR increasing in smaller thalli and declining in larger thalli. The present study measured the RGR of thalli in relation to thallus size of four crustose lichens, including a larger sample of *R. geographicum* thalli, in Gwynedd, north Wales, an area in which crustose lichens grow relatively rapidly (Armstrong, 1973; 1983). The principle objective was to test the hypothesis that the relationship between RGR and thallus diameter in crustose species differs from that in foliose species.

2. Materials and Methods

Site

The study was conducted in the field in an area of Ordovician slate rock in

Gwynedd, north Wales, UK (Nat. Grid Ref. SN 6196) (Armstrong, 1974b). Populations of crustose lichens are frequent on boulders and rock outcrops at this site (Armstrong, 1974b) and are important constituents of the lichen communities typical of nutrient-poor siliceous rock in the north and west of the UK (James et al., 1977).

Lichen species

Four of the most common crustose species at the site were chosen for study (Table 1): *Buellia aethalia* (Ach.) Th. Fr., *Lecidea tumida* Massal., *Rhizocarpon geographicum* (L.) DC., and *Rhizocarpon reductum* Th. Fr. Each of the four species comprises a more or less areolate thallus, containing the phycobiont, located on a fungal hypothallus that extends beyond the edge of the areolae (Armstrong and Smith, 1987). Identification to species can be particularly difficult in the yellow-green *R. geographicum* group and thalli are often identified to the section level using the criteria of Poelt (1988). Using the broadly circumscribed criteria of Purvis et al. (1992), however, the populations included in this study were identified as *R. geographicum* (L.) DC. In addition, the suggestion that *R. reductum* should be used for the small spored thalli normally referred to as *R. obscuratum* has been followed (Fryday, 2000). Samples of thalli of the four species were collected, each thallus on a piece of smooth slate, from several rock surfaces and placed on horizontal boards at an unshaded site in a private garden. Thalli were allowed to equilibrate for a year before commencing growth measurements.

Table 1. Details of lichen thalli used in the study.

Species	Number of thalli (N)	Size range (cm)	SD
Buellia aethalia	29	0.20–1.70	0.42
Lecidea tumida	27	0.30–4.0	0.37
Rhizocarpon geographicum	53	0.30–7.0	0.27
Rhizocarpon reductum	25	0.20–2.4	0.45

Growth measurements

Radial growth was measured from the edge of the hypothallus at three-month intervals from Oct 1 1995 until March 1 1997 using previously described methods (Armstrong, 1973; 1975). Five locations were selected at random around the thallus perimeter and averaged for each thallus. Growth increments were added together to obtain a RGR (mm 1.5 yr^{-1}) for each thallus. RGR of each thallus was then plotted against thallus diameter to obtain the growth curves.

Data analysis

Two types of curve fitting were applied to the growth data. First, the Aplin and Hill growth model, which provides the best fit to the growth curves of foliose species, was fitted to the data as follows (Aplin and Hill, 1979; Hill, 1981): 1) the data were grouped into size classes, 2) mean RGR in each size class ($r_2 - r_1$) was plotted as a function of $\log_e r_2 - \log_e r_1$, and 3) the degree of linearity in the relationship was tested using Pearson's correlation coefficient. This model was fitted to all thalli and to the smaller thalli only, i.e., those up to and including the thallus diameter exhibiting maximum RGR. Second, a polynomial curve (STATISTICA Software, Statsoft Inc., 2300 East 14th St, Tulsa, OK 74104, USA) up to and including the fourth-order were fitted successively to all thalli of each species. At each stage, the goodness of fit of the curve to the data was tested using correlation methods and analysis of variance. A more complex curve was accepted as a better fit to the data if it resulted in a significant increase in Pearson's correlation coefficient ('r') and a significant reduction in the residual sums of squares compared with the preceding curves (Snedecor and Cochran, 1980). To test whether RGR declined in larger thalli, polynomial curves were also fitted to the data for the larger thalli only. The thallus diameter exhibiting maximum RGR was identified and all thalli equal to or larger than this size included in this analysis.

