Growth rates of *Rhizocarpon geographicum* lichens: A review with new data from Iceland

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Abstract

This article reviews evidence from previous growth-rate studies on lichens of the yellow-green species of Subgenus *Rhizocarpon* – the family most commonly used in lichenometric dating. New data are presented from *Rhizocarpon* section *Rhizocarpon* thalli growing on a moraine in southern Iceland over a period of 4.33 years. Measurements of 38 lichen thalli, between 2001 and 2005, show that diametral growth rate (DGR, mm yr^{-1}) is a function of thallus size. Growth rates increase rapidly in small thalli (<10 mm diameter), remain high (c. 0.8 mm/yr) and then decrease gradually in larger thalli (>50 mm diameter). Mean DGR in southern Iceland, between 2001 and 2005, was 0.64 mm yr^{-1} (SD = 0.24). The resultant growth-rate curve is parabolic and is best described by a third-order polynomial function. The striking similarity between these findings in Iceland and those of Armstrong (1983) in Wales implies that the shape of the growth-rate curve may be characteristic of *Rhizocarpon geographicum* lichens. The difference between the absolute growth rate in southern Iceland and Wales (c. 66% faster) is probably a function of climate and micro-environment between the two sites. These findings have implications for previous lichenometric-dating studies; namely, that those studies which assume constant lichen growth rates over many decades are probably unreliable.

Key words: lichenometry, *Rhizocarpon* section *Rhizocarpon*, climate, dating

Introduction

Lichens are valuable dating tools for geoscientists. The combination of extremely slow growth in certain crustose species and their wide distribution in nature have been key factors in most lichenometric dating studies. Knowledge of a species' growth rate can be used to estimate the age of the surface on which they are growing, assuming that lichen colonisation occurs immediately after exposure. Lichenometric-dating studies have been performed by numerous workers to answer a wide range of geochronological questions since the technique was pioneered by Beschel in 1950 (Table 1). Most lichenometric-dating studies have focused on the yellow-green species of *Rhizocarpon*, more precisely known as Rhizocarpon *Ram. em. Th. Fr. subgenus* Rhizocarpon (Poelt, 1988).

Despite the numerous dating studies that have utilised the growth rate of crustose lichens (Table 1), few attempts have been made to analyse the actual growth mechanisms or to study the growth history of a *Rhizocarpon* lichen thallus. Such a relatively poor understanding has led to considerable controversy regarding the use of lichenometry, particularly amongst biologists. Given the current popularity of lichenometric-dating studies in the earth sciences (eg. Noller and Locke, 2001; McCarthy, 2003; Solomina and Calkin, 2003; Lowell *et al*., 2005, Matthews, 2005), a review of measured lichen-growth rates within the *Rhizocarpon* species seems timely. In addition, we present new data from Iceland regarding the growth curve of *Rhizocarpon geographicum*.

Review of previous growth-rate studies

The direct method

Twelve articles have reported growth data measured over a period of 12 months or more for species within the *Rhizocarpon* subgenus:– Hausmann (1948), Ten Brink (1973), Hooker (1980), Armstrong (1983), Proctor (1983), Rogerson *et al*., (1986), Haworth *et al*., (1986), Matthews (1994), Winchester & Chaujar (2002), McCarthy (2003), Sancho and Pintado (2004) and Armstrong (2005). With the exception of Matthews' and McCarthy's studies, all the measurements refer to thalli of '*Rhizocarpon geographicum*'.

Ethel Hausmann (1948) was probably the first to publish information regarding the growth rate of *Rhizocarpon geographicum*. Her observations of a single *R. geographicum* 'map lichen' growing near the summit of Mt. Monadnock, New Hampshire, showed that the growth rate of *R. geographicum* over a four-year period was slow, typically around 0.5 mm yr^{-1}. She also made a basic physiological assumption that the rock-lichens in question grew fastest in the wettest year when the mountain was "more swathed in clouds" than normal.

Roland Beschel (1956, 1961) measured and photographed *Rhizocarpon* lichens in west Greenland. Ten Brink (1973) revisited Beschel's control sites and determined the growth rate of several *Rhizocarpon geographicum* thalli over the intervening 12-year period using the photogrammetric method. The results show that growth rates had been very slow, averaging 0.1-0.2 mm yr^{-1}. No conclusions were drawn in these studies regarding the growth history of the plants.

Antarctic crustose lichens are presumed to be amongst the slowest-growing and, hence, longest-living organisms on Earth. Hooker's photogrammetric studies on the South Orkney Islands between 1972 and 1977 were published in 1980. He detected no measurable growth during a 2.5-year period in any of the 63 *Rhizocarpon geographicum* thalli being monitored. However, after a subsequent three-year period, small amounts of radial growth were recorded, optimally around 0.1 mm yr^{-1}. Using this data he estimated average radial growth rates in the maritime sub-Antarctic to be of the order of 4 mm 100 yr^{-1}. Hooker (1980) was unable to demonstrate any significant effect of thallus size on growth rate.

Armstrong's (1983) observations on the growth of *Rhizocarpon geographicum* in North Wales comprise the first major study of the growth curve of a crustose lichen. He measured the radial growth of 39 thalli over a period of 1.5 years, using a graduated scale under high magnification. Armstrong's results detected three distinct phases of growth – an initial phase where radial growth rates increased rapidly, a second phase where radial growth rates are high and relatively constant, and a declining phase where growth rates fell. The statistical representation of this growth rate decline has been questioned (Innes, 1985). However, the growth rate of each of the thalli over 55 mm in diameter falls below the mean growth rate of thalli between

15 and 55 mm in diameter. Armstrong's evidence suggested that a phase of declining growth occurs in thalli over ~50 mm in diameter and hence that growth is a size (age) dependent phenomenon in *Rhizocarpon geographicum*.

