Invited Review

LICHENOMETRIC DATING (LICHENOMETRY) AND THE BIOLOGY OF THE LICHEN GENUS *RHIZOCARPON*: CHALLENGES AND FUTURE DIRECTIONS

Richard A. Armstrong

Dept. of Vision Sciences, Aston University, Birmingham B4 7ET, United Kingdom,
E-mail: R.A.Armstrong@aston.ac.uk
ABSTRACT. Lichenometric dating (lichenometry) involves the use of lichen measurements to estimate the age of exposure of various substrata. Because of low radial growth rates [RaGR] and considerable longevity, species of the crustose lichen genus *Rhizocarpon* have been the most useful in lichenometry. The primary assumption of lichenometry is that colonization, growth, and mortality of *Rhizocarpon* are similar on surfaces of known and unknown age so that the largest thalli present on the respective faces are of comparable age. This review describes the current state of knowledge regarding the biology of *Rhizocarpon* and considers two main questions: (1) to what extent does existing knowledge support this assumption and (2) what further biological observations would be useful both to test its validity and to improve the accuracy of lichenometric dates? A review of the *Rhizocarpon* literature identified gaps in knowledge regarding early development, the growth rate/size curve, mortality, regeneration, competitive effects, colonization, and succession on rock surfaces. The data suggest that these processes may not be comparable on different rock surfaces, especially in regions where growth rates and thallus turnover are high. In addition, several variables could differ between rock surfaces and influence maximum thallus size including rate and timing of colonization, RaGR, environmental differences, thallus fusion, allelopathy, thallus mortality, colonization, and competition. Comparative measurements of these variables on surfaces of known and unknown age may help to determine whether the basic assumptions of lichenometry are valid. Ultimately, it may be possible to take these differences into account when interpreting estimated dates.

*Key Words: Lichenometry, Rhizocarpon, Development, Growth rate-size curve, Senescence, Mortality, Competition*
Introduction

Lichenometric dating (lichenometry) involves the use of lichen measurements to estimate the age of exposure of various substrata. It is a widely used method of dating the surface age of substrata and has had many applications over the last 50 years including the dating of rock surfaces, boulders, walls, and archaeological remains (Locke et al. 1979, Innes 1981, 1985, Matthews 1994, Benedict, 2009). Although opinion is divided as to the optimal time scale over which lichenometry may be effective (Miller and Andrews 1972, Gordon and Sharp 1983, Innes 1985, Noller and Locke 2000, Winchester and Chaufer 2002, Benedict 2009), the method has been especially important in dating late Holocene glacial events although the majority of the most successful studies which claim precision involve dating events over the last few centuries (Oerlemans 1994, Narama 2002, Solomina and Calkin 2003, Yi et al. 2007, McKay and Kaufman 2009, Sikorski et al. 2009, Wiles et al. 2010). Nevertheless, almost since its inception, lichenometry has had its critics and various theoretical limitations have been identified (Jochimsen 1973, Worsley 1981, McCarthy 1999), yet it has remained popular; yielding dates which are often confirmed by other methods (Solomina and Calkin 2003, Levy et al. 2004, Young et al. 2009, Dąbski and Angiel 2010). Other studies, however, have taken an even more critical view, either by highlighting the apparent inaccuracy, imprecision, and non-reproducibility of the ages derived (Curry 1969, Clark and Gillespie 1997, Kirkbride and Dugmore 2001, Jomelli et al. 2006, Bowerman and Clark 2011) or by questioning the validity of the fundamental assumptions of lichenometry (Osborn et al. 2015).

The most important ‘primary’ assumption of lichenometry is that if the age of lichen thalli can be estimated, then a minimum date can be obtained for surface exposure based on the size of either the single largest or a sample of the largest thalli present (Webber and Andrews 1973, Matthews 1974, 1975, 1977, Calkin and Ellis 1980, Innes 1984, Sikorski et al. 2009, Osborn et al. 2015). There are four potential methods of estimating the age of the largest thallus: (1) calibrating lichen size against surfaces of known age (‘indirect lichenometry’) (Locke et al. 1979, Innes 1981, 1985, Matthews 1994, Benedict 2009), (2) by establishing a lichen growth rate/size curve from direct measurement of lichen growth (‘direct lichenometry’) (Armstrong 1976, Trenbirth and Matthews 2010, Armstrong 2014), (3) using radiocarbon (C-14) dating
(Maguas and Brugnoli 1996, Clark et al. 2000, Bench et al. 2001, Garnett and Bradwell 2010), and (4) by measuring lichen ‘growth rings’ where present (Hale 1973, Hooker 1980a, Armstrong and Bradwell 2010a, 2015). Indirect lichenometry has been the most frequently used method to date, direct lichenometric studies being relatively rare (Trenbirth and Matthews 2010, Armstrong 2014), while RC dating and lichen growth rings have been little used and are still under investigation (Armstrong and Bradwell 2015). In indirect lichenometry, the primary assumption that the largest thallus is an indicator of age would only be strictly true if the timing of initial colonization and then the subsequent processes of growth, senescence, and mortality were comparable on unknown surfaces and the surfaces of known age used for calibration. An important issue therefore is the degree to which the assumptions may be correct and therefore what level of accuracy is possible using lichenometry.

Although many lichen species have been used in lichenometry, it is members of the crustose genus *Rhizocarpon* (Poelt 1988, Benedict 1988, Purvis et al. 1992, Smith et al. 2009), and especially the ‘yellow-green’ species, that have been most frequently employed (Armstrong 2011). The most common subgenus, *Rhizocarpon* Ram. Em. Th. Fr. subgen. *Rhizocarpon*, is subdivided into four sections, viz., *Superficiale*, *Alpicola*, *Viridiatrum*, and *Rhizocarpon* (Poelt, 1988). Thalli can be identified to section level fairly easily using identification criteria suggested by Benedict (1988). Hence, many studies discussed in this review refer to species identified within *Rhizocarpon* section *Rhizocarpon* (L.) DC. Identification to species level within the *Rhizocarpon* section, however, can be more difficult. Nevertheless, using broadly circumscribed criteria (Purvis et al. 1992, Smith et al. 2009), many studies identify the 'species' under investigation as *R. geographicum* (L.) DC. Given the critiques of lichenometry (Jochimsen 1973, Worsley 1981, McCarthy 1999, Osborn et al. 2015), it would appear timely to review the current state of knowledge regarding the life cycle of *Rhizocarpon* and to consider two main questions: (1) to what extent does existing knowledge support the basic assumption of lichenometry and (2) what further biological observations would be useful both to test its validity and improve the accuracy of lichenometric dates?

**Initial colonization by Rhizocarpon**
Different species exhibit various colonization-extinction dynamics (Johansson et al. 2013), and lichens are likely to exhibit long time-lags before colonization of a new surface. Nevertheless, there have been relatively few studies which have specifically estimated these time-lags. Armstrong (1981) found that two foliose and one crustose lichen species colonized permanent plots on newly-exposed slate after six years, with significantly greater colonization where small cracks were present. In addition, lag-times before colonization by Rhizocarpon species were estimated in Iceland and varied among sites with a range of 5 – 16 years (Evans and Archer 1999), the latter close to the 18 years estimated from dated gravestones in North Wales (Winchester and Chaujer 2002).

