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4   **LICHENOMETRIC DATING (LICHENOMETRY) AND THE BIOLOGY OF**

5   **THE LICHEN GENUS *RHIZOCARPON*: CHALLENGES AND FUTURE**

6   **DIRECTIONS**

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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 Chaujer 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 lichenomety, 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*

109   Different species exhibit various colonization-extinction dynamics (Johansson et al

110   2013), and lichens are likely to exhibit long time-lags before colonization of a new

111   surface. Nevertheless, there have been relatively few studies which have specifically

112   estimated these time-lags. Armstrong (1981) found that two foliose and one crustose

113   lichen species colonized permanent plots on newly-exposed slate after six years, with

114   significantly greater colonization where small cracks were present. In addition, lag-

115   times before colonization by *Rhizocarpon* species were estimated in Iceland and

116   varied among sites with a range of 5 − 16 years (Evans and Archer 1999), the later

117   close to the 18 years estimated from dated gravestones in North Wales (Winchester

118   and Chaujer 2002).

119

120   The stages in the life cycle of *Rhizocarpon* colonizing a rock surface are summarized

121   in Fig. 1. Species of *Rhizocarpon* do not produce obvious vegetative propagules

122   ('diaspores') such as thallus fragments (Armstrong 1981), isidia (Armstrong 1981), or

123   soredia (Armstrong 1987), which propagate both the algal and fungal components of

124   the symbiosis. Spore-producing apothecia, however, are abundant on most thalli and it

125   is likely that new thalli initially colonize a surface as a result of 'lichenization', i.e.,

126   germinating fungal spores contacting suitable algal cells, in this case a green alga of

127   the genus *Trebouxia*. On quartzite in the North Cascade mountains, Washington State,

128   USA, the earliest stages of colonization by *Rhizocarpon* are small 'wefts' of black

129   fungal hyphae, most of which do not appear to be associated with algal cells and tend

130   to be relatively short lived (Fig. 2). Free-living *Trebouxia* cells, however, are often the

131   first organisms to colonize a bare substratum and such cells can be detected before

132   any lichen thallus has become established (Mukhtar *et al*. 1994). In addition, scanning

133   electron microscope studies of rock-inhabiting algae and fungi in a region recovering

134   from fire revealed the presence of three types of unicellular green algae, one free-

135   living micro-fungus, and many lichen ascospores (Garty 1992). Hence, random

136   contact between some of the fungal 'wefts' and early colonizing algae presumably

137   result in the first thalli of *Rhizocarpon* to appear on a rock surface.

138

139   **Early development**

140

141   In the earliest stages of development, wefts of fungus are probably loosely associated

142   with algal cells and only later is the typical integrated symbiosis actually formed (Ott

143   1987). Early development has been studied in *Rhizocarpon lecanorinum* (Flörke ex

144   Körb) Anders, a member of the section *Rhizocarpon* (Clayden 1998). The first stage

145   is a compact granule in which fungal hyphae associate with a compatible species of

146   *Trebouxia*. Thallus differentiation subsequently occurs resulting in the formation of a

147   typical areola. The hypothallus or prothallus is then formed, initiated from the basal

148   margin of the primary areola, and which grows out to form a marginal ring. Hence,

149   the earliest clearly identifiable stage of a *Rhizocarpon* thallus on a recently exposed

150   surface is likely to comprise a single areola surrounded by the fungal prothallus (Fig.

151   3).

152

153   **Growth to maturity**

154

155   A fully mature thallus of *Rhizocarpon* (Fig. 4), however small, consists of the basal

156   prothallus together with discrete areolae largely covering its surface. The prothallus is

157   evident both between individual areolae and especially at the margin where it often

158   extends to form a ring of variable width (1 - 2 mm) (Armstrong and Bradwell 2001).

159   Areolae which develop on the marginal prothallus are called 'primary' or 'pioneer'

160   areolae and are punctate or verrucose (warty) in shape (Armstrong 2013). By contrast,

161   areolae in the centre of the thallus are called 'mature' or 'secondary' areolae and have

162   a more complex morphology, often being described as angular or lobed (Armstrong

163   2013). Within each areola, there is a cortical layer 10 - 80 μm in depth, an algal layer,

164   and fungal medullary tissue (Armstrong and Bradwell 2010b).

165

166   After initial thallus establishment, primary areolae continue to develop on the

167   marginal prothallus as it advances (Asta and Letrouit-Galinou 1995). A number of

168   processes may be involved in the formation of new areolae. First, in the crustose

169   genus *Pertusaria* DC., a lichen with a similar growth form to *Rhizocarpon*, algal cells

170   originating in the central areolae may be 'pushed' towards the thallus margin. Hence,

171   the thallus a few millimetres from the edge is composed of radially elongated hyphae

172   and a few algal cells could then be pushed forwards into this region by specialised

173   hyphae (Nienberg 1926). Second, *Trebouxia* form zoospores that could swim from the

174   central areolae and colonize the prothallus (Slocum *et al*. 1980). Third, zoospores

175   from neighbouring thalli may colonize the prothallus. Fourth, the marginal prothallus

176 could trap free-living algal cells on the surface as it gradually extends. In experiments

177 carried out by Armstrong and Smith (1987), new areolae developed on isolated

178 prothalli over three years at a similar rate whether or not the mature areolae in the

179 centre were completely removed or separated from the margin by a 2 mm or 5 mm

180 wide gap. Hence, central areolae may not be involved in the formation of primary

181 areolae and it is likely that areolae at the margin develop from free-living algal cells

182 'trapped' by the prothallus as it advances (Hill 1981). By contrast, new areolae

183 forming in gaps in the centre of the thallus are more likely to develop from zoospores

184 originating from pre-existing areolae (Slocum *et al*. 1980, Armstrong and Bradwell

185 2010b, Armstrong, 2013).