Proctor (1983) studied the growth rate of thalli growing on the moraines of an Alpine glacier in Switzerland. He took photographs of numerous sites at four-year intervals and using these, calculated the radial growth rate of 22 *Rhizocarpon geographicum* thalli. He then constructed a curve of mean radial growth increment against thallus radius showing that smaller thalli (<10 mm) grew significantly more slowly than larger thalli. Unfortunately, Proctor's dataset does not include any thalli of more than 36 mm in diameter. In addition, Proctor assumed constant growth rates in thalli over ~10 mm in diameter and extrapolated the linear part of his growth curve for thalli up to 60 mm in diameter, without any further measurements. The statement then made regarding the growth curve of *Rhizocarpon geographicum* would seem to be over-optimistic, viz., "That lichen thalli can grow with a near-constant radial increment for periods of many years is now established beyond question" (1983: 258).

Rogerson *et al*. (1986) photographed and measured 7 thalli of *Rhizocarpon* section *Rhizocarpon geographicum* growing on rocks in the coastal mountains of northern Labrador in 1978 and again in 1983. Diameter increases of 0.10 – 0.58 mm yr^{-1} were derived using the photogrammetric method of Locke *et al*. (1979). They reported an average diameter increase of 0.34 mm yr^{-1} over the five-year period, with a range from 0.10 to 0.54 mm yr^{-1}. Due to the small number of thalli measured, including only two greater than 50 mm in diameter, their study sheds little new light on the relationship between thallus size and growth rate.

Haworth *et al*. (1986) measured 92 *Rhizocarpon geographicum* 'sensu lato' thalli over a 4-6-year period in the Central Brooks Range, Alaska. They determined mean annual change in diameter using a combination of photogrammetric and tracing techniques. Diametral growth rates ranged from 0 to 0.35 mm yr^{-1} with variability being high within and between sites. Their study, like Armstrong's (1983), also found evidence, though poorly defined, for an inverse relationship between thallus growth rate and thallus size. The authors reached the following conclusion (1986: 294):

"The growth curve developed for *Rhizocarpon geographicum* shows continuously slowing increases in diameter throughout the life of the thallus."

Haworth *et al*., (1986) also stated that lichen age was only one of many factors contributing to variations in growth rate, along with substrate lithology, micro-climate and competition between thalli.

Matthews (1994) presented direct measurements of 63 thalli of the *Rhizocarpon* subgenus (probably only species within sections *Rhizocarpon* and *Alpicola*, (Matthews, *pers. comm*. 2000)). His measurements were conducted over a five-year period on the outermost moraine at Nigardsbreen, southern Norway. Dial callipers were used to measure the long axes of only well-defined thalli. Matthews found no indication of a decline in growth rate with increasing thallus size. However, the extreme scatter within the dataset precludes the identification of any possible trends. Furthermore, the use of an “aggregate species” may cause any growth rate decline in *Rhizocarpon geographicum* to be obscured amongst data from species within different lichen groups (i.e. *Rhizocarpon alpicola*; (see Innes, 1983; 1985)). The reported linear growth rate in *Rhizocarpon* thalli up to 120 mm in diameter should therefore be viewed with caution.

Winchester and Chaujar (2002) measured *Rhizocarpon geographicum* lichens on gravestones in North Wales, as part of a lichenometric study on mass movement deposits. Measurements were made with a flexible tape accurate to ±1 mm. They recorded thallus diameter increases from 2 to 11 mm over a 4.25 yr period, with an average of 1.47 mm yr^{-1}. Winchester and Chaujar (2002) found no relationship between thallus size and growth rate. However, their study of 32 lichens only included two below 20 mm in diameter, and also combined data from two sites 8 km apart.

McCarthy (2003) has provided the largest dataset on *Rhizocarpon* growth rates to date. 105 *Rhizocarpon* section *Rhizocarpon* thalli, ranging from 5-50 mm in diameter, were measured at annual intervals over a four-year period. (McCarthy states that most of the 105 thalli belonged to the species *Rhizocarpon lecanorinum* Anders.) The lichens were growing on boulders on a moraine crest in front of the Illecillewaet Glacier, British Columbia. Measurements were made using digital calipers accurate to

±0.02 mm. His measurements showed that mean radial growth rates, between 1996 and 2000, ranged from 0.26 to 0.41 mm yr^{-1}. However, there was considerable scatter around the mean in every year (range = ~1.0 mm yr^{-1}). McCarthy found that thallus size was a poor predictor of thallus growth rate. Only weak positive correlations ($r^2 < 0.3$) were found between radial growth and thallus diameter. However, it should be remembered that all but 2 of the thalli were under 45 mm in diameter in McCarthy's dataset, and none was over 50 mm in diameter. Consequently, any growth-rate decline in large thalli (>50 mm), as suggested by Armstrong (1983), is unlikely to have been detected in McCarthy's (2003) study.

Leopoldo Sancho measured and photographed *Rhizocarpon geographicum* (L). DC. thalli in 1991 on Livingston Island in the maritime Antarctic. Revisiting the same boulders on moraines in 2002 he was able to calculate the diametral growth rate of around 400 crustose lichens over 11 years, including ~100 *Rhizocarpon geographicum* (Sancho and Pintado, 2004). Measurments were made with digital calipers accurate to ±0.1 mm. This study deduced mean growth of 0.50 mm yr^{-1} for the five largest thalli between 1991 and 2002. Unfortunately, the diameters of the thalli were not included in the results table making it difficult to draw conclusions about the role of lichen size on growth rate. However, all the *Rhizocarpon* lichens in the study were less than 20 mm in diameter (Sancho and Pintado, 2004). Interestingly, this study highlights faster than expected growth rates in a maritime, subantarctic environment.

Most recently, Armstrong (2005) measured the growth of 39 yellow-green *Rhizocarpon* section *Rhizocarpon* lichens on boulders in the Cascade Mountains of Washington State, USA. Measurements were made between 1988 and 1994 using a micrometer scale under x8 magnification. His study found slow radial growth rates in this high-altitude montane environment (typically c. 0.1 mm yr^{-1}), probably as a direct result of the short snow-free periods experienced. In this environment, Armstrong found no relationship between lichen size and growth rate, which may have been masked by the slow growth rates recorded during the 6-yr study (Armstrong, 2005).