The stages in the life cycle of Rhizocarpon colonizing a rock surface are summarized in Fig. 1. Species of Rhizocarpon do not produce obvious vegetative propagules (‘diaspores’) such as thallus fragments (Armstrong 1981), isidia (Armstrong 1981), or soredia (Armstrong 1987), which propagate both the algal and fungal components of the symbiosis. Spore-producing apothecia, however, are abundant on most thalli and it is likely that new thalli initially colonize a surface as a result of ‘lichenization’, i.e., germinating fungal spores contacting suitable algal cells, in this case a green alga of the genus Trebouxia. On quartzite in the North Cascade mountains, Washington State, USA, the earliest stages of colonization by Rhizocarpon are small ‘wefts’ of black fungal hyphae, most of which do not appear to be associated with algal cells and tend to be relatively short lived (Fig. 2). Free-living Trebouxia cells, however, are often the first organisms to colonize a bare substratum and such cells can be detected before any lichen thallus has become established (Mukhtar et al. 1994). In addition, scanning electron microscope studies of rock-inhabiting algae and fungi in a region recovering from fire revealed the presence of three types of unicellular green algae, one free-living micro-fungus, and many lichen ascospores (Garty 1992). Hence, random contact between some of the fungal ‘wefts’ and early colonizing algae presumably result in the first thalli of Rhizocarpon to appear on a rock surface.

**Early development**

In the earliest stages of development, wefts of fungus are probably loosely associated with algal cells and only later is the typical integrated symbiosis actually formed (Ott
Early development has been studied in *Rhizocarpon lecanorinum* (Flörke ex Körb) Anders, a member of the section *Rhizocarpon* (Clayden 1998). The first stage is a compact granule in which fungal hyphae associate with a compatible species of *Trebouxia*. Thallus differentiation subsequently occurs resulting in the formation of a typical areola. The hypothallus or prothallus is then formed, initiated from the basal margin of the primary areola, and which grows out to form a marginal ring. Hence, the earliest clearly identifiable stage of a *Rhizocarpon* thallus on a recently exposed surface is likely to comprise a single areola surrounded by the fungal prothallus (Fig. 3).

**Growth to maturity**

A fully mature thallus of *Rhizocarpon* (Fig. 4), however small, consists of the basal prothallus together with discrete areolae largely covering its surface. The prothallus is evident between individual areolae and especially at the margin where it often extends to form a ring of variable width (1 - 2 mm) (Armstrong and Bradwell 2001). Areolae which develop on the marginal prothallus are called ‘primary’ or ‘pioneer’ areolae and are punctate or verrucose (warty) in shape (Armstrong 2013). By contrast, areolae in the centre of the thallus are called ‘mature’ or 'secondary' areolae and have a more complex morphology, often being described as angular or lobed (Armstrong 2013). Within each areola, there is a cortical layer 10 - 80 μm in depth, an algal layer, and fungal medullary tissue (Armstrong and Bradwell 2010b).

After initial thallus establishment, primary areolae continue to develop on the marginal prothallus as it advances (Asta and Letrouit-Galinou 1995). A number of processes may be involved in the formation of new areolae. First, in the crustose genus *Pertusaria* DC., a lichen with a similar growth form to *Rhizocarpon*, algal cells originating in the central areolae may be ‘pushed’ towards the thallus margin. Hence, the thallus a few millimetres from the edge is composed of radially elongated hyphae and a few algal cells could then be pushed forwards into this region by specialised hyphae (Nienberg 1926). Second, *Trebouxia* form zoospores that could swim from the central areolae and colonize the prothallus (Slocum et al. 1980). Third, zoospores from neighbouring thalli may colonize the prothallus. Fourth, the marginal prothallus
could trap free-living algal cells on the surface as it gradually extends. In experiments carried out by Armstrong and Smith (1987), new areolae developed on isolated prothalli over three years at a similar rate whether or not the mature areolae in the centre were completely removed or separated from the margin by a 2 mm or 5 mm wide gap. Hence, central areolae may not be involved in the formation of primary areolae and it is likely that areolae at the margin develop from free-living algal cells ‘trapped’ by the prothallus as it advances (Hill 1981). By contrast, new areolae forming in gaps in the centre of the thallus are more likely to develop from zoospores originating from pre-existing areolae (Slocum et al. 1980, Armstrong and Bradwell 2010b, Armstrong, 2013).

Radial growth rate [RaGR]

There are considerable variations in reported lichen growth rates which reflect not only real differences among sites and regions but also the different methods of measuring growth and the time-span over which measurements are made. Different methods have been employed to measure lichen growth in the field depending on growth form and substratum type. Hence, the foliose and crustose lichens, which are largely used in lichenometry, exhibit a flat dorsi-ventral thallus and similar methods can be used to measure their growth (Armstrong and Bradwell 2011). The most accurate current techniques enable measurements of foliose lichen growth to be made over relatively short time intervals such as weeks and months (Hale 1973). This involves measuring the advance of the thallus perimeter, either the tip of a lobe in foliose species or the edge of the hypothallus in many crustose species, with reference to fixed markers on the rock. Digital photography (Hooker 1980a, Proctor 1983) and an image analysis system (Image-J) (Armstrong 2013) can then be used to measure growth increments. Measurements can be made over various time scales, viz., one month for faster-growing foliose (Armstrong and Bradwell 2011) and three months for slower-growing crustose species (Armstrong and Bradwell 2010b). Many studies have employed an absolute measure of growth such as radial growth, diameter growth, area growth (Roof and Werner 2011), or dry weight gain. The most popular measure in many studies of foliose lichens has been RaGR (e.g., mm yr$^{-1}$). A limitation of RaGR, however, is that it is strongly correlated with thallus size and exhibits a high degree of variability both within and between thalli (Armstrong 2014).
As a consequence, measurement of relative growth rate has been used to compensate for these variations in size, growth being scaled to an existing thallus measure such as increase in area per unit of area in unit time (mm$^2$ mm$^{-2}$, time$^{-1}$) (Armstrong 1973, 1976).

Following initial colonization, there is a long period of radial growth resulting in the formation of a fully mature thallus. A plot showing the approximate location of various growth studies carried out in the Northern Hemisphere, with the range of RaGR recorded at each site, is shown in Fig 5. The slowest radial growth rates [RaGR] of *Rhizocarpon* have been reported from high latitudes and elevations and especially in dry, continental Arctic and Alpine environments (Beschel 1958, 1961, Denton and Karlen 1973, Ten Brink 1973). Of these, possibly the slowest RaGR yet recorded by direct measurement is by Benedict (2008) in a study of *Rhizocarpon superficiale* (Schaer.) Vain. carried out over 16 years at high elevation from the Front Range in Colorado, USA, an overall average RaGR of 0.006 mm yr$^{-1}$ being reported. Most studies of crustose lichens in these environments have confirmed that RaGR is very slow. Hence, in a 6-year study in the Cascade Mountains of Washington State, USA, an average RaGR of 0.1 mm yr$^{-1}$ was obtained for thalli of *R. geographicum* (Armstrong 2005a). Hooker (1980b) studied 63 thalli of *R. geographicum* in South Orkney Island and found no measurable growth over three years. Nevertheless, small amounts of growth were recorded during the next three-year period of approximately 0.1 mm yr$^{-1}$. Higher RaGR of *Rhizocarpon*, however, were recorded by Rogerson *et al.* (1986) in Northern Labrador [0.17 mm yr$^{-1}$], and by Haworth *et al.* (1986) in the Central Brooks Range, Alaska [0 - 0.18 mm yr$^{-1}$]. Significantly higher growth rates have also been recorded from the Southern Hemisphere, most notably some maritime regions of the Antarctic. On Livingston Island, for example, RaGR of 0.25 mm yr$^{-1}$ has been reported (Sancho and Pinta 2004) and similar high growth rates in Tierra del Fuego (Sancho *et al.* 2011).