186

187 *Radial growth rate [RaGR]*

188

189 There are considerable variations in reported lichen growth rates which reflect not

190 only real differences among sites and regions but also the different methods of

191 measuring growth and the time-span over which measurements are made. Different

192 methods have been employed to measure lichen growth in the field depending on

193 growth form and substratum type. Hence, the foliose and crustose lichens, which are

194 largely used in lichenometry, exhibit a flat dorsi-ventral thallus and similar methods

195 can be used to measure their growth (Armstrong and Bradwell 2011). The most

196 accurate current techniques enable measurements of foliose lichen growth to be made

197 over relatively short time intervals such as weeks and months (Hale 1973). This

198 involves measuring the advance of the thallus perimeter, either the tip of a lobe in

199 foliose species or the edge of the hypothallus in many crustose species, with reference

200 to fixed markers on the rock. Digital photography (Hooker 1980a, Proctor 1983) and

201 an image analysis system (Image-J) (Armstrong 2013) can then be used to measure

202 growth increments. Measurements can be made over various time scales, viz., one

203 month for faster-growing foliose (Armstrong and Bradwell 2011) and three months

204 for slower-growing crustose species (Armstrong and Bradwell 2010b). Many studies

205 have employed an absolute measure of growth such as radial growth, diameter

206 growth, area growth (Roof and Werner 2011), or dry weight gain. The most popular

207 measure in many studies of foliose lichens has been RaGR (e.g., mm yr^{-1}). A

208 limitation of RaGR, however, is that it is strongly correlated with thallus size and

209 exhibits a high degree of variability both within and between thalli (Armstrong 2014).

210   As a consequence, measurement of relative growth rate has been used to compensate

211   for these variations in size, growth being scaled to an existing thallus measure such as

212   increase in area per unit of area in unit time (mm^2 mm^{-2}, $time^{-1}$) (Armstrong 1973,

213   1976).

214

215   Following initial colonization, there is a long period of radial growth resulting in the

216   formation of a fully mature thallus. A plot showing the approximate location of

217   various growth studies carried out in the Northern Hemisphere, with the range of

218   RaGR recorded at each site, is shown in Fig 5. The slowest radial growth rates

219   [RaGR] of *Rhizocarpon* have been reported from high latitudes and elevations and

220   especially in dry, continental Arctic and Alpine environments (Beschel 1958, 1961,

221   Denton and Karlen 1973, Ten Brink 1973). Of these, possibly the slowest RaGR yet

222   recorded by direct measurement is by Benedict (2008) in a study of *Rhizocarpon*

223   *superficiale* (Schaer.) Vain. carried out over 16 years at high elevation from the Front

224   Range in Colorado, USA, an overall average RaGR of 0.006 mm yr^{-1} being reported.

225   Most studies of crustose lichens in these environments have confirmed that RaGR is

226   very slow. Hence, in a 6-year study in the Cascade Mountains of Washington State,

227   USA, an average RaGR of 0.1 mm yr^{-1} was obtained for thalli of *R. geographicum*

228   (Armstrong 2005a). Hooker (1980b) studied 63 thalli of *R. geographicum* in South

229   Orkney Island and found no measurable growth over three years. Nevertheless, small

230   amounts of growth were recorded during the next three-year period of approximately

231   0.1 mm yr^{-1}. Higher RaGR of *Rhizocarpon*, however, were recorded by Rogerson *et*

232   *al*. (1986) in Northern Labrador [0.17 mm yr^{-1}], and by Haworth *et al*. (1986) in the

233   Central Brooks Range, Alaska [0 - 0.18 mm yr^{-1}]. Significantly higher growth rates

234   have also been recorded from the Southern Hemisphere, most notably some maritime

235   regions of the Antarctic. On Livingston Island, for example, RaGR of 0.25 mm yr^{-1}

236   has been reported (Sancho and Pintado 2004) and similar high growth rates in Tierra

237   del Fuego (Sancho *et al*. 2011).

238

239   In lower latitudes, studies have reported significantly greater RaGR. McCarthy

240   (2003), for example, reported RaGR for *R. geographicum* in British Columbia of 0.26

241   - 0.42 mm yr^{-1}. Higher rates of growth have also been reported from Mount

242   Monadnock, New Hampshire [0.4 mm yr^{-1}] (Hausman 1948), Southern Norway [0.18

243   – 0.44 yr^{-1}] (Trenbirth and Matthews 2010), from Iceland [0.09 – 0.37 mm yr^{-1}]

244   (Bradwell and Armstrong 2007), and Switzerland [maximum 0.5 mm yr^{-1}] (Proctor

245   1983).

246

247   Sites in Europe and especially in the UK report some of the highest recorded RaGR

248   for *R. geographicum*. Hence, Bradwell (2010) measured thalli in a maritime subpolar

249   environment in Scotland. In thalli greater than 10 mm in diameter, growth rates were

250   0.67 mm yr^{-1} while thalli less than 10 mm had growth rates of 0.29 mm yr^{-1}.

251   Winchester and Chaujar (2002) studied the growth of *R. geographicum* spp.

252   *prospectans* on gravestones in North Wales and estimated RaGR to be 0.74 mm yr^{-1}.

253   Comparable results have been reported in the studies of Topham (1976) (0.5 mm yr^{-1})

254   and Armstrong (1983, 2005b) in North Wales in which RaGR was in the range 0.03 –

255   0.94 mm yr^{-1}, depending on thallus size. Nevertheless, not all studies in Wales have

256   reported high growth rates, e.g., Hawksworth and Chater (1979) (0 – 0.20, mm yr^{-1}).

257

258   *Growth rate/size curve*

259

260   It has not been possible to study the growth of any single thallus of *Rhizocarpon* over

261   more than a very small part of its life cycle. Hence, a 'cross-sectional' method has

262   been used, i.e., RaGR is measured at a single interval of time over a range of thallus

263   size to represent increasing age, a direct correlation between thallus size and age

264   being assumed, the result being a 'growth rate/size curve'. Such a growth curve may

265   not reflect the growth of any single individual throughout its life. In addition,

266   variation in RaGR can be considerable and obscure changes attributable to size so that

267   only large changes in growth may be detected (Armstrong 2014). In addition, such

268   studies are often carried out over relatively short time intervals (usually 1 – 3 years)

269   and therefore, ignore potential long-term effects of climate on growth rate, a major

270   limitation of direct lichenometry (Armstrong and Bradwell 2010b, Armstrong 2014).

271

272   In many lichen growth studies, variability in RaGR, slow growth rates, and small

273   sample sizes have made it difficult to establish the shape of the growth rate/size curve

274   of *Rhizocarpon* (Proctor 1983, Haworth *et al*. 1986, Matthews 1994, McCarthy 2003,

275   Armstrong 2005a). The growth rate/size curve of faster-growing foliose lichen

276   species, i.e., those which possess marginal 'leaf-like' lobes, is well documented and is

277   asymptotic in shape (Aplin and Hill 1979, Childress and Keller 1980, Armstrong and

278   Smith 1996, Armstrong and Bradwell 2011). Hence, in foliose lichens, RaGR

279   increases in smaller thalli and becomes more constant, approaching an 'asymptotic'

280   value in larger individuals. There is usually no evidence of a declining growth phase

281   in many larger foliose thalli even during senescence characterised by fragmentation of

282   the thallus centre (Aplin and Hill 1979, Armstrong 1973, Armstrong and Smith 1996,

283   1997, Armstrong and Bradwell 2011).