The Indirect method

Earth scientists interested in dating recently exposed rock surfaces have contributed valuable information on lichen growth rates. Measuring the size of lichen thalli on surfaces of known age offers a method of studying the growth rates of slow-growing lichens over periods of many decades. The majority of workers have derived non-linear dating curves using *Rhizocarpon* species (eg. Beschel, 1958, 1961; Miller, 1969; Miller and Andrews, 1972; Mottershead and White, 1972; Denton and Karlén, 1973; Matthews, 1974; Innes, 1985; Benedict, 1985; Bull and Brandon, 1998; Bradwell, 2001a; Solomina and Calkin, 2003; Larocque and Smith, 2004; Lowell *et al*., 2004). These age-size curves provide *indirect* evidence that lichen growth slows with time, possibly as a function of thallus size. Those workers who report a linear relationship between exposure age and lichen size, using *Rhizocarpon* lichens, have probably identified only part of a larger curve or have extrapolated growth rates without justification (eg. Burrows, 1975; Gordon and Sharp, 1983; Maizels and Dugmore, 1985; Kugelmann, 1991; Evans *et al*., 1999; Kirkbride and Dugmore, 2001).

Two recent indirect growth-rate studies should be discussed at this point. Karlén and Black (2002) revisited surfaces hosting *Rhizocarpon geographicum* lichens, originally measured by Karlén in 1970-71 (Karlén, 1973). Lichen measurements were conducted in the year 2000 on “close to identical surfaces” as those used in 1970. The results indicate that growth rates were apparently similar in large and small thalli. Karlén and Black (2002) found diameter increases in lichens on 14 surfaces equivalent to ‘growth rates’ of 0.17 - 0.62 mm yr^{-1}. This experiment provides a good proxy for lichen growth rates over the intervening 30 years. However, the measurements were not made on exactly the same thalli and therefore are not actual, *directly measured*, lichen growth rates. Karlén and Black (2002: 229) also stated that the “maximum lichen diameter may have been underestimated in 2000” due to snow restricting the observable area. Furthermore, the inclusion of lichens from other sections within the subgenus (including *R. alpicola*) could not be ruled out.

A second recent study by O’Neal and Schoenenberger (2003) revisited surfaces in the Cascade Mountains hosting *Rhizocarpon geographicum,* originally measured by Porter (1981). They constructed a growth curve from repeated measurements of ‘largest lichens’ diameters at three sites: Mt Hood, Mt Rainier and Mt Baker. The resultant growth curve was curvilinear, implying increasing, then constant, then decreasing growth rates. Interestingly, the implied decrease in growth rate occurred in thalli >60 mm in diameter. When the role of thallus size on growth rate over the ~25 year period is examined, lichens <40 mm in diameter appeared to grow at c. 0.5 mm yr^{-1}; whilst the largest lichens (>50 mm) increased in diameter by only c.0.25 mm yr^{-1}.

New growth rate data from Iceland

A direct study of lichen growth rates was conducted on the terminal moraine complex at Gigjökull, southern Iceland, over a 4.33-year period between May 2001 and September 2005.

Study site

Gigjökull is a steep glacier flowing from the summit of the ice-capped Eyjafjöll volcano. Parts of the Eyjafjalljökull ice cap receive in excess of 4000 mm precipitation a year, although the valleys and outwash plains to the north and east experience considerably less (<2500 mm yr)(Figure 1; B). Rainfall data from Basar, 10 km east of Gigjökull, records an annual mean of 2350 mm yr^{-1} (between 1991-2001). The study site experiences a mean annual temperature of c. 3°C, and a mean annual temperature range of 11°C (Einarson, 1991) (Figure 1, B).

Four, large, porphyritic basalt, boulders were selected: two near the base of the ice-proximal slope and two on the broad crest of the terminal moraine, 300 m away. These are referred to as measurement stations 1 and 2, respectively (Figure 1, C). Yellow-green *Rhizocarpon* lichens were selected for measurement on gently sloping north and west-facing boulder surfaces. Lichens on horizontal surfaces or in small depressions were avoided, as these could act as collection points for rainwater. The area is free from human disturbance, has no trees and is 300 m from the nearest stream. Hence, all thalli are thought to share the same microclimatic conditions.

Methods

41 non-competing, approximately circular, *Rhizocarpon* section *Rhizocarpon* thalli were marked and photographed in early May 2001. All lichens had sharp margins with clearly defined hypothalli. All thalli were identified in the field, using the criteria

of Poelt (1988), as *Rhizocarpon* section *Rhizocarpon* (formerly the *Geographicum* group of Runemark (1956)). Although chemical identification to species level was not undertaken in Iceland, all 41 thalli were examined using a x8 handlens against the broadly circumscribed criteria of Purvis *et al*. (1992); most could be identified as *Rhizocarpon geographicum* (L.) DC. Furthermore, each thalli was examined to ensure that it did not comprise two or more intergrown individuals. Identification marks were made with white oil-based paint and Rotring pen, several millimetres away from the edge of the thallus margin (as done by Benedict, 1988; McCarthy, 2003). Each lichen was numbered – GIG01 to GIG41. Measurements of thallus diameter, longest axis and 90 degrees to the longest axis, were made in the field using a clear flexible rule with 0.1 mm graduations and x8 handlens (Figure 2, A). Measurement precision using this technique is probably only ±0.5 mm, particularly on larger thalli and rough surfaces. All measurements were made by the same operator. Photographs were taken with a Canon EOS 35mm camera on Fujicolour slide film. The distance from lichen to camera was kept below 10 cm using a Sigma macro lens to minimise photographic distortion. The lichens were re-photographed and re-measured in September 2005. Slide photographs from 2001 and 2005 were scanned using a Sony film scanner UYS100. To obtain more precise measurements of lichen growth, the images were enlarged 400% in Adobe Photoshop and accurately overlaid, using the identification marks as reference points. Minor corrections were made for geometric distortion using the method outlined by Locke *et al.* (1979). Tracings of the thallus margin in 2001 and 2005 allowed the lichen growth to be visualised and quantified. On-screen measurements of thallus diameter, longest axis and 90 degrees to the longest axis, were made for all thalli from photographs taken in 2001 and 2005 (Figure 2, B). Using this photogrammetic technique, measurement precision increases to ±0.05 mm.