3. Results

A summary of the RGR data for each species is shown in Table 2. With the exception of a single thallus of *L. tumida*, all thalli exhibited positive RGR over a period of 18 months. On average, thalli of *R. reductum* displayed the fastest and *L. tumida* the slowest RGR. Variations between thalli, as indicated by the coefficient of variation, were greater in *B. aethalia* and *L. tumida* compared with *R. reductum* and *R. geographicum*.

The relationship between RGR and thallus diameter for each species is shown in Figs. 1–4. All four species showed essentially the same type of growth curve, viz., an increasing phase of RGR in smaller thalli, most evident in *B. aethalea* (Fig. 1) and *R. geographicum* (Fig. 3) reaching a maximum, and then a phase of declining RGR in larger thalli. The results of the curve fitting analyses are shown in Table 3.

Table 2. Summary of the radial growth rates (RGR, mm 1.5 yr^{-1} with annual RGR in parentheses) of four species of crustose lichens in Gwynedd, north Wales (SD = standard deviation, CV = coefficient of variation).

Species	Mean RGR (mm 1.5 yr^{-1})	Range of RGR	SD	CV (%)
Buellia aethalia	1.21 (0.81)	0.23–2.10	0.53	43.8
Lecidea tumida	0.78 (0.52)	0–1.56	0.37	47.4
Rhizocarpon geographicum	0.80 (0.53)	0.05–1.41	0.27	33.4
Rhizocarpon reductum	1.26 (0.84)	0.47–3.0	0.45	35.7

Table 3. Data analysis of the growth curves of four foliose lichen species in Gwynedd, north Wales. (Data in parentheses are the goodness of fits of the curves to the data; isd = insufficient data to test fit to model, *P<0.05, ***P<0.001, ns = not significant).

Species	Polynomial model		Aplin/Hill model	
	All data	Large thalli	All data	Small thalli
Buellia aethalia	2nd order (r = 0.74***)	Linear (r = –0.0.72*)	r = 0.13 ns	r = 0.47 ns
Lecidea tumida	2nd order (r = 0.53*)	Linear (r = –0.60*)	r = 0.15 ns	isd
Rhizocarpon geographicum	2nd order (r = 0.54*)	Linear (r = –0.69**)	r = 0.49 ns	r = 0.10 ns
Rhizocarpon reductum	2nd order (r = 0.46*)	Linear (r = –0.72*)	r = 0.02 ns	isd

The Aplin and Hill model did not successfully fit the data as a whole for any species. There were sufficient thalli of *B. aethalea* and *R. geographicum* to fit the Aplin and Hill model to the growth of the smaller thalli only. In neither case was a significant fit achieved. The relationship between RGR and thallus diameter for all four species was fitted best by a second-order (quadratic) polynomial; the best fit to this model being shown by *B. aethalea* (r = 0.74, P<0.001) (Fig 1). In addition, a significant linear regression of negative slope was fitted to the RGR data in larger thalli consistent with the presence of a declining phase of growth in all four species. This phase was most evident in *B. aethalea* (Fig. 1) and least apparent in *R. geographicum* (Fig. 3).

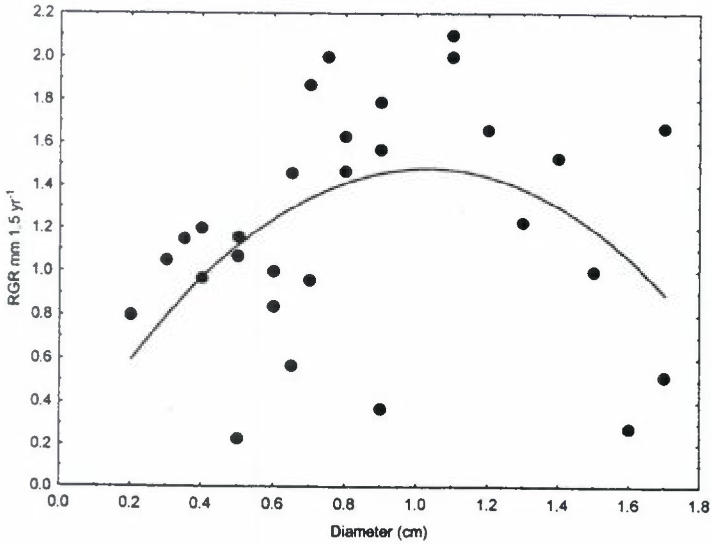

Figure 1. The relationship between radial growth rate (RGR) (mm 1.5 yr^{-1}) for thalli of *Buellia aethalea*. (Goodness of fit r = 0.74, P<0.001).