In lower latitudes, studies have reported significantly greater RaGR. McCarthy (2003), for example, reported RaGR for *R. geographicum* in British Columbia of 0.26 - 0.42 mm yr$^{-1}$. Higher rates of growth have also been reported from Mount Monadnock, New Hampshire [0.4 mm yr$^{-1}$] (Hausman 1948), Southern Norway [0.18 – 0.44 yr$^{-1}$] (Trenbirth and Matthews 2010), from Iceland [0.09 – 0.37 mm yr$^{-1}$]
Sites in Europe and especially in the UK report some of the highest recorded RaGR for *R. geographicum*. Hence, Bradwell (2010) measured thalli in a maritime subpolar environment in Scotland. In thalli greater than 10 mm in diameter, growth rates were 0.67 mm yr$^{-1}$ while thalli less than 10 mm had growth rates of 0.29 mm yr$^{-1}$.

Winchester and Chaujar (2002) studied the growth of *R. geographicum* spp. *prospectans* on gravestones in North Wales and estimated RaGR to be 0.74 mm yr$^{-1}$. Comparable results have been reported in the studies of Topham (1976) (0.5 mm yr$^{-1}$) and Armstrong (1983, 2005b) in North Wales in which RaGR was in the range 0.03 – 0.94 mm yr$^{-1}$, depending on thallus size. Nevertheless, not all studies in Wales have reported high growth rates, e.g., Hawksworth and Chater (1979) (0 – 0.20, mm yr$^{-1}$).

**Growth rate/size curve**

It has not been possible to study the growth of any single thallus of *Rhizocarpon* over more than a very small part of its life cycle. Hence, a ‘cross-sectional’ method has been used, i.e., RaGR is measured at a single interval of time over a range of thallus size to represent increasing age, a direct correlation between thallus size and age being assumed, the result being a ‘growth rate/size curve’. Such a growth curve may not reflect the growth of any single individual throughout its life. In addition, variation in RaGR can be considerable and obscure changes attributable to size so that only large changes in growth may be detected (Armstrong 2014). In addition, such studies are often carried out over relatively short time intervals (usually 1 – 3 years) and therefore, ignore potential long-term effects of climate on growth rate, a major limitation of direct lichenometry (Armstrong and Bradwell 2010b, Armstrong 2014).

In many lichen growth studies, variability in RaGR, slow growth rates, and small sample sizes have made it difficult to establish the shape of the growth rate/size curve of *Rhizocarpon* (Proctor 1983, Haworth *et al.* 1986, Matthews 1994, McCarthy 2003, Armstrong 2005a). The growth rate/size curve of faster-growing foliose lichen species, i.e., those which possess marginal ‘leaf-like’ lobes, is well documented and is asymptotic in shape (Aplin and Hill 1979, Childress and Keller 1980, Armstrong and

Early studies of growth rate/size curves of crustose species often assumed that they were asymptotic. Hence, the placodioid lichen Buellia (Diploicia) canescens (Dicks.) DNot., which comprises a crustose centre but a lobed margin, does exhibit an essentially asymptotic growth curve (Proctor 1977). Similarly, on glacial moraines in Switzerland, the Rhizocarpon growth curve appeared asymptotic and similar to that of B. canescens (Proctor 1977) but this study did not include thalli larger than 36 mm in diameter. Hence, although there is evidence that the growth rate/size curves of placodioid and foliose species are similar (Hill 1981, Benedict 2008), this may not be the case in Rhizocarpon (Innes 1985).

In other studies of Rhizocarpon growth (Bradwell and Armstrong 2007), between-thallus variability was often too great to establish the shape of the growth rate/size curve with any certainty. Hence, Hooker (1980b) was unable to demonstrate any significant effect of thallus size on RaGR in South Orkney while the studies of Rogerson et al. (1986) in northern Labrador shed little light on the relationship between growth and size. Similar conclusions were reported by Matthews (1994), Winchester and Chaujar (2002), Sancho and Pintado (2004), and Armstrong (2005a).

In corticolous lichen communities in Long Island, New York growth rates of larger crustose thalli (>40 mm diameter) were lower compared with smaller thalli (10 – 30 mm diameter) (Brodo 1965). A decline in RaGR in large thalli was also suggested in a study of R. geographicum growing at a site in North Wales, UK (Armstrong 1983) in which the growth-rate size curve was essentially parabolic (Fig. 6). More substantial evidence for declining growth rates in larger thalli was obtained from four crustose lichen species growing in North Wales (Armstrong 2005b) and R. geographicum in Iceland (Bradwell and Armstrong 2007). In all species, which included R. geographicum and R. reductum Th. Fr., RaGR increased to a maximum and then
declined in larger-diameter thalli, a second-order polynomial curve best describing data (Armstrong 2005b) (Fig. 6). Nevertheless, Roof and Werner (2011) found that radial growth increased with size while several different growth-rate size curves for *Rhizocarpon* were observed in South Norway (Trenbirth and Matthews 2010, Matthews and Trenbirth 2011). On different surfaces, annual growth rates remained relatively constant or increased with size up to a diameter of 12 cm, describing essentially a linear growth curve. Hence, the growth-rate size curve of *R. geographicum* may be quite variable, differing between sites or even at the same site in different years, with implications for the basic assumption of lichenometry.

That larger crustose thalli may grow more slowly than smaller individuals has also been suggested by growth rates derived from indirect lichenometry. Lichen growth curves obtained in early indirect studies were reviewed by Porter (1981). Prior to 1980, growth curves were described as linear (Andersen and Sollid 1971, Burrows and Orwin 1971), exponential (Mottershead and White 1972, Luckman 1977), exponential-linear (Benedict 1967, Denton and Karlen 1973), or ‘irregular’ (Curry 1969). Several later studies often suggested a declining phase of growth in larger thalli. Hence, Birkeland (1981) demonstrated at Mount Cook in New Zealand, that growth rates of *R. geographicum* decreased with time. Furthermore, Bull and Brandon (1998) studied the growth of *Rhizocarpon* subgenus *Rhizocarpon* in the Southern Alps in New Zealand observing non-linear growth. Hence, colonization was followed by exponential growth for approximately 20 years and then a phase of slower linear growth. A similar type of growth curve of *R. geographicum* provided by indirect lichenometry to that obtained by direct measurement (Armstrong 1983, 2005a) was reported by O’Neal and Schoenenberger (2003). Surfaces in the Cascade mountains, USA, originally measured by Porter (1981), were revisited and it was observed that the growth curve was curvilinear with phases of increasing, constant, and then decreasing RaGR.