Results

38 of the lichens showed measurable growth over the study period. Two thalli could not be positively identified in 2005; one had died and disintegrated. The diametral growth rate (DGR) of 38 individual thalli was calculated assuming constant growth throughout the 4.33-year period (ie. total diameter increase divided by 52 months) and expressed in mm yr^{-1}. The average maximum growth rate of each lichen thallus has been plotted against its respective maximum diameter in May 2001 (Figure 3). The

resultant graph shows DGR between thalli varies from 0.23 mm to 1.39 mm yr^{-1}; the mean DGR in the 38 thalli being 0.65 mm yr^{-1}. The range (1.16) and standard deviation of the dataset (0.24) reveal a moderate degree of scatter around the mean.

The data reveal a distinct relationship between thallus size and DGR in *Rhizocarpon geographicum*, with growth appearing to be most rapid in 10-40 mm diameter thalli. Whilst slower DGR were recorded in the smallest thalli (<10 mm in diameter) and in the largest thalli (>50 mm in diameter). The shape of the growth-rate curve is optimally described (r^2 = 0.44) by a third-order polynomial curve, initially accelerating to a peak around 30 mm before gradually declining, possibly in an asymptotic way. Linear regression (r^2 = 0.004) and a second-order polynomial (r^2 = 0.34) yield weaker best-fit values. The evidence for slower radial growth in the smallest thalli is clear, as all 7 thalli <10 mm in diameter have DGR less than the average of the whole dataset. The evidence for slower growth in large thalli is also clear with 9 out of the 10 largest thalli (>40 mm) having DGR less than the mean of the whole dataset. The mean DGR of lichens in the 40-80 mm size range is 30% less than the mean DGR of those in the 10-40 mm size range (0.54 mm yr^{-1} cf. 0.78 mm yr^{-1}). Furthermore, three of the four largest lichens, all >60 mm in diameter, have growth rates of <0.45 mm yr^{-1}; which is appreciably slower than those thalli in the 10-40 mm size range.

Discussion

The new growth study described above was set up in 2001, following lichenometric investigations by one of the authors in southern Iceland (Bradwell, 2001a, 2004, Bradwell *et al*., 2006), to determine whether the growth rate of *Rhizocarpon* lichens was linear over time or a function of thallus size. Previous direct-measurement studies have revealed considerable uncertainty over the exact shape of the growth curve of *Rhizocarpon geographicum,* with some studies suggesting that growth rates decline in larger thalli (Armstrong, 1983; Haworth *et al*, 1986), whilst others found no evidence of this decline (Matthews, 1994; Winchester and Chaujar, 2002).

The present study suggests that in south Iceland *Rhizocarpon geographicum* thalli conform to a parabolic growth-rate curve. The steep rising limb corresponds to accelerating DGR in small, younger thalli; the crest of the curve corresponds to the period of maximum DGR; and the slowly declining phase represents a growth rate decline in larger, older thalli. This model of growth fits well with *indirect* lichen growth-rate studies that predict accelerating growth, followed by rapid, then exponentially decreasing growth (eg. Matthews, 1975; Thompson and Jones, 1986; Bradwell, 2001a; O'Neal and Schoenenberger, 2002; Larocque and Smith, 2004).

The new data from Iceland can be compared with the results of a similar study carried out in north Wales almost 25 years ago (Armstrong, 1983). Armstrong's dataset (1983) involved 40 lichen thalli of *R. geographicum*, ranging in size from 3 – 65 mm, measured over an 18-month period. The trend was best described by a third-order polynomial function ($r^2 = 0.48$). The similarity between the growth-rate curve of Armstrong's dataset (1983) and the present study is striking (Figure 4). (Armstrong's dataset has been normalised to show growth rates over a 12-month period). Both curves display an increasing growth phase, followed by a maximum at ~30 mm and a more gentle declining phase. The coincidence of the maxima and the overall shape of the curves implies strongly similar growth curves in the two contrasting environments. The growth curves can be broadly divided into four phases of growth: an initial phase of lichen **establishment**; followed by increasing growth rates in the **juvenile** phase; relatively rapid, constant growth rates during **maturation**; and declining growth rates during **maturity/senescense** (Armstrong, 1974; Bradwell, 2001b) (Figure 5; a-d).

Naturally, the absolute growth rates at the two sites differ markedly. This difference in lichen growth rate is highly significant, being 66% greater at the maximum in north Wales than southern Iceland. Faster average growth rates in north Wales are likely to be attributable to environmental conditions being more favourable to growth at temperate latitudes – consistent with the results of other workers (eg. Beschel, 1950, 1961; Rydzak, 1961; Armstrong, 1973; Benedict, 1990). In particular, the combination of a longer snow-free growing season (Benedict, 1990), higher frequency of rain days (Lawrey and Hale, 1977), and warmer average daytime temperatures (Kershaw, 1985) in north Wales will all tend to promote faster growth than in Iceland.

We propose that the form of the growth curve identified in the present study, together with the study of Armstrong (1983), and supported by lichenometric studies conducted on five continents, is characteristic of this lichen species (and possibly subgenus). The shape of this growth-rate curve has wider implications; firstly for the growth of *Rhizocarpon geographicum* in other climatic zones, and secondly for the use of lichens as a dating tool.