284

285   Early studies of growth rate/size curves of crustose species often assumed that they

286   were asymptotic. Hence, the placodioid lichen *Buellia* (*Diploicia) canescens* (Dicks.)

287   DNot., which comprises a crustose centre but a lobed margin, does exhibit an

288   essentially asymptotic growth curve (Proctor 1977). Similarly, on glacial moraines in

289   Switzerland, the *Rhizocarpon* growth curve appeared asymptotic and similar to that of

290   *B. canescens* (Proctor 1977) but this study did not include thalli larger than 36 mm in

291   diameter. Hence, although there is evidence that the growth rate/size curves of

292   placodioid and foliose species are similar (Hill 1981, Benedict 2008), this may not be

293   the case in *Rhizocarpon* (Innes 1985).

294

295   In other studies of *Rhizocarpon* growth (Bradwell and Armstrong 2007), between-

296   thallus variability was often too great to establish the shape of the growth rate/size

297   curve with any certainty. Hence, Hooker (1980b) was unable to demonstrate any

298   significant effect of thallus size on RaGR in South Orkney while the studies of

299   Rogerson *et al*. (1986) in northern Labrador shed little light on the relationship

300   between growth and size. Similar conclusions were reported by Matthews (1994),

301   Winchester and Chaujar (2002), Sancho and Pintado (2004), and Armstrong (2005a).

302

303   In corticolous lichen communities in Long Island, New York growth rates of larger

304   crustose thalli (>40 mm diameter) were lower compared with smaller thalli (10 – 30

305   mm diameter) (Brodo 1965). A decline in RaGR in large thalli was also suggested in a

306   study of *R. geographicum* growing at a site in North Wales, UK (Armstrong 1983) in

307   which the growth-rate size curve was essentially parabolic (Fig. 6). More substantial

308   evidence for declining growth rates in larger thalli was obtained from four crustose

309   lichen species growing in North Wales (Armstrong 2005b) and *R. geographicum* in

310   Iceland (Bradwell and Armstrong 2007). In all species, which included *R.*

311   *geographicum* and *R. reductum* Th. Fr., RaGR increased to a maximum and then

312   declined in larger-diameter thalli, a second-order polynomial curve best describing

313   data (Armstrong 2005b) (Fig. 6). Nevertheless, Roof and Werner (2011) found that

314   radial growth increased with size while several different growth-rate size curves for

315   *Rhizocarpon* were observed in South Norway (Trenbirth and Matthews 2010,

316   Matthews and Trenbirth 2011). On different surfaces, annual growth rates remained

317   relatively constant or increased with size up to a diameter of 12 cm, describing

318   essentially a linear growth curve. Hence, the growth-rate size curve of *R.*

319   *geographicum* may be quite variable, differing between sites or even at the same site

320   in different years, with implications for the basic assumption of lichenometry.

321

322   That larger crustose thalli may grow more slowly than smaller individuals has also

323   been suggested by growth rates derived from indirect lichenometry. Lichen growth

324   curves obtained in early indirect studies were reviewed by Porter (1981). Prior to

325   1980, growth curves were described as linear (Andersen and Sollid 1971, Burrows

326   and Orwin 1971), exponential (Mottershead and White 1972, Luckman 1977),

327   exponential-linear (Benedict 1967, Denton and Karlen 1973), or 'irregular' (Curry

328   1969). Several later studies often suggested a declining phase of growth in larger

329   thalli. Hence, Birkeland (1981) demonstrated at Mount Cook in New Zealand, that

330   growth rates of *R. geographicum* decreased with time. Furthermore, Bull and Brandon

331   (1998) studied the growth of *Rhizocarpon* subgenus *Rhizocarpon* in the Southern

332   Alps in New Zealand observing non-linear growth. Hence, colonization was followed

333   by exponential growth for approximately 20 years and then a phase of slower linear

334   growth. A similar type of growth curve of *R. geographicum* provided by indirect

335   lichenometry to that obtained by direct measurement (Armstrong 1983, 2005a) was

336   reported by O'Neal and Schoenenberger (2003). Surfaces in the Cascade mountains,

337   USA, originally measured by Porter (1981), were revisited and it was observed that

338   the growth curve was curvilinear with phases of increasing, constant, and then

339   decreasing RaGR.

340

341   A further question regarding the long-term growth of *Rhizocarpon* is whether thalli

342   grow continuously over long periods of time or whether there are likely to be

343   disruptions to growth attributable to environmental disturbance. Hence, Caseldine and

344   Baker (1998) studied the size-frequency distributions of *R. geographicum* thalli at

345   seven sites in Northern Iceland. All frequency distributions were similar with four

346   identifiable points of 'disruption' over the last 120 years, attributable largely to phases
347   of increased lichen competition. This study also provides evidence that establishment
348   and survival may be comparable on different rock surfaces within a region, a support
349   for the main assumption of lichenometry.

350

351   **Environmental growth effects**

352

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

364

365   *Climate*

366

367   The effects of climate on *Rhizocarpon* have been studied by either measuring the
368   growth of different species within the same region or in contrasting environments.
369   Beschel's detailed lichenometric studies (Beschel 1958, 1961) emphasised the
370   important role played by climate on lichen growth, the same species of *Rhizocarpon*
371   growing considerably more slowly in Greenland than the Swiss Alps. Re-
372   measurement of Beschel's lichens 12 years after the original measurements (Ten
373   Brink 1973) confirmed that growth of *R. geographicum* was more than 50% slower at
374   sites furthest from the sea. Subsequently, indirect lichenometric studies from the
375   Northern hemisphere have identified similar trends. Hence, Innes (1983) found a
376   decrease in RaGR of *Rhizocarpon* section *Rhizocarpon* thalli from west to east in
377   Scotland. John (1989) measured the size of the largest thalli of three *Rhizocarpon*
378   (subgroup *Rhizocarpon*) species growing at a single site and found them to be
379   significantly different, suggesting each species was responding differently to the local

380 climate. In addition, Bradwell (2001a, 2001b) suggested a growth rate gradient across

381 Iceland and Matthews (2005) found a similar phenomenon in Southern Norway,

382 possibly reflecting reduced moisture availability associated with a diminishing

383 maritime influence. In a further study, Trenbirth and Mathews (2010) found that

384 variations in RaGR were correlated with winter but not summer mean temperatures

385 but there was a less strong correlation with annual summer and winter rainfall. A

386 substantial change in growth rate has also been observed in Antarctica from the

387 warmer, wetter peninsula to the cold, dry central valleys, reflecting differences in

388 annual moisture availability and temperature (Sancho *et al*. 2007).