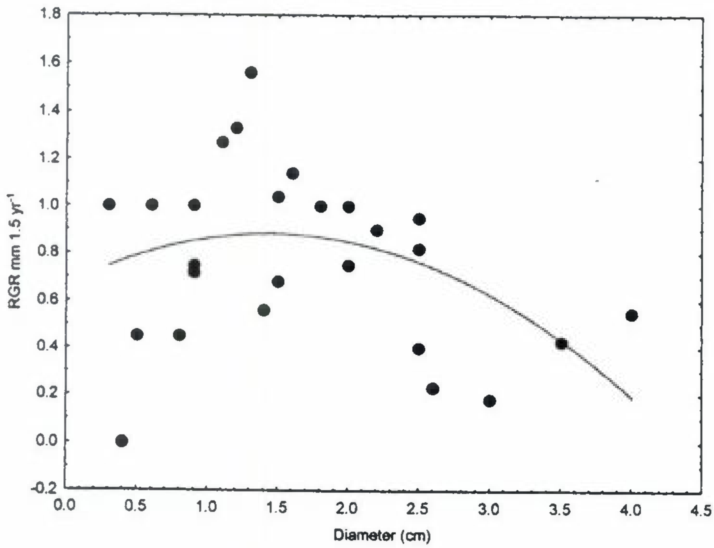

Figure 2. The relationship between radial growth rate (RGR) (mm 1.5 yr^{-1}) for thalli of *Lecidea tumida*. (Goodness of fit r = 0.53, P<0.05).

4. Discussion

The Aplin and Hill model (1979) successfully describes the asymptotic growth curve of many foliose and placodiod lichen species (Armstrong, 1974a; Hale, 1974; Aplin and Hill, 1979; Armstrong and Smith, 1996a) but does not

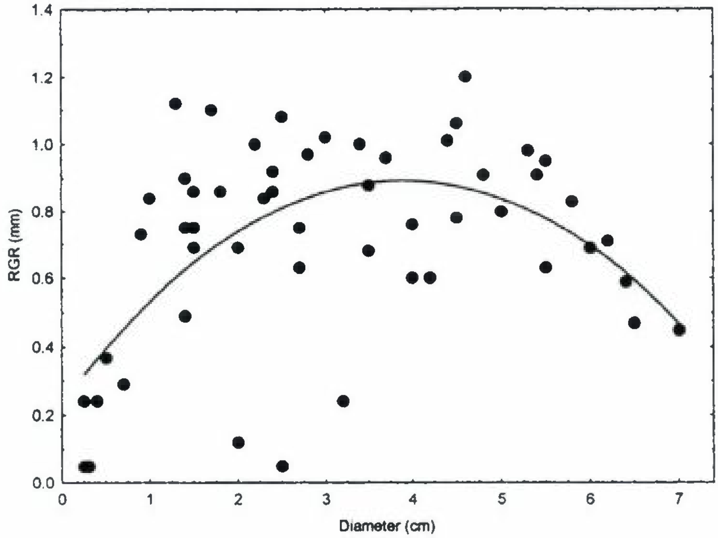

Figure 3. The relationship between radial growth rate (RGR) (mm 1.5 yr^{-1}) for thalli of *Rhizocarpon geographicum*. (Goodness of fit r = 0.54, P<0.05).