In more arid regions, where environmental conditions are not conducive to rapid growth, meangrowth rates may be relatively low, thus flattening the growth curve (Figure 5; curve 4). Where growth is extremely slow (DGR <0.2 mm yr^{-1}), such as in parts of Greenland and Antarctica (Ten Brink, 1973; Hooker, 1980), the growth curve would be almost completely flat, thus effectively obscuring the 3 stages (Figure 5; curve 5). In sharp contrast, where mean *R. geographicum* growth rates are particularly rapid (DGR > 1.5 mm yr^{-1}), for example in parts of maritime western Europe, New Zealand and South America, the curve would be 'stretched', emphasising the parabolic nature of lichen growth (Figure 5; curve 1).

Lichenometric studies that report a linear relationship between lichen age and lichen size in *Rhizocarpon* lichens over many decades should be viewed with caution. The overwhelming majority of lichenometric, and some lichenological, studies find the age-size relationship to be non-linear, slowing with time. Hence, studies that report a linear relationship may have identified only part of a larger curve or may have extrapolated growth rates without justification. In the latter cases, serious doubt should be placed on the estimated lichenometric ages reported.

Conclusions

Thirteen studies have now reported directly measured growth rates of lichens in the *Rhizocarpon* subgenus. Of these, ten studies have examined the role of thallus size on growth rates. Three of these studies (Armstrong, 1983; Haworth *et al*., 1986; Bradwell and Armstrong, *this study*) show evidence for a decline in the growth rate of large thalli; whilst three do not include large thalli (>50 mm) (Proctor, 1983; McCarthy, 2003; Sancho and Pintado, 2004); one is inconclusive owing to the size of the dataset (Rogerson *et al*., 1986); and a further three studies show no evidence for a growth-rate decline (Matthews, 1994; Winchester and Shaujar, 2002; Armstrong, 2005), although Matthews (1994) used an aggregate *Rhizocarpon* 'species'; and Armstrong (2005) recorded very slow growth rates. Both of these factors are likely to obscure growth-rate trends. On balance, these direct studies suggest that larger *Rhizocarpon* *geographicum* thalli grow more slowly than smaller thalli (excluding the smallest thalli <10 mm). In addition, new data (this study) suggests initially increasing then gradually decreasing growth rates, probably describing an asymptotic curve with a long tail.

The striking similarity between these new data from Iceland and those of Armstrong (1983) in Wales implies that the shape of the growth-rate curve of *Rhizocarpon geographicum* is probably characteristic of this species (and possibly subgenus). The difference between the absolute growth rates is probably a function of climate and microenvironment between the two sites. We find that, at its optimum, the same species grows ~66% more rapidly in a more oceanic climate – probably as a result of the higher frequency of rain days and longer growing season in north Wales than in southern Iceland. This study highlights the need for correction factors when using lichen-growth curves across different climatic regions.

Finally, indirect lichenometric studies lend further support for a growth rate decline in larger thalli. A consensus finds a **non-linear** relationship between lichen size and age. Hence, those studies that assume a constant relationship between lichen growth and time over many decades are probably unreliable. However, indirect studies still leave question marks surrounding the role played by climatic change and the effects of ecological competition. Further long-term direct observations are required from different climatic regions to show, beyond reasonable doubt, that age is the primary control on the growth rate of lichens within the *Rhizocarpon* family.

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Figure captions

Figure 1: A. Location map of the study site in Southern Iceland. B. Climatic setting of the study site at Gigjökull (G). Shaded values show mean annual precipitation (1960-1990); dashed lines show mean annual air temperature isotherms (°C) (1960-1990) (Einarsson, 1991). Ice caps: M = Myrdalsjökull; E = Eyjafjallajökull. Central volcanoes shown as triangles. C. Detailed map of the study site at Gigjökull showing the location of lichen measurements stations (1) and (2). D. Photograph of the moraines at Gigjökull in September 2005 (taken from x on map C). Note that the ice margin has receded c. 1.5 km since 1996.

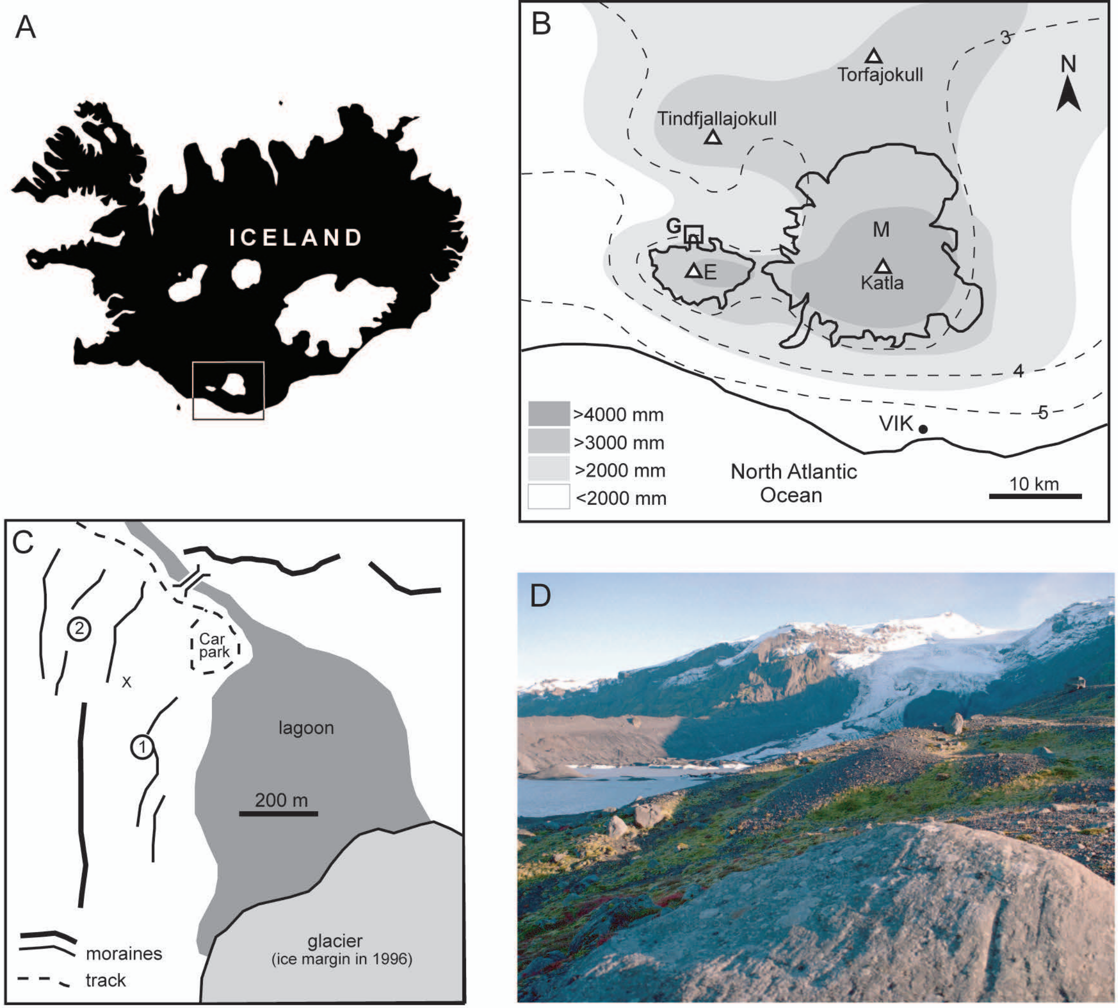
Figure 2: A. Photographs of *Rhizocarpon geographicum* thalli (GIG31 & GIG33) measured in this study (taken in September 2005). The paint marks around the edge were made in 2001 as reference points. B. The outline of the thallus traced from photographs taken in May 2001 and September 2005. Measurement axes are also shown. Note the change in diameter over the intervening period (c. 4-6 mm).