389

390 The study of annual and seasonal growth fluctuations have been particularly useful in

391 assessing the effects of climatic factors, especially on faster-growing foliose species,

392 but there are few comparable data for crustose lichens (Armstrong 1973, 1993a).

393 However, the RaGR of a sample of *R. geographicum* thalli was measured *in situ* at

394 three-month intervals over 51 months on a southeast-facing rock surface in North

395 Wales (Armstrong 2006). There were five periods of significant growth: July-

396 September of 1993, 1994 and 1995, in January-March of 1996, and in April-June of

397 1997. In four of these periods, growth maxima coincided with a mean temperature

398 maximum [Tmax] over a three-month period exceeding 15°C and three of the maxima

399 also coincided with greater than 450 sunshine hours. Two of the growth maxima

400 coincided with three-month periods of total rainfall exceeding 300 mm and one with

401 greater than 50 rain days. There were no significant linear correlations between RaGR

402 and the climatic variables measured, but significant non-linear relationships were

403 detected, e.g., between RaGR and Tmax, mean temperature minimum [Tmin], total

404 number of air and ground frosts, and number of rain days in a growth period, the

405 relationship with Tmax being the most significant. Coxon and Kershaw (1983)

406 studied changes in photosynthetic capacity of a related species, viz. *R. superficiale*

407 over a single year in Canada. This species showed a broad response to temperature

408 and a high resistance to heat stress, but there were no significant seasonal changes in

409 photosynthetic capacity.

410

411 *Aspect and slope*

412

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

432

433 *Snowfall*

434

435 Snowfall is likely to be an important factor in many lichenometric studies and may
436 have both positive and negative effects on growth. Under snow, thalli may exhibit
437 normal rates of respiration but due to poor light penetration, low rates of
438 photosynthesis and RaGR (MacFarlane and Kershaw 1980), and consequently, thalli
439 smaller than expected (Innes 1985). Hence, thallus diameter often increases with
440 distance from the centres of snow patches (Pitman 1973). At some sites, however, the
441 effects of increasing moisture associated with snow patches may be advantageous and
442 counter some of the negative influence of snow. Snow-kill effects were elegantly
443 demonstrated by Benedict (1990a, 1990b). Lines of lichen-covered rocks were
444 installed in two semi-permanent snow patches in the Colorado Front Range (Benedict
445 1990a, 1990b). All thalli of *R. geographicum* disappeared 5 to 8 years after
446 transplanting, with an average duration of snow cover exceeding 40 to 43 weeks while

14

447 thalli of *Rhizocarpon riparium* Räsänen, survived to the end of the study and were

448 more snow tolerant. The effect of snow on long-term lichen growth at high elevations

449 has also been studied by measuring the size of *R. geographicum* thalli along transects

450 which included snow-free and snow-accumulation areas (Benedict 1991). No changes

451 in maximum thallus diameter were observed despite large differences in the duration

452 of snow cover. These results suggest that the zoned lichen communities observed

453 adjacent to snow patches are more likely to be attributable to episodic snow kill rather

454 than to slow growth under seasonal cover (Benedict 1991).

455

456 *Pollution and anthropogenic factors*

457

458 Despite the reinvasion of many urban sites by lichens in the last twenty years, polluted

459 sites still have significantly lower lichen diversity than rural sites, a testament to the

460 powerful effect that air pollution has had on lichen growth. Samples of foliose and

461 crustose species, the latter including *R. geographicum* were transplanted on rock

462 fragments from north Wales to a city centre site in Birmingham UK; no measurable

463 growth was recorded, all thalli exhibiting evidence of fragmentation within seven days

464 of transplantation, all disappearing completely within one month (Armstrong

465 unpublished data). In addition, Mahaney *et al*. (1995) observed marginal bleaching of

466 *Rhizocarpon* thalli in Sweden and although various causal factors were discussed, acid

467 rain was thought to be the most likely. It is also possible that depletion of stratospheric

468 ozone, observed over the Antarctic since 1974 and the Arctic since 2005, could

469 damage lower plants such as lichens and influence long-term trends in growth

470 (Rozema *et al* 2005).

471

472 There have been no studies which have directly investigated anthropogenic nitrogen

473 fertilisation on the growth of *Rhizocarpon*. However, the response of *Xanthoria*

474 *parietina* to variations in nitrogen was studied by Gaio-Oliveira et al. (2005). Thallus

475 specific weight was similar in all thalli without any significant effect of added nitrogen

476 suggesting that this species may respond more to changes in pH than to nitrogen

477 consistent with previous data (Armstrong 1990). The relationship between nitrogen

478 concentration and growth was also studied in *Nephroma arcticum* (L.) Torss. and

479 *Peltigera aphthosa* (L.) Willd. (Sundberg et al. 2001). Control and nitrogen-fertilized

480 thalli of *Nephroma arcticum* increased in area by 0.2 m^2 m^{-2} and *Peltigera aphthosa*

15

481 by 0.4 m^2 m^{-2} after 4 months growth. Slower growth in *Nephroma arcticum* was
482 explained by lower nitrogen and chlorophyll A concentration and as a consequence,
483 substantially lower light-energy conversion efficiency. The interaction between
484 nitrogen availability and light exposure was also studied in *Platismatia glauca* (L.)
485 WL Culb. & CF Culb. (Palmqvist and Dahlman 2006). Growth was significantly
486 enhanced by nitrogen supply, variations in performance being most significantly
487 accounted for by Chlorophyll A concentration. Hence, *Platismatia glauca* may
488 respond to increasing nitrogen concentration by increasing growth rate and carbon
489 assimilation capacity through encouraging the production of algal cells. Hence, studies
490 are need on the effect of nitrogen on *R. geographicum*, generally a species of nutrient
491 poor substrata.