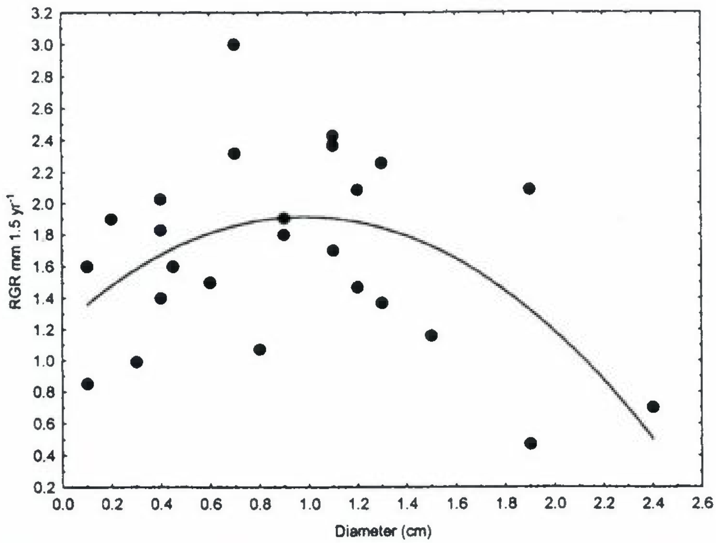

Figure 4. The relationship between radial growth rate (RGR) (mm 1.5 yr^{-1}) for thalli of *Rhizocarpon reductum*. (Goodness of fit r = 0.46, P<0.05).

appear to describe the relationship between RGR and thallus size in the crustose species studied. Instead a parabolic type of growth curve is present with phases of increasing and declining RGR. The Aplin and Hill model could describe the growth curves of crustose lichens in the earliest stages of growth

(Armstrong, 1983). Because of the small number of thalli in the smaller size classes, it was only possible to test this model on two of the species, a poor fit to the model being obtained.

Previous studies of the growth curves of crustose lichens studied by direct measurement have resulted in conflicting results. Two studies of the growth curve of *R. geographicum* (Armstrong, 1983; Haworth et al., 1986) suggest a declining phase of RGR in larger thalli, although in both studies, the decline is not well defined (Innes, 1985; Bradwell, 2001). By contrast, Proctor (1983) studied the RGR of thalli growing on the moraines of an Alpine glacier in Switzerland. Smaller thalli grew significantly more slowly than larger thalli and there was no evidence of a declining phase. Thalli larger than 36 mm in diameter were not included in this study and the data were extrapolated up to 60 mm to determine the growth curve. Mathews (1994) reported growth measurements of species within the *Rhizocarpon* and *Alpicola* subgenera over a five year period and found no evidence of a decline in growth rate. The extreme variability of the data, however, low RGR, and the use of an aggregate species made it difficult to identify possible growth phases in this study.

Lichenometric studies also provide indirect information on the growth curves of crustose species. In many of these studies, non-linear dating curves have been established suggesting a declining phase in RGR with increasing thallus size (Miller and Andrews, 1972; Mottershead and White, 1972; Denton and Karlin, 1973; Mathews, 1974; Innes, 1985; Benedict, 1985; Bull and Brandon, 1998). The present data are therefore consistent with some cross-sectional growth studies and with many lichenometric studies.

A number of factors could explain the slower RGR of the larger thalli. First, if the centers of the thalli contribute carbohydrate for radial growth at the margin, senescence and disintegration of the centers of larger thalli could result in a decline in RGR. It is unlikely, however, that declining RGR can be explained by disintegration of the thallus center (Innes, 1985; Armstrong and Smith, 1997) since only entire thalli were included in the present study and there was no evidence of degeneration during the growth period. Furthermore, in foliose species, disintegration of the thalli is not associated with declining growth rates (Armstrong, 1974a; 1979).

In addition, there are few published data on the width of the peripheral growth zone in crustose lichens. However, radial growth of *R. geographicum* thalli was significantly reduced only when areolae were removed to within 1 mm and 2 mm of the hypothallus suggesting the presence of a narrow rather than a wide annulus (Armstrong and Smith, 1996b). Second, the crustose lichens studied comprise more or less distinct areolae and a marginal hypothallus, a common type of growth form in crustose lichens especially in the genera *Verrucaria*, *Lecidea*, *Rhizocarpon*, and *Lecanora*. The declining RGR in larger thalli could be attributable to the marginal areolae having to supply a greater area of hypothallus as the thallus enlarges. However, there is no evidence of an increase or reduction in hypothallus width in *R. geographicum* with thallus size (Armstrong and Bradwell, 2001).