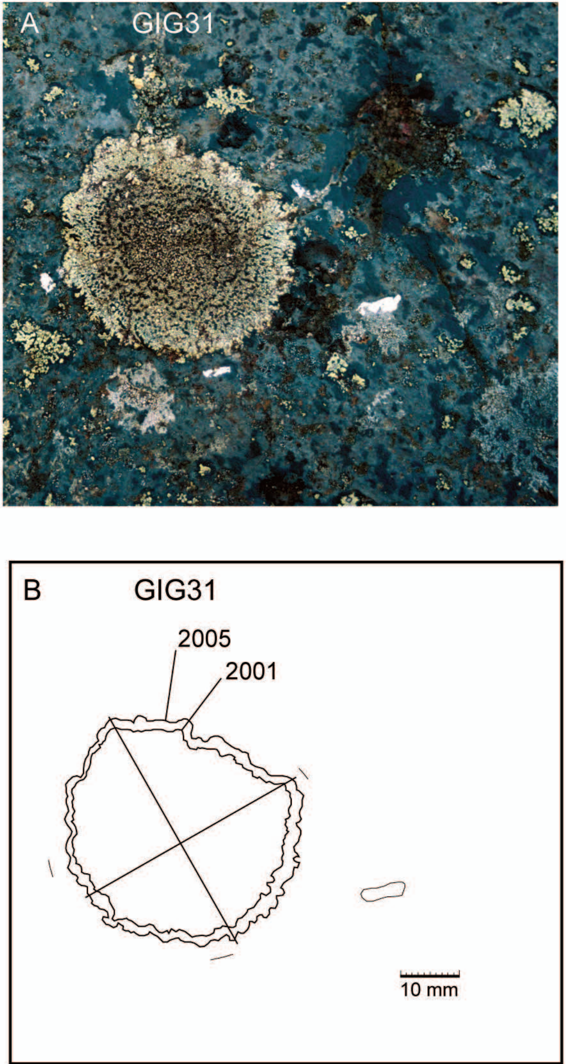
Figure 3: Diametral growth rate of *Rhizocarpon geographicum* (mm/yr) plotted against lichen diameter (mm in 2001), from Gigjökull, southern Iceland.

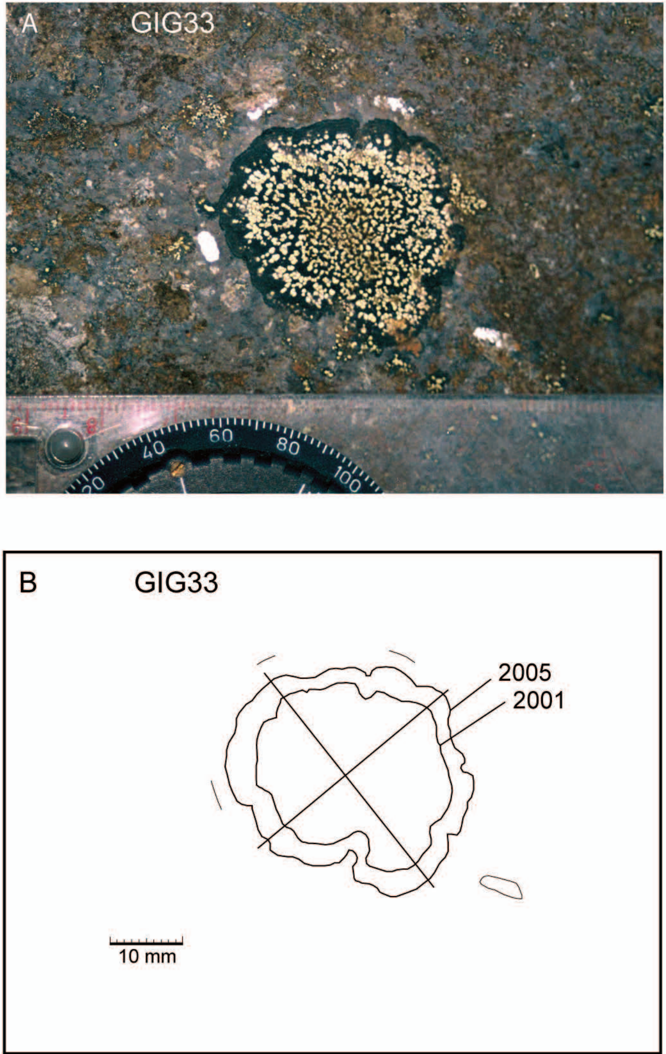
Figure 4: Comparison of diametral growth rates of *Rhizocarpon geographicum* from Armstrong (1983) (grey dots) and this study (black dots). (Armstrong's (1983) radial growth rate data have been converted to DGR (ie. multiplied by 2) and scaled to mm/12 months for direct comparison with this study).