492

493 *Substratum*

494

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

508

509 **Fusion, senescence and mortality**

510

511 Two further life-cycle processes may have implications for lichenometry. First, as
512 individual thalli grow to maturity, they may fuse together to form larger individuals.
513 Hence, in North Wales, *R. geographicum* forms mosaics of sharply delimited
514 individual thalli (Fig 7) while *R. lecanorinum* thalli may merge with one another

16

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

17

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 parella* (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

18

583   cessation of growth when two lichen thalli meet, especially in crustose communities,

584   leading to a 'truce' condition, a process likely to contribute to the formation of lichen

585   mosaics (Pentecost 1980).

586

587   In North Wales, a more complex relationship between the growth of *R.*

588   *geographicum*, competition, and rock surface aspect was revealed (Armstrong 2002).

589   Hence, *R. geographicum* is abundant on south-facing surfaces at this site but exhibits

590   significantly greater RaGR on northwest-facing surfaces. The size-frequency

591   distributions of the thalli also differed with aspect, with a higher percentage of thalli

592   in the smallest size classes and a more restricted range of size on the northwest

593   surfaces. In addition, the rate of mortality of the thalli was greater on northwest

594   surfaces. It was concluded that the aspect distribution of *R. geographicum* could not

595   be explained by differences in RaGR and that the differing competitive environments

596   on the two surfaces was the more likely explanation. These data also imply that

597   competitive processes in lichen populations can vary on closely adjacent surfaces

598   which differ in aspect (Armstrong 2002).

599

600   The growth of *R. geographicum* may also be inhibited by the presence of other types

601   of vegetation. Hence, the occurrence of the alga *Trentepohlia* Mart. on boulders can

602   interfere with colonization by *R. geographicum* (Ellis *et al*. 1981). Reduced growth

603   (Gellately 1982), and increased mortality of *R. geographicum* thalli have also been

604   observed as a consequence of vegetation encroachment (Reger and Péwé 1969).

605

606   *Allelopathy*

607

608   Slow growing lichens, such as *Rhizocarpon*, may be potentially overgrown and out-

609   competed by faster-growing foliose species (Armstrong and Welch 2007). Crustose

610   species, however, are often dominant, not only on recently exposed surfaces, but also

611   on more mature faces. In New Zealand, for example, species of *Rhizocarpon* achieve

612   dominance on many rock surfaces and actually occur on a greater number of rocks

613   than any other species (Orwin 1970). The abundance and widespread distribution of

614   *Rhizocarpon* could be attributable to its high tolerance of harsh conditions but it is

615   also possible that it may have a competitive advantage due to the production of toxic

616   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 *Alpicola*. 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

20

651 minimum period of exposure before colonization (Innes 1983). Erratic establishment
652 and colonization of a foliose lichen, viz. *Xanthoparmelia cumberlandisma* (Gyeln.)
653 Hale, has also been observed in a Tulsa cemetery, recruitment being particularly
654 sporadic (Golm *et al*. 1993).

655

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

664

665 Successional processes on rock surfaces may be affected by three additional
666 phenomena. First, there may be changes in abundance with height on vertical or near
667 vertical surfaces (Yarranton and Green 1966, Armstrong 1974, 2014) suggesting a
668 microclimatic gradient down the surface (Hess 1959, Harris 1971a, 1971b, Armstrong
669 2014). On vertically inclined tombstones and monuments, however, initial
670 colonization may occur at the top, the lichens then spreading down the face. In
671 addition, on near vertical slate rock surfaces in north Wales, *R. geographicum* can
672 exhibit quite different vertical distributions at sites a short distance apart (Armstrong
673 1974). For example, on surface A (Fig. 10), *R. geographicum* thalli occur exclusively
674 at the top of the face whereas on surface B, there is a peak of abundance close to the
675 top but then a declining trend of abundance down the face. Furthermore, there may be
676 a gradient of thallus size from top to bottom on some faces, largest thalli occurring at
677 the top, but with little significant difference in measurable RaGR down the face
678 (Armstrong 1978, 2014). These results support initial colonization of the upper part of
679 the face, possibly from diaspores carried by birds, and subsequent colonization down
680 the rock from propagules carried in surface runoff (Armstrong 1978, 1981). These
681 observations have implications for sampling strategies in lichenometry, e.g., whether
682 to sample the upper surfaces of boulders, thus avoiding the bases of the rocks, or to
683 sample the crests only, the assumed initial site of colonization (Matthews 1974,

684   Eriksted and Sollid 1980, Hallet and Putkonen 1994, Bradwell 2001b, Allen and

685   Smith 2007, Sikorski *et al*. 2009).

686

687   Second, on more unstable substrata, such as slate, portions of rock may flake off

688   (Armstrong 1974, Innes 1985) resulting in a surface which is a mosaic of different

689   ages. Hence, different successional stages could coexist on the same surface and

690   observed variations in lichen size over a rock surface could be partly explained by this

691   process (Armstrong 2014).

692

693   Third, there may be natural cyclic changes in abundance of lichens on rock surface

694   which have been little studied to date. Hence, Hale (1967) observed cycles in surface

695   cover of the foliose species *Xanthoparmelia conspersa* (Fr. Ex Duby) Hale, with a

696   wavelength of 20 years suggesting the population exhibited both building and

697   declining phases. Whether such cyclic changes occur in populations of *Rhizocarpon*

698   remains to be established.

699

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

701

702   Although progress has been made in understanding the life cycle of *Rhizocarpon* in

703   the last thirty years (Armstrong 2011), this review has also identified many gaps in

704   knowledge. First, the duration of the time interval between surface exposure, actual

705   colonization, and the appearance of the first 'detectable' thalli is uncertain and is

706   important in the application of direct lichenometry. There have also been few

707   experimental studies on the early developmental stages of *Rhizocarpon* and therefore,

708   little information on how to recognise and identify to species the first colonizers of

709   recently exposed surfaces.

710

711   Second, there is uncertainty regarding the shape of the growth rate/size curve of

712   *Rhizocarpon* over the life span which is particularly important for direct lichenometry.

713   The growth curve is usually based on growth measurements made over short intervals

714   of time (Trenbirth and Mathews 2010, Armstrong 2014). In addition, between-thallus

715   variability in RaGR is often larger among similarly-sized thalli than the growth-size

716   fluctuations themselves (Armstrong 2014). Hence, different models have been

717   proposed for the shape of the growth-rate size curve of *Rhizocarpon* (Bradwell and

718   Armstrong 2007, Trenbirth and Matthews 2010) including those suggesting parabolic,

719   linear, or increasing RaGR over time. It is also possible that *Rhizocarpon* exhibits

720   different types of growth curve at different sites or even at the same site in successive

721   years (Trenbirth and Matthews 2010), thus limiting the application of directly

722   established lichen growth curves across different regions.