A further question regarding the long-term growth of *Rhizocarpon* is whether thalli grow continuously over long periods of time or whether there are likely to be disruptions to growth attributable to environmental disturbance. Hence, Caseldine and Baker (1998) studied the size-frequency distributions of *R. geographicum* thalli at seven sites in Northern Iceland. All frequency distributions were similar with four
identifiable points of ‘disruption’ over the last 120 years, attributable largely to phases of increased lichen competition. This study also provides evidence that establishment and survival may be comparable on different rock surfaces within a region, a support for the main assumption of lichenometry.

Environmental growth effects

A major source of growth rate variation in mature lichen thalli is differential environmental effects (Armstrong 2015). Understanding these effects on lichen growth is important in lichenometry for two reasons. First, in direct lichenometry, where growth rates are measured over relatively few years compared with the overall longevity of *Rhizocarpon*, to understand how longer-term changes in climate may have affected RaGR. Second, in indirect lichenometry to understand how local changes in the environment associated with rock aspect, slope, or type of substratum may have differentially affected growth on surfaces of known and unknown age (Armstrong 2014). In addition, decadal and century scale climate change is likely to increasingly affect lichen growth rates, i.e., increasing or decreasing RaGR depending on site and therefore likely to impact indirect lichenometry (Roof and Werner 2011).

Climate

The effects of climate on *Rhizocarpon* have been studied by either measuring the growth of different species within the same region or in contrasting environments. Beschel's detailed lichenometric studies (Beschel 1958, 1961) emphasised the important role played by climate on lichen growth, the same species of *Rhizocarpon* growing considerably more slowly in Greenland than the Swiss Alps. Re-measurement of Beschel’s lichens 12 years after the original measurements (Ten Brink 1973) confirmed that growth of *R. geographicum* was more than 50% slower at sites furthest from the sea. Subsequently, indirect lichenometric studies from the Northern hemisphere have identified similar trends. Hence, Innes (1983) found a decrease in RaGR of *Rhizocarpon* section *Rhizocarpon* thalli from west to east in Scotland. John (1989) measured the size of the largest thalli of three *Rhizocarpon* (subgroup *Rhizocarpon*) species growing at a single site and found them to be significantly different, suggesting each species was responding differently to the local
In addition, Bradwell (2001a, 2001b) suggested a growth rate gradient across Iceland and Matthews (2005) found a similar phenomenon in Southern Norway, possibly reflecting reduced moisture availability associated with a diminishing maritime influence. In a further study, Trenbirth and Mathews (2010) found that variations in RaGR were correlated with winter but not summer mean temperatures but there was a less strong correlation with annual summer and winter rainfall. A substantial change in growth rate has also been observed in Antarctica from the warmer, wetter peninsula to the cold, dry central valleys, reflecting differences in annual moisture availability and temperature (Sancho et al. 2007).

The study of annual and seasonal growth fluctuations have been particularly useful in assessing the effects of climatic factors, especially on faster-growing foliose species, but there are few comparable data for crustose lichens (Armstrong 1973, 1993a). However, the RaGR of a sample of *R. geographicum* thalli was measured in situ at three-month intervals over 51 months on a southeast-facing rock surface in North Wales (Armstrong 2006). There were five periods of significant growth: July-September of 1993, 1994 and 1995, in January-March of 1996, and in April-June of 1997. In four of these periods, growth maxima coincided with a mean temperature maximum [Tmax] over a three-month period exceeding 15°C and three of the maxima also coincided with greater than 450 sunshine hours. Two of the growth maxima coincided with three-month periods of total rainfall exceeding 300 mm and one with greater than 50 rain days. There were no significant linear correlations between RaGR and the climatic variables measured, but significant non-linear relationships were detected, e.g., between RaGR and Tmax, mean temperature minimum [Tmin], total number of air and ground frosts, and number of rain days in a growth period, the relationship with Tmax being the most significant. Coxon and Kershaw (1983) studied changes in photosynthetic capacity of a related species, viz. *R. superficiale* over a single year in Canada. This species showed a broad response to temperature and a high resistance to heat stress, but there were no significant seasonal changes in photosynthetic capacity.

Aspect and slope
A number of studies have reported the effects of aspect on growth of *R. geographicum*, often an important source of local variation in lichenometric studies (Jochimsen 1973). Hence, Dąbrowski (2007) studied the size-frequency distribution of *Rhizocarpon* agg. in South-east Iceland and found different distributions on the proximal, distal, and upper sides of boulders, suggesting different growth rates. In the Brooks Range, Alaska, RaGR of *R. geographicum* at sites with high to moderate light intensities was twice that at shaded locations (Haworth *et al.* 1986). Similarly, Bradwell (2001b) observed that the largest thalli of *R. geographicum* in Iceland were found on south-facing surfaces of boulders, as previously reported (Pentecost 1979, Trenbirth and Mathews 2010) and presumably a consequence of their longer thermal operating period and higher temperatures. In the Cascade Mountains, Washington State, RaGR of *Rhizocarpon* section *Rhizocarpon* thalli on scree-slope boulders was significantly greater on east-southeast and south-southeast facets compared with north-facing facets of the boulders (Armstrong 2005a), the slope of the facet not appearing to influence growth. These studies suggest that at northern hemisphere sites, well-lit, south-facing surfaces may be optimal for the growth of *R. geographicum*. By contrast, Haeberli *et al.* (1979) found that *R. geographicum* avoided south-facing slopes in the Swiss Alps suggesting a more complex association with aspect in some areas (Armstrong 2002).

**Snowfall**

Snowfall is likely to be an important factor in many lichenometric studies and may have both positive and negative effects on growth. Under snow, thalli may exhibit normal rates of respiration but due to poor light penetration, low rates of photosynthesis and RaGR (MacFarlane and Kershaw 1980), and consequently, thalli smaller than expected (Innes 1985). Hence, thallus diameter often increases with distance from the centres of snow patches (Pitman 1973). At some sites, however, the effects of increasing moisture associated with snow patches may be advantageous and counter some of the negative influence of snow. Snow-kill effects were elegantly demonstrated by Benedict (1990a, 1990b). Lines of lichen-covered rocks were installed in two semi-permanent snow patches in the Colorado Front Range (Benedict 1990a, 1990b). All thalli of *R. geographicum* disappeared 5 to 8 years after transplanting, with an average duration of snow cover exceeding 40 to 43 weeks while
thalli of *Rhizocarpon riparium* Räsänen, survived to the end of the study and were more snow tolerant. The effect of snow on long-term lichen growth at high elevations has also been studied by measuring the size of *R. geographicum* thalli along transects which included snow-free and snow-accumulation areas (Benedict 1991). No changes in maximum thallus diameter were observed despite large differences in the duration of snow cover. These results suggest that the zoned lichen communities observed adjacent to snow patches are more likely to be attributable to episodic snow kill rather than to slow growth under seasonal cover (Benedict 1991).

**Pollution and anthropogenic factors**

Despite the reinvasion of many urban sites by lichens in the last twenty years, polluted sites still have significantly lower lichen diversity than rural sites, a testament to the powerful effect that air pollution has had on lichen growth. Samples of foliose and crustose species, the latter including *R. geographicum* were transplanted on rock fragments from north Wales to a city centre site in Birmingham UK; no measurable growth was recorded, all thalli exhibiting evidence of fragmentation within seven days of transplantation, all disappearing completely within one month (Armstrong unpublished data). In addition, Mahaney et al. (1995) observed marginal bleaching of *Rhizocarpon* thalli in Sweden and although various causal factors were discussed, acid rain was thought to be the most likely. It is also possible that depletion of stratospheric ozone, observed over the Antarctic since 1974 and the Arctic since 2005, could damage lower plants such as lichens and influence long-term trends in growth (Rozema et al. 2005).