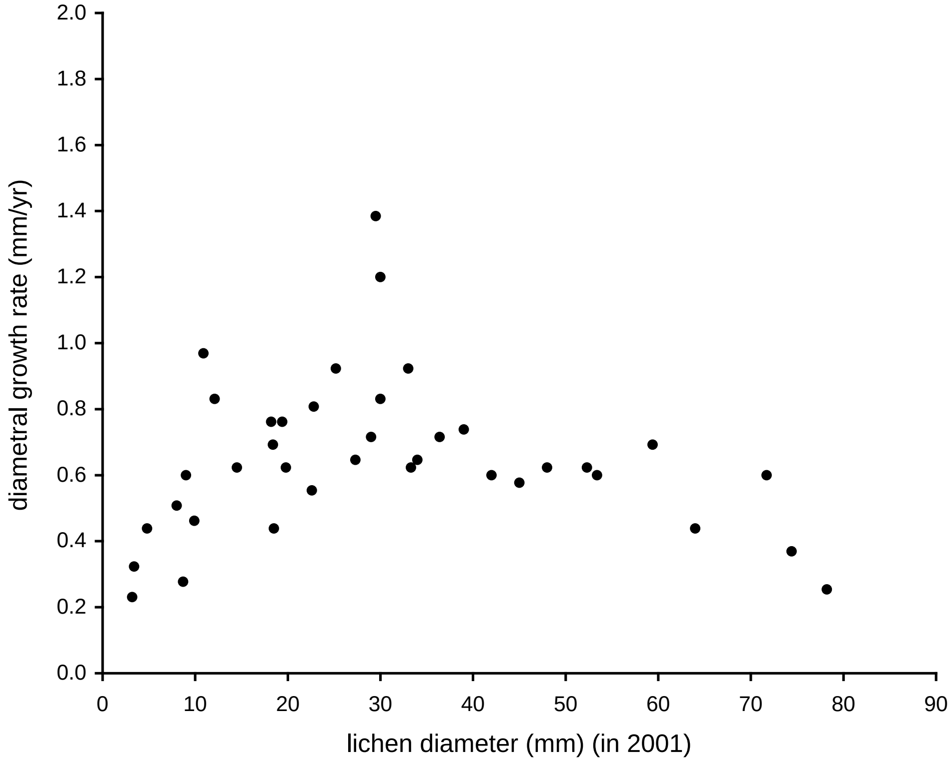
Figure 5: Growth-rate curves of *R. geographicum* from different climates. (1) South Island, New Zealand (hypothesised); (2) north Wales (Armstrong, 1983); (3) south Iceland (this study); (4) north Iceland (hypothesised); (5) west Greenland, 68°N (hypothesised). Letters denote phases of lichen growth – a: establishment; b: juvenile; c: maturation; d: maturity or senescense. DGR – diametral growth rate.

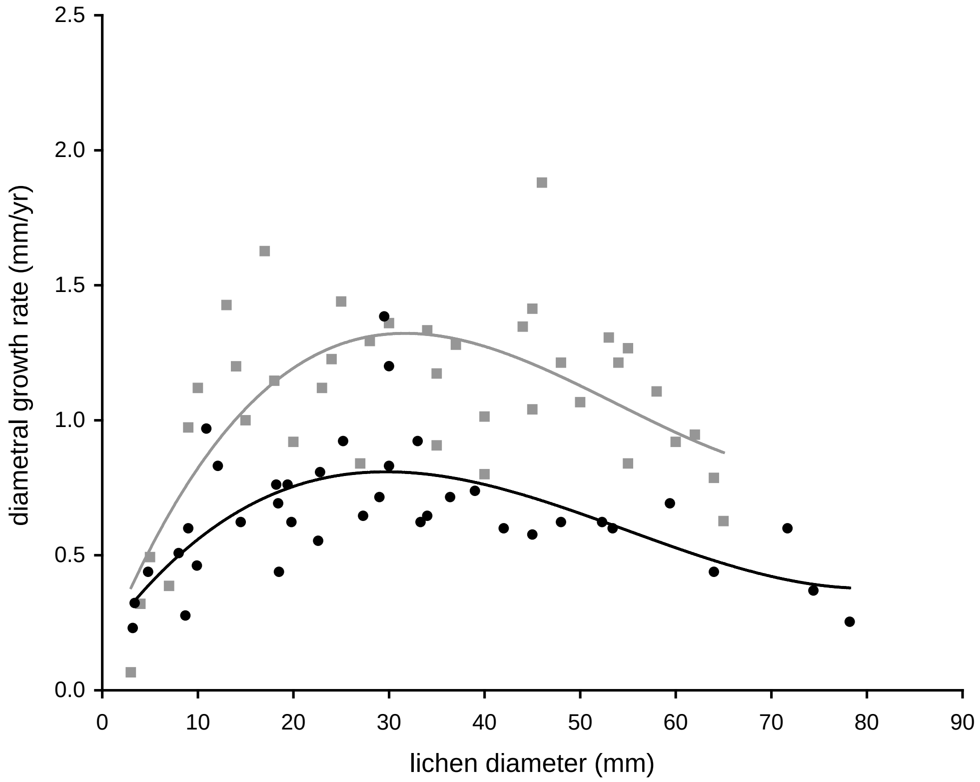
Table 1: Some worldwide applications of lichenometric dating.