723

724   Third, as in foliose lichens (Armstrong 1973, 1993a)*, Rhizocarpon* may exhibit

725   seasonal fluctuations in growth and significant annual variations in RaGR (Armstrong

726   2006). These variations may correlate with specific climatic and microclimatic factors

727   (Armstrong 2006, Trenbirth and Matthews 2010) and further studies of such

728   relationships are needed to enable climatic variations between sites to be taken into

729   account.

730

731   Fourth, there can be substantial mortality of young *Rhizocarpon* thalli on a rock

732   surface (Loso and Doak 2006) resulting in relatively few survivors of the first

733   colonists. Whether or not any of the initial colonizers actually survive to maturity will

734   depend on the shape of the mortality curve of the population, a factor little studied in

735   lichens. Hence, further studies of thallus senescence, mortality, and survival on a

736   variety of surfaces are needed to improve demographic models of *Rhizocarpon* (Loso

737   *et al*. 2014).

738

739   Fifth, there has been debate regarding the impact of lichen competition on the

740   processes of colonization, growth, and mortality (Armstrong and Welch 2007). On

741   older surfaces, increased competition can lead to overgrowth, mortality, cessation of

742   growth, and the formation of lichen 'mosaics' (Armstrong and Welch 2007). Hence,

743   Bradwell (2010) measured the growth of *R. geographicum* at two contrasting sites in

744   Scotland, and found that more intensive competition at one site ruled out a meaningful

745   comparison between the two. In addition, the rate of lichen growth may decline on

746   older surfaces as a consequence of increased competition, which has implications for

747   dating surfaces with a high lichen cover (Gellatly 1982). Increased competition may

748   also be a factor determining increased variability of lichen sizes and lower growth

749   rates on older surfaces. Haines-Young (1988) observed that spatial competition was a

750   factor influencing the structure and dynamics of a lichen community within 100 years

751   of deglaciation. Hence, in the pre-competition phase, there was a positive correlation

752   between thallus size and density whereas in a closed community, further growth could

753   only occur after a corresponding reduction in the lichen mosaic. Although

754   experimental studies of lichen competition involving foliose species have been

755   reported (Armstrong and Welch 2007), there have been no comparable studies

756   involving *Rhizocarpon* or other crustose species.

757

758   Sixth, there are few data regarding how species of *Rhizocarpon* colonize a surface, at

759   which stage of a succession, and whether there are natural cyclic changes in

760   abundance over time (Hale 1967). Existing data are limited but suggest that species of

761   *Rhizocarpon* may not necessarily be the first colonizers (Orwin 1970), may establish

762   on the upper part of a face initially, subsequently spreading downwards over the

763   remaining part of the surface (Armstrong 1978). However, Haines-Young (1983)

764   found that the maximum thallus diameter of *Rhizocarpon* species was largest at the

765   proximal slope of moraine ridges whereas Mahaney and Spence (1984) showed that

766   lichen size and cover decreased downslope into depressions. Hence, studies of the

767   vertical distribution of *Rhizocarpon* on surfaces of different age are needed to take

768   this factor into account.

769

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

771

772   From its inception, lichenometry used slow-growing crustose species such as

773   *Rhizocarpon*, and the method was applied in regions in which very low RaGR had

774   been recorded and exceptionally large individual thalli reported. Roland Beschel was

775   one of the first lichenometrists to investigate lichen growth in such regions. In West

776   Greenland, for example, for the first seven decades after colonization of a rock

777   surface, RaGR of *R. geographicum* was very slow and the largest thalli occurred on

778   glacial moraines greater than about 1000 years of age (Beschel 1958, 1961). In

779   addition, at Disko Island in the same region, some individuals appeared to have not

780   increased in size since 1896, whereas the fastest growing thalli may have increased by

781   a maximum of 1 - 4 mm in diameter. Beschel concluded from these data that some

782   thalli of *R. geographicum* could be at least 4500 years old. Similarly, *R. alpicola* was

783   studied at sites in the White River Valley, Skolai Pass, Southern Alaska (Denton and

784   Karlen 1973). There was an initial rapid increase in diameter followed, after a few

785   centuries, by a longer interval of approximately linear growth, a recorded RaGR of

24

786 3.4 mm 100 yr^{-1} being typical. Extrapolating from these data, an individual of

787 diameter 15.5 cm could be 3700 years old and the largest recorded *R. alpicola* thallus

788 found in the region, viz., 480 mm in diameter, potentially 9000 years old. Hence, in

789 regions characterized by particularly low RaGR, rock surfaces could support their

790 initial colonizers, thus supporting a main assumption of lichenometry.

791

792 The data suggest caution, however, especially in regions of higher RaGR and where

793 population turnover is likely to be more rapid. Studies of RaGR and the growth-rate

794 size curve of *Rhizocarpon* reveal three potential concerns: (1) uncertainty regarding

795 the shape and reproducibility of the growth curve (Trenbirth and Matthews 2010), (2)

796 considerable variation in growth rates both among and within thalli at a site

797 (Armstrong 2014), and (3) variation in RaGR between sites (Trenbirth and Matthews

798 2010). In addition, in environments characterised by rapid RaGR, several cycles of

799 growth and senescence followed by regeneration may have occurred since exposure.

800 Hence, a rock surface is unlikely to have its original colonizers and therefore could be

801 significantly older than the lichens it supports (Osborn *et al*. 2015). This is not

802 necessarily a 'fatal challenge' to lichenometry if the various life-cycle processes were

803 similar on the different surfaces thus increasing the probability that they have resulted

804 in the same outcome: a comparable maximum thallus size.

805

806 Some studies have shown similar size-frequency distributions of *Rhizocarpon* thalli

807 on different surfaces (Caseldine and Baker 1998) supporting the assumption that

808 population dynamics may be similar, whereas other studies have reported that there

809 could be significant variations on different surfaces within the same region

810 (Armstrong 2002). In addition, Griffin and Conran (1994) studied populations of

811 corticolous lichens on *Pinus radiata* at five sites in Australia and reported significant

812 differences in size-class frequency distributions among sites.