There have been no studies which have directly investigated anthropogenic nitrogen fertilisation on the growth of *Rhizocarpon*. However, the response of *Xanthoria parietina* to variations in nitrogen was studied by Gaio-Oliveira et al. (2005). Thallus specific weight was similar in all thalli without any significant effect of added nitrogen suggesting that this species may respond more to changes in pH than to nitrogen consistent with previous data (Armstrong 1990). The relationship between nitrogen concentration and growth was also studied in *Nephroma arcticum* (L.) Torss. and *Peltigera aphthosa* (L.) Willd. (Sundberg et al. 2001). Control and nitrogen-fertilized thalli of *Nephroma arcticum* increased in area by 0.2 m^2 m^-2 and *Peltigera aphthosa*
by 0.4 m$^2$ m$^{-2}$ after 4 months growth. Slower growth in *Nephroma arcticum* was explained by lower nitrogen and chlorophyll A concentration and as a consequence, substantially lower light-energy conversion efficiency. The interaction between nitrogen availability and light exposure was also studied in *Platismatia glauca* (L.) WL Culb. & CF Culb. (Palmqvist and Dahlman 2006). Growth was significantly enhanced by nitrogen supply, variations in performance being most significantly accounted for by Chlorophyll A concentration. Hence, *Platismatia glauca* may respond to increasing nitrogen concentration by increasing growth rate and carbon assimilation capacity through encouraging the production of algal cells. Hence, studies are need on the effect of nitrogen on *R. geographicum*, generally a species of nutrient poor substrata.

**Substratum**

The physical and chemical nature of the substratum has a profound influence on the establishment, growth, and distribution of many lichens (Brodo 1973). Although it has been possible to investigate the influence of the substratum on growth of foliose lichens using transplant experiments in which thalli are removed from one surface and glued onto another (Armstrong 1993b), this has not been possible with species of *Rhizocarpon*, which cannot be separated intact from the rock. *R. geographicum*, however, does appear to be able to grow on a wide variety of siliceous and non-siliceous rocks of different textures (Innes 1985). In addition, observations suggest *R. geographicum* may exhibit faster RaGR on sandstone than gneiss (Belloni 1973) and faster on andesite compared with granodiorite (Porter 1981). By contrast, there was little variation in RaGR of *R. geographicum* on two slate rock surfaces in North Wales attributable to a lack of differences in porosity or texture of the surface (Armstrong 2014).

**Fusion, senescence and mortality**

Two further life-cycle processes may have implications for lichenometry. First, as individual thalli grow to maturity, they may fuse together to form larger individuals. Hence, in North Wales, *R. geographicum* forms mosaics of sharply delimited individual thalli (Fig 7) while *R. lecanorinum* thalli may merge with one another...
leaving no visible trace of their initial boundaries (Clayden 1997). In *R. geographicum*, it is possible that there is somatic incompatibility between genotypes, whereas in *R. lecanorinum*, somatic compatibility exists but only between genetically identical or closely-related thalli (Clayden 1997). In addition, thalli of different species may fuse to form a lichen mosaic, a feature of many communities dominated by crustose species, growth often ceasing at points of contact (Hawksworth and Chater 1979, Pentecost 1980). A lichenometric consequence of the formation of mosaics is that growth will be severely restricted so that thalli may not achieve a size commensurate with their anticipated RaGR.

Second, lichen thalli increase in thickness with age, the thalli blistering as they grow, with dead algal cells accumulating in the cortex beneath the living algal zone (Hill 1981). Degeneration and flaking off of the centres of old *R. geographicum* thalli may be the final stage of senescence, the space or ‘windows’ in the centres of thalli becoming potential surfaces for colonization (Armstrong and Smith 1997). By contrast, in central Sweden, both small and large thalli of *Rhizocarpon* section *Rhizocarpon* exhibited damage to the thallus margin rather than the centre, acid rain probably being the cause (Mahaney *et al.*. 1995). These processes result in a further challenge to the main assumption of lichenometry, i.e., that the initial colonizers may not have survived to the present. Hence, the initial colonizers may have disintegrated and it is their surviving fragments that have grown to maturity and are present on rock surfaces (Armstrong 1979), a phenomenon frequently observed in foliose lichen species (Honnegar 1996, Honnegar *et al.*. 1996), but also present in *R. geographicum* (Armstrong 2011) (Fig. 8).

Understanding the processes of senescence and mortality is the study of ‘population dynamics’, and has rarely been carried out in lichens. However, size frequency distributions of lichen thalli were used by Loso and Doak (2006) to fit demographic models to lichen populations, *R. geographicum* being shown to exhibit substantial mortality of 2 – 3% per year. It was suggested that the results could explain the ‘contradiction’ between lichenometry and lichen biology, i.e., the period of ‘great growth’ could be explained by mortality which ensures that early colonists are rarely found on the oldest surfaces. The size frequency distributions were then used to date the terminal moraines of an Alaskan glacier (Loso *et al.* 2014). A sign of senescence is
fragmentation of the thallus centre, a process which gradually spreads to affect the perimeter (Armstrong and Smith 1997). Hence, McCarthy (1989) observed in several lichens, including the crustose species *Ochrolechia parea* (L.) Massal., that all thalli with evidence of central fragmentation completely disappeared from a surface after 26 months. In addition, in a study of foliose lichens in North Wales, the percentage of fragmenting thalli present increased with thallus size, the size class at which 50% and 100% of thalli had fragmenting centres varying significantly among populations within the same area (Armstrong and Smith 1997). Hence, the size-frequency distribution of senescent thalli could be used as an indicator of the pattern of mortality in a population. Examples of ‘survival curves’ for two contrasting populations of *R. geographicum* growing in North Wales, based on the size-frequency distribution of fragmenting thalli and calculated using the Kaplan-Meier product limit estimator, are shown in Fig. 9. In population A, 75% of thalli ≤ 3.0 cm were fragmenting and estimated maximum thallus diameter in the population at the time of sampling was 4.5 cm while in population B, 75% of thalli ≤ 4.25 cm were fragmenting and maximum diameter was 7.5 cm. These data suggest that at sites in north Wales where growth rates are high, there is significant mortality of thalli and the probability that an individual thallus will survive to achieve a larger size quite low. Hence, in such environments, it is more likely that a rock surface will not have its original colonizers and therefore, a surface could be much older than the lichens it supports, with considerable implications for indirect lichenometry (Osborn *et al.* 2015).

**Species interactions**

**Competition**

Competition has a significant effect on the growth of *Rhizocarpon* and therefore, on potential thallus size (Armstrong and Welch 2007). As lichens colonize a surface, the margins of thalli eventually contact each other. Pentecost (1980) described various outcomes resulting from such lichen contacts: (1) one species overgrows another, (2) neither species grows at the point of contact (‘truce’ condition), and (3) one species may grow on the surface of another as an epiphyte. Considerable evidence for thallus overgrowth involving foliose species has been obtained from field observations and experiments (Armstrong and Welch 2007). Nevertheless, there is also evidence for
cessation of growth when two lichen thalli meet, especially in crustose communities, leading to a ‘truce’ condition, a process likely to contribute to the formation of lichen mosaics (Pentecost 1980).