A
ICELAND
B
3
Torfajokull
N
Tindfjallajokull
G
M
E
Katla
4
5
VIK
>4000 mm
>3000 mm
>2000 mm
<2000 mm
North Atlantic
Ocean
10 km
C
2
Car
park
x
1
lagoon
200 m
moraines
track
glacier
(ice margin in 1996)
D

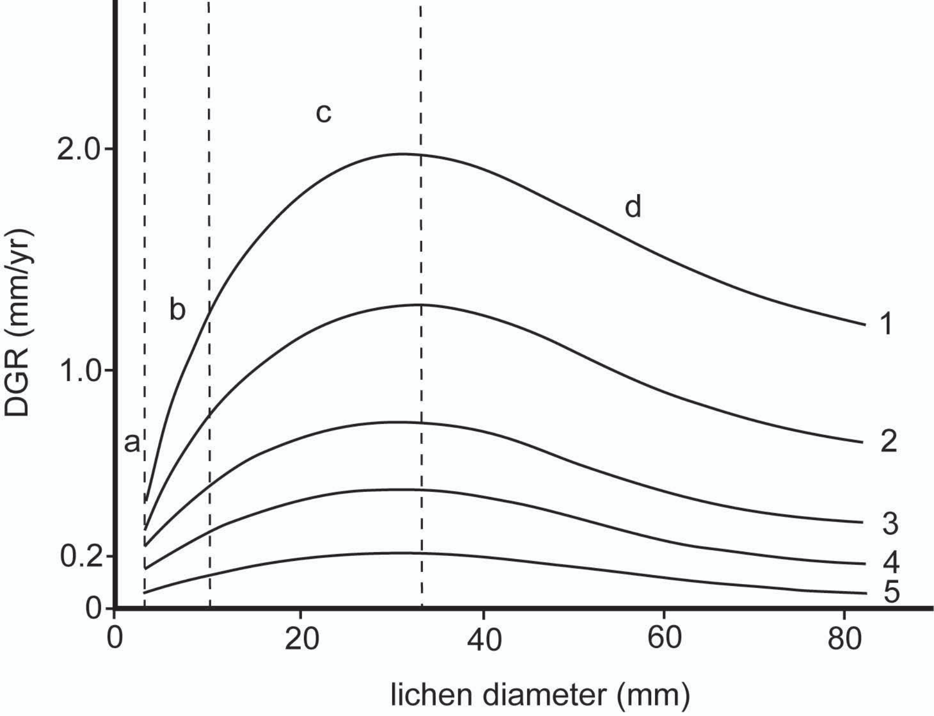

A
GIG31
B
GIG31
2005
2001
10 mm


A
GIG33
40
60
80
100
B
GIG33
2005
2001
10 mm


2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
diametral growth rate (mm/yr)
0
10
20
30
40
50
60
70
80
90
lichen diameter (mm) (in 2001)



diametral growth rate (mm/yr)
0.0
0.5
1.0
1.5
2.0
2.5
0
10
20
30
40
50
60
70
80
90
lichen diameter (mm)



DGR (mm/yr)
2.0
1.0
0.2
0
0
20
40
60
80
lichen diameter (mm)
a
b
c
d
1
2
3
4
5

Type of surface	*Location*	*Author(s)*
River channels (abandoned)	England	Macklin (1986);
		Macklin *et al.* (1993)
River terraces	England	Merrett and Macklin (1999)
	Iceland	Maizels and Dugmore (1985);
		Thompson and Jones (1986)
	Norway	Maizels and Petch (1985)
Flood deposits	Greece	Maas & Macklin (2002)
	Corsica	Gob *et al.* (2003)
Lake shorelines	Norway	Matthews *et al.* (1986)
	Spitsbergen	Andre (1985, 1986)
	Iceland	Evans *et al.* (1999)
Raised beaches	Gulf of Bothnia	Broadbent and Bergqvist (1986)
Rock glaciers	Norway	Vere and Matthews (1985)
	Iceland	Martin *et al.* (1994)
	Swiss Alps	Haeberli *et al.* (1979);
		Burga *et al.* (2004)
Protalus ramparts	Norway	Shakesby *et al.* (1987)
Patterned ground	Norway	Cook-Talbot (1991)
Talus	Spitsbergen	Andre (1985, 1986)
Debris flows	Scotland	Innes (1982)
	Poland	Jonasson *et al.* (1991)
Landslides	Italian Alps	Porter and Orombelli (1981)
	Norway	Dawson *et al.* (1986)
Statues	Easter Island	Follmann (1961)
Stone walls	England	Laundon (1980)
	Colorado	Benedict (1985)
Stone circles	England	Winchester (1984, 1988)

Type of surface	*Location*	*Author(s)*
Earthquake-induced faults/disruptions	Tadjikistan	Nikonov and Shebalina (1979); Smirnova and Nikonov (1990);
	California	Bull (1996)
Earthquake-induced rockfalls	Russia	Nikonov (1988)
	New Zealand	Bull *et al.* (1994); Bull and Brandon (1998)
Snow-free areas	Colorado	Benedict (1993)
Moraines	Iceland	Thompson (1988); Evans *et al.* (1999);
		Caseldine (1990, 1991); Kugelmann (1991)
		Bradwell (2004); Bradwell *et al.* (2006)
		McKinzey *et al.* (2004)
	Norway	Denton and Karlen (1973);
		Matthews (1974, 1977, 1994, 2005)
		Innes (1986); Erikstad and Sollid (1986);
		McCarroll (1994); Ballantyne (1990);
		Bickerton and Matthews (1992); Winkler *et al.* (2003)
	Spitsbergen	Werner (1990)
	Greenland	Beschel (1958, 1961); Geirsdottir *et al.* (2000)
	Alaska	Denton and Karlen (1973); Solomina and Calkin (2003)
	Canada	Luckmann (1977); Smith *et al.* (1995)
		Larocque and Smith (2004)
	Patagonia	Winchester and Harrison (1994, 2000)
		Winchester *et al.* (2001)
	New Zealand	Burrows (1975); Gellatly (1982)
		Winkler (2000); Lowell *et al.* (2005)
	Kenya	Spence and Mahaney (1988)
	Peru	Rodbell (1992)
	Antarctica	Sancho and Valadares (1993); Goodwin (1996)