Third, there may be competition on the rock surface between the hypothallus and other microorganisms for inorganic nutrients and older thalli may be less able to compete than younger thalli. Field experiments have suggested that the hypothallus of *R. geographicum* can utilize exogenous nutrients consistent with this hypothesis (Armstrong and Smith, 1996b). Fourth, the decline in RGR could be attributable to a reduction in carbohydrate transfer from the algae to the hypothallus with age. Within the discrete areolae of *R. geographicum*, for example, there is a cortical layer 15–80 µm thick, an algal layer consisting of *Trebouxia*, and medullary tissue. Nutrient transfer may occur only within the immediate vicinity of each individual areola (Innes, 1985). The levels of ribitol, arabitol, and mannitol are several times higher in the areolae of *R. geographicum* compared with the marginal hypothallus throughout the year (Armstrong and Smith, 1987) consistent with relatively restricted transport from areolae to hypothallus. Hence, increasing inhibition of transport as the thallus ages could explain the declining phase of RGR in crustose lichens. Further research should establish whether the parabolic growth curve is typical of crustose lichens as a whole or only those with a marginal hypothallus. In addition, the morphology of algal and fungal cells could be studied in thalli of different size to establish whether there is increased senescence of these cells in the marginal areolae and hypothallus.

These results also have implications for lichenometry. Non-linear growth curves are a consistent feature of many lichenometric studies from around the world that employ species of *Rhizocarpon* (Miller and Andrews, 1972; Mottershead and White, 1972; Denton and Karlin, 1973; Mathews, 1974; Innes, 1985; Benedict, 1985; Bull and Brandon, 1998). Two hypotheses can be proposed to explain these lichenometric growth curves. First, that the curves reflect mainly environmental change over the last 300 years, i.e., a tendency for either more rapid growth to have occurred in the last 100 years or slower growth over the preceding 200 years. Second, that the growth curve results from a declining phase of RGR in older thalli. The present study provides some evidence to support the latter hypothesis and suggests that more detailed knowledge of the growth curves of crustose lichens could increase the accuracy of the lichenometric method.

REFERENCES

Aplin, P.S. and Hill, D.J. 1979. Growth analysis of circular lichen thalli. *Journal of Theoretical Biology* **78**: 347–363.

Armstrong, R.A. 1973. Seasonal growth and growth rate colony size relationships in six species of saxicolous lichens. *New Phytologist* **72**: 1023–1030.

Armstrong, R.A. 1974a. Growth phases in the life of a lichen thallus. *New Phytologist* **73**: 913–918.

Armstrong, R.A. 1974b. The descriptive ecology of saxicolous lichens in an area of South Merionethshire, Wales. *Journal of Ecology* **62**: 33–45.

Armstrong, R.A. 1975. The influence of aspect on the pattern of seasonal growth in the lichen *Parmelia glabratula* ssp. *fuliginosa* (Fr. ex Duby) Laund. *New Phytologist* **75**: 245–251.

Armstrong, R.A. 1979. Growth and regeneration of lichen thalli with the central portions artificially removed. *Environmental and Experimental Botany* **21**: 116–120.

Armstrong, R.A. 1983. Growth curve of the lichen *Rhizocarpon geographicum*. *New Phytologist* **94**: 619–622.

Armstrong, R.A. and Smith, S.N. 1987. Growth and development of the lichen *Rhizocarpon geographicum* (L.) DC. *Symbiosis* **3**: 287–300.

Armstrong, R.A. and Smith, S.N. 1996a. Factors determining the growth curve of the foliose lichen *Parmelia conspersa*. *New Phytologist* **134**: 517–522.

Armstrong, R.A. and Smith, S.N. 1996b. Experimental studies of hypothallus growth in the lichen *Rhizocarpon geographicum*. *New Phytologist* **132**: 123–126.

Armstrong, R.A. and Smith, S.N. 1997. Factors associated with degeneration of the thallus centre in foliose lichens. *Symbiosis* **22**: 293–302.

Armstrong, R.A. and Bradwell, T. 2001. Variation in hypothallus width and the growth of the lichen *Rhizocarpon geographicum* (L.)DC. *Symbiosis* **30**: 317–328.

Benedict, J.B. 1985. Arapaho Pass. Research report 3, Centre for Mountain Archeology, Ward, Colorado.