In North Wales, a more complex relationship between the growth of *R. geographicum*, competition, and rock surface aspect was revealed (Armstrong 2002). Hence, *R. geographicum* is abundant on south-facing surfaces at this site but exhibits significantly greater RaGR on northwest-facing surfaces. The size-frequency distributions of the thalli also differed with aspect, with a higher percentage of thalli in the smallest size classes and a more restricted range of size on the northwest surfaces. In addition, the rate of mortality of the thalli was greater on northwest surfaces. It was concluded that the aspect distribution of *R. geographicum* could not be explained by differences in RaGR and that the differing competitive environments on the two surfaces was the more likely explanation. These data also imply that competitive processes in lichen populations can vary on closely adjacent surfaces which differ in aspect (Armstrong 2002).

The growth of *R. geographicum* may also be inhibited by the presence of other types of vegetation. Hence, the occurrence of the alga *Trentepohlia* Mart. on boulders can interfere with colonization by *R. geographicum* (Ellis et al. 1981). Reduced growth (Gellately 1982), and increased mortality of *R. geographicum* thalli have also been observed as a consequence of vegetation encroachment (Reger and Péwé 1969).

**Allelopathy**

Slow growing lichens, such as *Rhizocarpon*, may be potentially overgrown and out-competed by faster-growing foliose species (Armstrong and Welch 2007). Crustose species, however, are often dominant, not only on recently exposed surfaces, but also on more mature faces. In New Zealand, for example, species of *Rhizocarpon* achieve dominance on many rock surfaces and actually occur on a greater number of rocks than any other species (Orwin 1970). The abundance and widespread distribution of *Rhizocarpon* could be attributable to its high tolerance of harsh conditions but it is also possible that it may have a competitive advantage due to the production of toxic chemicals (allelopathy). It has been observed that some species of *Rhizocarpon*
appear to be surrounded by ‘zones of inhibition’ 1 – 5 cm wide (Beschel and Weideck 1973, Benedict 2009). Faster-growing foliose species that invade this space often disintegrate on the outer rim of the bare area suggesting that allelopathy may have been responsible (Beschel and Weideck 1973). The lichenometrical significance of allelopathy is that it may increase the chance that Rhizocarpon thalli can continue to grow even in relatively ‘closed’ communities (Armstrong and Welch, 2007).

Succession and colonization

Changes in species composition of lichens on a surface occur over long periods of time making it difficult to study successional processes directly either by observing newly-exposed surfaces or clearing lichen vegetation on established surfaces and studying its redevelopment (Armstrong 1974). Lichen succession has been studied by investigating surfaces of known age (Degelius 1964, Beschel 1965, Orwin 1970) or by studying a ‘zonation’ where environmental gradients have rendered a temporal succession spatially (Karenlampi 1966). Hence, there is a considerable degree of uncertainty regarding the likely sequence of succession on most surfaces and particularly the role of Rhizocarpon, often assumed to be one of the first colonizers of newly-exposed rock (Armstrong 2011). In eastern Nearctic, however, Beschel (1965) observed that R. geographicum was not the first colonizer but often replaced earlier faster-growing species. Similarly, studies suggested there may be a delay of at least 5 - 18 years before the colonization of gravestones by R. geographicum (Evans and Archer 1999, Winchester and Chaujer 2002).

Different species within the Rhizocarpon genus may colonize a surface at different rates. Hence, species in section Rhizocarpon may establish earlier than those in section Alpica. Nevertheless, R. alpicola (Anzi) Rabenh., exhibits a faster RaGR than members of the Rhizocarpon section and may ultimately become the largest lichen on a surface (Innes, 1985). In addition, colonization may occur continuously or in distinct phases. Innes (1986) studied the size-frequency distribution of thalli of R. alpicola in southwest Norway and found evidence that colonization only occurred during limited periods. In addition, colonization was restricted at the time of observation, even on relatively young surfaces. Further studies on gravestones in highland Scotland also revealed that establishment was erratic and that there was a
minimum period of exposure before colonization (Innes 1983). Erratic establishment and colonization of a foliose lichen, *viz.* *Xanthoparmelia cumberlandis* (Gyeln.) Hale, has also been observed in a Tulsa cemetery, recruitment being particularly sporadic (Golm *et al.* 1993).

On rocks in New Zealand, the number of lichen species and degree of lichen cover of the surface were positively correlated with surface age, some of the variation among resulting communities being attributable to the surface area of the rock (Orwin 1970). There was also evidence that *R. geographicum* was not present on the youngest (5 years) or oldest (40 years) surfaces, but on surfaces of intermediate age, with maximum thallus area and number of individuals being observed on approximately 30 year-old surfaces. Similar results were observed on slate rock surfaces in north Wales, UK (Armstrong 1974).

Successional processes on rock surfaces may be affected by three additional phenomena. First, there may be changes in abundance with height on vertical or near vertical surfaces (Yarranton and Green 1966, Armstrong 1974, 2014) suggesting a microclimatic gradient down the surface (Hess 1959, Harris 1971a, 1971b, Armstrong 2014). On vertically inclined tombstones and monuments, however, initial colonization may occur at the top, the lichens then spreading down the face. In addition, on near vertical slate rock surfaces in north Wales, *R. geographicum* can exhibit quite different vertical distributions at sites a short distance apart (Armstrong 1974). For example, on surface A (Fig. 10), *R. geographicum* thalli occur exclusively at the top of the face whereas on surface B, there is a peak of abundance close to the top but then a declining trend of abundance down the face. Furthermore, there may be a gradient of thallus size from top to bottom on some faces, largest thalli occurring at the top, but with little significant difference in measurable RaGR down the face (Armstrong 1978, 2014). These results support initial colonization of the upper part of the face, possibly from diaspores carried by birds, and subsequent colonization down the rock from propagules carried in surface runoff (Armstrong 1978, 1981). These observations have implications for sampling strategies in lichenometry, e.g., whether to sample the upper surfaces of boulders, thus avoiding the bases of the rocks, or to sample the crests only, the assumed initial site of colonization (Matthews 1974,
Second, on more unstable substrata, such as slate, portions of rock may flake off (Armstrong 1974, Innes 1985) resulting in a surface which is a mosaic of different ages. Hence, different successional stages could coexist on the same surface and observed variations in lichen size over a rock surface could be partly explained by this process (Armstrong 2014).

Third, there may be natural cyclic changes in abundance of lichens on rock surface which have been little studied to date. Hence, Hale (1967) observed cycles in surface cover of the foliose species 
Xanthoparmelia conspersa
(Fr. Ex Duby) Hale, with a wavelength of 20 years suggesting the population exhibited both building and declining phases. Whether such cyclic changes occur in populations of 
Rhizocarpon
remains to be established.