813

814 The study of competitive effects also has implications for lichenometry. First,

815 increasing competition intensity could increase mortality (Armstrong and Welch

816 2007) thus reducing the probability that an early colonizer will survive to become the

817 largest thallus. Second, growth may cease for long periods at points of contact,

818 resuming only if a competitor itself fragments and disappears, thus freeing the surface

819 for further growth. Such a thallus would therefore be smaller than expected from its

820 RaGR and longevity on a rock surface. If however species of *Rhizocarpon* are
821 allelopathic, which remains to be experimentally demonstrated, then some of these
822 potential competitive effects could be ameliorated resulting in more unconstrained
823 growth even in a competitive environment.

824

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

826

827 The most important determiners of success in obtaining accurate dates using indirect
828 lichenometry is the presence of surfaces of precisely known age which can be used for
829 age control and ensuring that variations in environmental conditions are held as
830 constant as possible. Ultimately, however, accuracy of a lichenometric date may also
831 depend on whether the processes of colonization, development, growth, and
832 senescence are comparable on surfaces of known and unknown age. On some closely-
833 adjacent rock surfaces in regions characterised by very low RaGR, life cycle
834 processes may have produced similar outcomes, which could explain some of the
835 more 'successful' indirect lichenometric studies, i.e., those in which dates have been
836 confirmed by other methods (Levy *et al*. 2004, Young *et al*. 2009, Dąbski and Angiel
837 2010). As conditions vary among different sites, it is only possible to assess accuracy
838 of estimated dates using levels of reproducibility or by comparing lichenometric dates
839 with other sources. Hence, Bickerton and Matthews (1993) studied complex-ridge
840 sequences in front of seven outlet glaciers dated using families of lichenometric
841 curves, established previously at an eighth site, and found good agreement with using
842 independent historical evidence for dates. Accurate lichenometric dates can also be
843 obtained on younger surfaces mainly because accurate control points can often be
844 established more readily. Nevertheless, studies of lichen biology and ecology suggest
845 considerable potential for differences in colonization, growth, senescence, and
846 mortality even on closely-adjacent rock surfaces, especially in those communities
847 with high RaGR (Armstrong 2002).

848

849 A number of factors can potentially influence the largest size of thallus achieved on a
850 rock surface (Fig. 11). First, differences in RaGR between known and unknown
851 surfaces may be attributable to a variety of factors including differences in aspect,
852 slope, size, texture, and surface stability of the face (Armstrong 2014). A sample of
853 directly measured growth rates could be made on the different surfaces to identify

854   potential differences in RaGR. This is a time consuming process as meaningful RaGR
855   measurements would need to be made over a period of at least 3 - 5 years. Such a
856   study may be a useful investment of time, however, if intensive studies are envisaged
857   in a region over many years. In addition, more rapid methods of directly estimating
858   RaGR by either utilising thallus growth rings where possible (Armstrong and
859   Bradwell 2010, 2015) or radiocarbon (C-14) dating (Maguas and Brugnoli 1996,
860   Clark *et al*. 2000, Bench *et al*. 2001, Garnett and Bradwell 2010) may become
861   possible in future. Second, the size-frequency distributions of thalli, and especially of
862   the fragmenting thalli can vary between rock surfaces and directly influence
863   maximum thallus size achieved by determining the pattern of mortality of a
864   population. These data can be used to construct survival curves for the populations on
865   known and unknown surfaces thus indicating potential differences in longevity
866   (Armstrong and Smith 1997). Moreover, Loso et al (2014) demonstrated how lichen
867   population studies involving measurement and statistical analysis of several thousand
868   thalli growing on surfaces of similar age can greatly increase understanding of
869   crustose lichen growth history, mortality, and longevity and thus expand the
870   opportunities for surface dating. Third, the presence of competition (Armstrong and
871   Welch 2007), lichen mosaics, and thallus fusion (Hawksworth and Chater 1979,
872   Pentecost 1980, Clayden 1997) can have considerable potential to restrict thallus
873   growth and ultimately, maximum thallus size. However, evidence of bare areas or
874   'zones of exclusion' around *Rhizocarpon* thalli (Beschel and Weideck 1973, Benedict
875   2009), which could indicate allelopathy, suggest that unrestricted growth may still be
876   possible even on surfaces with considerable lichen cover. However, how frequently
877   such zones of exclusion actually occur in crustose lichen communities is open to
878   question and may be so rare as to not have a significant effect on dating. Fourth, on
879   vertical or near vertical surfaces, colonization by *Rhizocarpon* may have occurred
880   from the top down and therefore, vertical location could indicate differences in the
881   timing of colonization on different surfaces and therefore, where the largest thallus is
882   likely to be located (Armstrong 1974).
883
884   Study of these variables, first on surfaces of known age and subsequently, on
885   unknown surfaces in a region may help to determine whether there are significant
886   differences among surfaces. The greater the discrepancy of these measurements
887   between surfaces of known and unknown age, the less reliable an estimated date.