Beschel, R.E. 1973. Lichens as a measure of the age of recent moraines. *Arctic and Alpine Research* **5**: 303–309.

Bradwell, T. 2001. Glacier fluctuations, lichenometry and climatic change in Iceland. PhD Thesis, University of Edinburgh.

Bull, W.T. and Brandon, M.T. 1998. Lichen dating of earthquake-generated regional rockfall events, Southern Alps, New Zealand. *Geological Society of America Bulletin* **110**: 60–84.

Childress, S. and Keller, J.B. 1980. Lichen growth. *Journal of Theoretical Biology* **32**: 157–165.

Denton, G.H. and Karlen, W. 1973. Lichenometry: Its application to Holocene moraine studies in southern Alaska and Swedish Lappland. *Arctic and Alpine Research* **5**: 347–372.

Fryday, A. 2000. On *Rhizocarpon obscuratum* (Ach.) Massal. With notes on some related species in the British Isles. *Lichenologist* **32**: 207–224.

Hale, M.E. 1974. *The Biology of Lichens*. Edward Arnold, London.

Haworth, L.A., Calkin, P.E., and Ellis, J.M. 1986. Direct measurement of lichen growth in the central Brooks Range, Alaska, USA and its application to lichenometric dating. *Arctic and Alpine Research* **18**: 289–296.

Hill, D.J. 1981. The growth of lichens with special reference to the modelling of circular thalli. *Lichenologist* **13**: 265–287.

Innes, J.L. 1985. Lichenometry. In: *Progress in Physical Geography*. B.W. Atkinson, ed. **9**: 187–254.

James, P.W., Hawksworth, D.L., and Rose, F. 1977. Lichen communities in the British Isles: a preliminary conspectus. In: *Lichen Ecology*. M.R.D. Seaward, ed. Academic Press, New York, pp. 295–419.

Mathews, J.A. 1994. Lichenometric dating: A review with particular reference to 'Little Ice Age' moraines in southern Norway. In: *Dating in Surface Context*. C. Beck, ed. New Mexico Press, Albuquerque, pp. 185–212.

Miller, G.H. 1973. Variations in lichen growth measurements: preliminary curves for *Alectoria miniscula* from Eastern Baffin Island, N.W.T. Canada. *Arctic and Alpine Research* **5**: 333–337.

Miller, G.H. and Andrews, J.T. 1972. Quaternary history of northern Cumberland peninsula, East Baffin Island, North West Territory, Canada. VI. Preliminary lichen growth curve. *Geological Society of America Bulletin* **83**: 1133–1138.

Mottershead, D.M. and White, I.D. 1972. The lichenometric dating of glacier recession, Tunsbergdalsbre, Southern Norway. *Geografiska Annaler* **54**: 47–52.

Poelt, J. 1988. *Rhizocarpon* Ram. Em. Th. Fr. Subgen. *Rhizocarpon* in Europe. *Arctic and Alpine Research* **20**: 292–298.

Porter, S.C. 1981. Lichenometric studies in the Cascade range of Washington: establishment of *Rhizocarpon geographicum* growth curves at Mount Rainier. *Arctic and Alpine Research* **13**: 11–23.

Proctor, M.C.F. 1977. The growth curve of the crustose lichen *Buellia canescens* (Dicks) De Not. *New Phytologist* **79**: 659–663.

Proctor, M.C.F. 1983. Sizes and growth rates of thalli of the lichen *Rhizocarpon geographicum* on the moraines of the Glacier de Valsorey, Valais, Switzerland. *Lichenologist* **15**: 249–261.

Purvis, O.W., Coppins, B.J., Hawksworth, D.L., James, P.W., and Moore, D.M. 1992. In: *The Lichen Flora of Great Britain and Ireland*. Natural History Museum Publications, London.

Snedecor, G.W. and Cochran, W.G. 1980. *Statistical Methods*. 7th ed., The Iowa State Press, Ames, Iowa, USA.

Trinci, A.P.J. 1971. Influence of the width of the peripheral growth zone on the radial growth rate of fungal colonies on solid media. *Journal of General Microbiology* **67**: 325–344.