**What do we not know about Rhizocarpon?**

Although progress has been made in understanding the life cycle of 
Rhizocarpon
in the last thirty years (Armstrong 2011), this review has also identified many gaps in knowledge. First, the duration of the time interval between surface exposure, actual colonization, and the appearance of the first ‘detectable’ thalli is uncertain and is important in the application of direct lichenometry. There have also been few experimental studies on the early developmental stages of 
Rhizocarpon
and therefore, little information on how to recognise and identify to species the first colonizers of recently exposed surfaces.

Second, there is uncertainty regarding the shape of the growth rate/size curve of 
Rhizocarpon
over the life span which is particularly important for direct lichenometry. The growth curve is usually based on growth measurements made over short intervals of time (Trenbirth and Mathews 2010, Armstrong 2014). In addition, between-thallus variability in RaGR is often larger among similarly-sized thalli than the growth-size fluctuations themselves (Armstrong 2014). Hence, different models have been proposed for the shape of the growth-rate size curve of 
Rhizocarpon
(Bradwell and
and Armstrong 2007, Trenbirth and Matthews 2010) including those suggesting parabolic, linear, or increasing RaGR over time. It is also possible that *Rhizocarpon* exhibits different types of growth curve at different sites or even at the same site in successive years (Trenbirth and Matthews 2010), thus limiting the application of directly established lichen growth curves across different regions.

Third, as in foliose lichens (Armstrong 1973, 1993a), *Rhizocarpon* may exhibit seasonal fluctuations in growth and significant annual variations in RaGR (Armstrong 2006). These variations may correlate with specific climatic and microclimatic factors (Armstrong 2006, Trenbirth and Matthews 2010) and further studies of such relationships are needed to enable climatic variations between sites to be taken into account.

Fourth, there can be substantial mortality of young *Rhizocarpon* thalli on a rock surface (Loso and Doak 2006) resulting in relatively few survivors of the first colonists. Whether or not any of the initial colonizers actually survive to maturity will depend on the shape of the mortality curve of the population, a factor little studied in lichens. Hence, further studies of thallus senescence, mortality, and survival on a variety of surfaces are needed to improve demographic models of *Rhizocarpon* (Loso et al. 2014).

Fifth, there has been debate regarding the impact of lichen competition on the processes of colonization, growth, and mortality (Armstrong and Welch 2007). On older surfaces, increased competition can lead to overgrowth, mortality, cessation of growth, and the formation of lichen ‘mosaics’ (Armstrong and Welch 2007). Hence, Bradwell (2010) measured the growth of *R. geographicum* at two contrasting sites in Scotland, and found that more intensive competition at one site ruled out a meaningful comparison between the two. In addition, the rate of lichen growth may decline on older surfaces as a consequence of increased competition, which has implications for dating surfaces with a high lichen cover (Gellatly 1982). Increased competition may also be a factor determining increased variability of lichen sizes and lower growth rates on older surfaces. Haines-Young (1988) observed that spatial competition was a factor influencing the structure and dynamics of a lichen community within 100 years of deglaciation. Hence, in the pre-competition phase, there was a positive correlation.
between thallus size and density whereas in a closed community, further growth could only occur after a corresponding reduction in the lichen mosaic. Although experimental studies of lichen competition involving foliose species have been reported (Armstrong and Welch 2007), there have been no comparable studies involving *Rhizocarpon* or other crustose species.

Sixth, there are few data regarding how species of *Rhizocarpon* colonize a surface, at which stage of a succession, and whether there are natural cyclic changes in abundance over time (Hale 1967). Existing data are limited but suggest that species of *Rhizocarpon* may not necessarily be the first colonizers (Orwin 1970), may establish on the upper part of a face initially, subsequently spreading downwards over the remaining part of the surface (Armstrong 1978). However, Haines-Young (1983) found that the maximum thallus diameter of *Rhizocarpon* species was largest at the proximal slope of moraine ridges whereas Mahaney and Spence (1984) showed that lichen size and cover decreased downslope into depressions. Hence, studies of the vertical distribution of *Rhizocarpon* on surfaces of different age are needed to take this factor into account.

**Do the biological data support the main assumption of lichenometry?**

From its inception, lichenometry used slow-growing crustose species such as *Rhizocarpon*, and the method was applied in regions in which very low RaGR had been recorded and exceptionally large individual thalli reported. Roland Beschel was one of the first lichenometrists to investigate lichen growth in such regions. In West Greenland, for example, for the first seven decades after colonization of a rock surface, RaGR of *R. geographicum* was very slow and the largest thalli occurred on glacial moraines greater than about 1000 years of age (Beschel 1958, 1961). In addition, at Disko Island in the same region, some individuals appeared to have not increased in size since 1896, whereas the fastest growing thalli may have increased by a maximum of 1 - 4 mm in diameter. Beschel concluded from these data that some thalli of *R. geographicum* could be at least 4500 years old. Similarly, *R. alpicola* was studied at sites in the White River Valley, Skolai Pass, Southern Alaska (Denton and Karlen 1973). There was an initial rapid increase in diameter followed, after a few centuries, by a longer interval of approximately linear growth, a recorded RaGR of
3.4 mm 100 yr⁻¹ being typical. Extrapolating from these data, an individual of diameter 15.5 cm could be 3700 years old and the largest recorded *R. alpicola* thallus found in the region, viz., 480 mm in diameter, potentially 9000 years old. Hence, in regions characterized by particularly low RaGR, rock surfaces could support their initial colonizers, thus supporting a main assumption of lichenometry.

The data suggest caution, however, especially in regions of higher RaGR and where population turnover is likely to be more rapid. Studies of RaGR and the growth-rate size curve of *Rhizocarpon* reveal three potential concerns: (1) uncertainty regarding the shape and reproducibility of the growth curve (Trenbirth and Matthews 2010), (2) considerable variation in growth rates both among and within thalli at a site (Armstrong 2014), and (3) variation in RaGR between sites (Trenbirth and Matthews 2010). In addition, in environments characterised by rapid RaGR, several cycles of growth and senescence followed by regeneration may have occurred since exposure. Hence, a rock surface is unlikely to have its original colonizers and therefore could be significantly older than the lichens it supports (Osborn et al. 2015). This is not necessarily a ‘fatal challenge’ to lichenometry if the various life-cycle processes were similar on the different surfaces thus increasing the probability that they have resulted in the same outcome: a comparable maximum thallus size.

Some studies have shown similar size-frequency distributions of *Rhizocarpon* thalli on different surfaces (Caseldine and Baker 1998) supporting the assumption that population dynamics may be similar, whereas other studies have reported that there could be significant variations on different surfaces within the same region (Armstrong 2002). In addition, Griffin and Conran (1994) studied populations of corticolous lichens on *Pinus radiata* at five sites in Australia and reported significant differences in size-class frequency distributions among sites.

The study of competitive effects also has implications for lichenometry. First, increasing competition intensity could increase mortality (Armstrong and Welch 2007) thus reducing the probability that an early colonizer will survive to become the largest thallus. Second, growth may cease for long periods at points of contact, resuming only if a competitor itself fragments and disappears, thus freeing the surface for further growth. Such a thallus would therefore be smaller than expected from its
RaGR and longevity on a rock surface. If however species of *Rhizocarpon* are allelopathic, which remains to be experimentally demonstrated, then some of these potential competitive effects could be ameliorated resulting in more unconstrained growth even in a competitive environment.

**What further measurements would be helpful in lichenometry?**

The most important determiners of success in obtaining accurate dates using indirect lichenometry is the presence of surfaces of precisely known age which can be used for age control and ensuring that variations in environmental conditions are held as constant as possible. Ultimately, however, accuracy of a lichenometric date may also depend on whether the processes of colonization, development, growth, and senescence are comparable on surfaces of known and unknown age. On some closely-adjacent rock surfaces in regions characterised by very low RaGR, life cycle processes may have produced similar outcomes, which could explain some of the more ‘successful’ indirect lichenometric studies, i.e., those in which dates have been confirmed by other methods (Levy *et al.* 2004, Young *et al.* 2009, Dąbski and Angiel 2010). As conditions vary among different sites, it is only possible to assess accuracy of estimated dates using levels of reproducibility or by comparing lichenometric dates with other sources. Hence, Bickerton and Matthews (1993) studied complex-ridge sequences in front of seven outlet glaciers dated using families of lichenometric curves, established previously at an eighth site, and found good agreement with using independent historical evidence for dates. Accurate lichenometric dates can also be obtained on younger surfaces mainly because accurate control points can often be established more readily. Nevertheless, studies of lichen biology and ecology suggest considerable potential for differences in colonization, growth, senescence, and mortality even on closely-adjacent rock surfaces, especially in those communities with high RaGR (Armstrong 2002).

A number of factors can potentially influence the largest size of thallus achieved on a rock surface (Fig. 11). First, differences in RaGR between known and unknown surfaces may be attributable to a variety of factors including differences in aspect, slope, size, texture, and surface stability of the face (Armstrong 2014). A sample of directly measured growth rates could be made on the different surfaces to identify
potential differences in RaGR. This is a time consuming process as meaningful RaGR measurements would need to be made over a period of at least 3 - 5 years. Such a study may be a useful investment of time, however, if intensive studies are envisaged in a region over many years. In addition, more rapid methods of directly estimating RaGR by either utilising thallus growth rings where possible (Armstrong and Bradwell 2010, 2015) or radiocarbon (C-14) dating (Maguas and Brugnoli 1996, Clark et al. 2000, Bench et al. 2001, Garnett and Bradwell 2010) may become possible in future. Second, the size-frequency distributions of thalli, and especially of the fragmenting thalli can vary between rock surfaces and directly influence maximum thallus size achieved by determining the pattern of mortality of a population. These data can be used to construct survival curves for the populations on known and unknown surfaces thus indicating potential differences in longevity (Armstrong and Smith 1997). Moreover, Loso et al (2014) demonstrated how lichen population studies involving measurement and statistical analysis of several thousand thalli growing on surfaces of similar age can greatly increase understanding of crustose lichen growth history, mortality, and longevity and thus expand the opportunities for surface dating. Third, the presence of competition (Armstrong and Welch 2007), lichen mosaics, and thallus fusion (Hawksworth and Chater 1979, Pentecost 1980, Clayden 1997) can have considerable potential to restrict thallus growth and ultimately, maximum thallus size. However, evidence of bare areas or ‘zones of exclusion’ around Rhizocarpon thalli (Beschel and Weideck 1973, Benedict 2009), which could indicate allelopathy, suggest that unrestricted growth may still be possible even on surfaces with considerable lichen cover. However, how frequently such zones of exclusion actually occur in crustose lichen communities is open to question and may be so rare as to not have a significant effect on dating. Fourth, on vertical or near vertical surfaces, colonization by Rhizocarpon may have occurred from the top down and therefore, vertical location could indicate differences in the timing of colonization on different surfaces and therefore, where the largest thallus is likely to be located (Armstrong 1974).

Study of these variables, first on surfaces of known age and subsequently, on unknown surfaces in a region may help to determine whether there are significant differences among surfaces. The greater the discrepancy of these measurements between surfaces of known and unknown age, the less reliable an estimated date.
Ultimately, it may be possible to take these differences into account when interpreting estimated dates.

In conclusion, lichenometry has been regarded as a simple, rapid, and successful method of dating substrata. Nevertheless, if the many criticisms of lichenometry are to be addressed, and especially those by Osborn et al. (2015), further research regarding establishment, growth, and population dynamics of the Rhizocarpon genus and other lichens may be needed. Ultimately, comparing life cycle differences on surfaces of known and unknown age may enable the complex combination of factors which influence thallus size to be taken into account. A major future challenge for lichenometry is whether these variables can be successfully modelled to improve the accuracy of estimated dates.

Corresponding Author: R.A. Armstrong, Vision Sciences, Aston University, Birmingham, B4 7ET, UK (Tel: 0121-359-3611; Fax: 0121-333-4220; Email: R.A.Armstrong@aston.ac.uk)

References


Figure 1. Stages in the life cycle of *Rhizocarpon* colonizing a rock surface.
Figure 2. Fungal ‘wefts’ (arrows), the earliest identifiable stages of colonization by the yellow-green lichen *Rhizocarpon geographicum* (L.) DC. growing on quartzite in the Cascade Mountains, Pacific northwest, USA, bar = 2mm.
Figure 3. Early stage in the development of *Rhizocarpon geographicum* (L.) DC. thalli growing on quartzite in the Cascade Mountains, Pacific northwest, USA comprising a single areole surrounded by prothallus (arrow), bar = 2 mm.
Figure 4. A mature thallus of *Rhizocarpon geographicum* (L.) DC. growing on quartzite in the Cascade Mountains, Pacific northwest, USA; Arrow indicates a marginal (‘pioneer’) areola, bar = 1 mm.
Figure 5. Approximate longitude and latitude of sites in the northern hemisphere where direct measurements of the growth of *Rhizocarpon geographicum* (L.) DC thalli have been made. Data opposite each point represent annual radial growth rates (RaGR) and where available, their range. (Symbols: * Corrected from diameter growth rates, ? = unclear whether diameter growth rate or RaGR measured)
Figure 6. Growth curve of the lichen *Rhizocarpon geographicum* (L.) DC. by direct measurement: a plot of radial growth rate [RaGR] versus thallus diameter on rock surfaces in north Wales. Three phases of growth were identified: (1) an early growth phase in which RaGR increased to a maximum, (2) a short phase in thalli 30 – 40 mm in diameter at which RaGR was maximal, and (3) a phase in which RaGR declined in thalli greater than approximately 50 mm in diameter (data from Armstrong 2012) (Data from Armstrong 2005b).
Figure 7. Fusion of adjacent thalli (arrows) of the lichen *Rhizocarpon geographicum* (L.) DC. growing in north Wales with bands of prothalli marking the original thalli, bar = 5 mm.
Figure 8. An older thallus of *Rhizocarpon geographicum* with degenerating centre. Arrows indicate surviving fragments which may develop into new individuals, bar = 10 mm.
Figure 9. Survival curves of two *Rhizocarpon geographicum* populations (A,B) growing on slate rock surfaces in north Wales, based on the Kaplan-Meier estimator (R.A. Armstrong, unpublished data).
Figure 10. Changes in the abundance (% cover) of the lichen *Rhizocarpon geographicum* (L.) DC. with vertical distance down the face on two southeast-facing rock surfaces (A,B), 50 m apart, in north Wales, UK. (R.A. Armstrong, unpublished data).
Figure 11. Variables influencing the size of largest thallus achieved on a rock surface (RaGR = Radial growth rate).