888   Ultimately, it may be possible to take these differences into account when interpreting
889   estimated dates.

890

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

900

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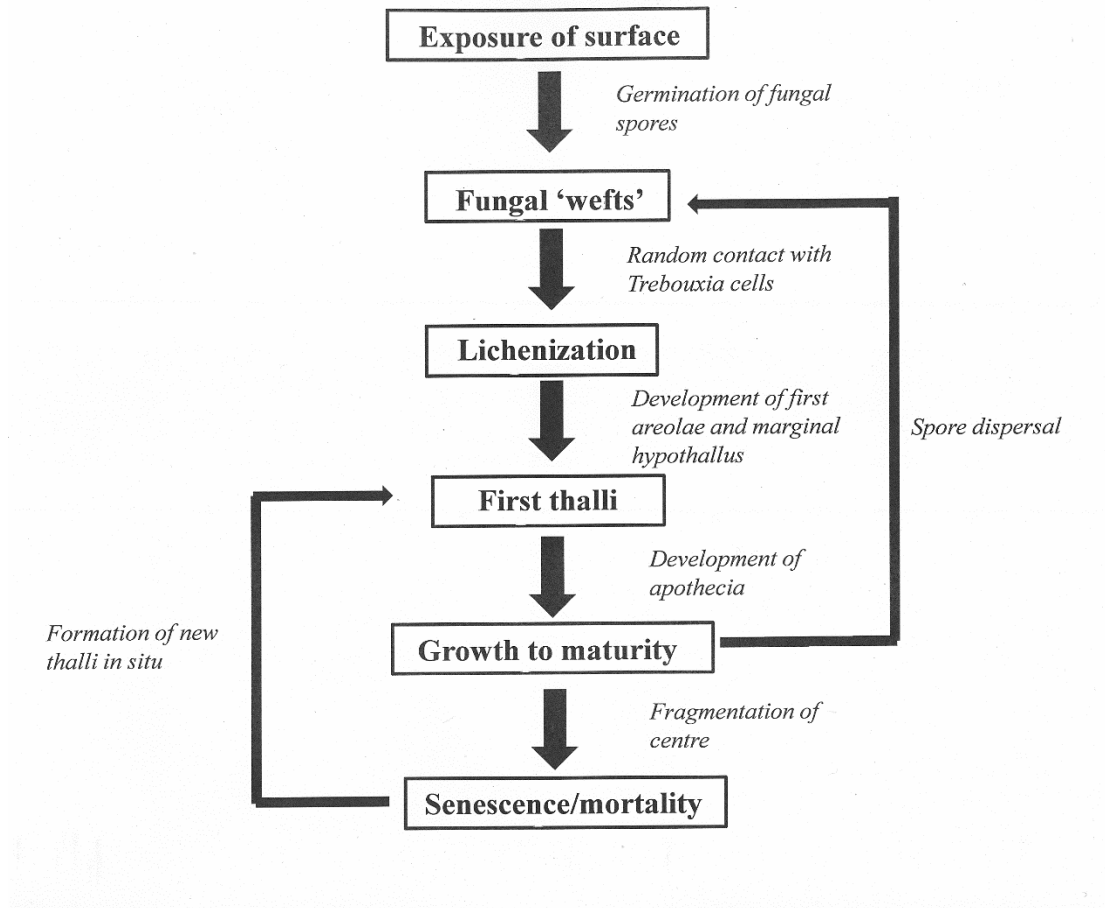1526   Revised and accepted d mmm; 20yy

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1529   **Legends to figures**

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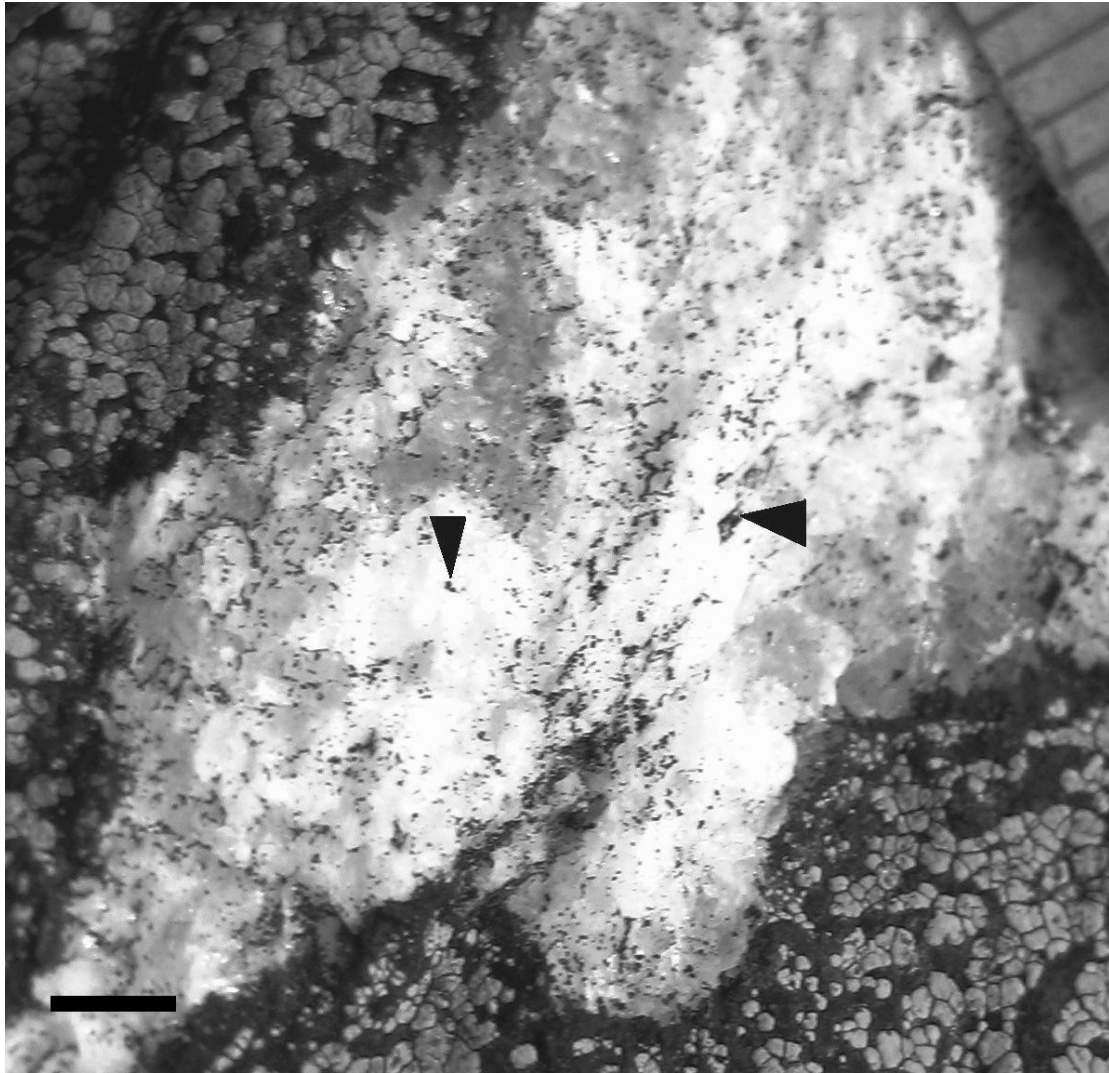1531   **Figure 1.** Stages in the life cycle of *Rhizocarpon* colonizing a rock surface.

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1535   **Figure 2.** Fungal 'wefts' (arrows), the earliest identifiable stages of colonization by

1536   the yellow-green lichen *Rhizocarpon geographicum* (L.) DC. growing on quartzite in

1537   the Cascade Mountains, Pacific northwest, USA, bar = 2mm.

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1541 **Figure 3**. Early stage in the development of *Rhizocarpon geographicum* (L.) DC.

1542 thalli growing on quartzite in the Cascade Mountains, Pacific northwest, USA

1543 comprising a single areole surrounded by prothallus (arrow), bar = 2 mm.
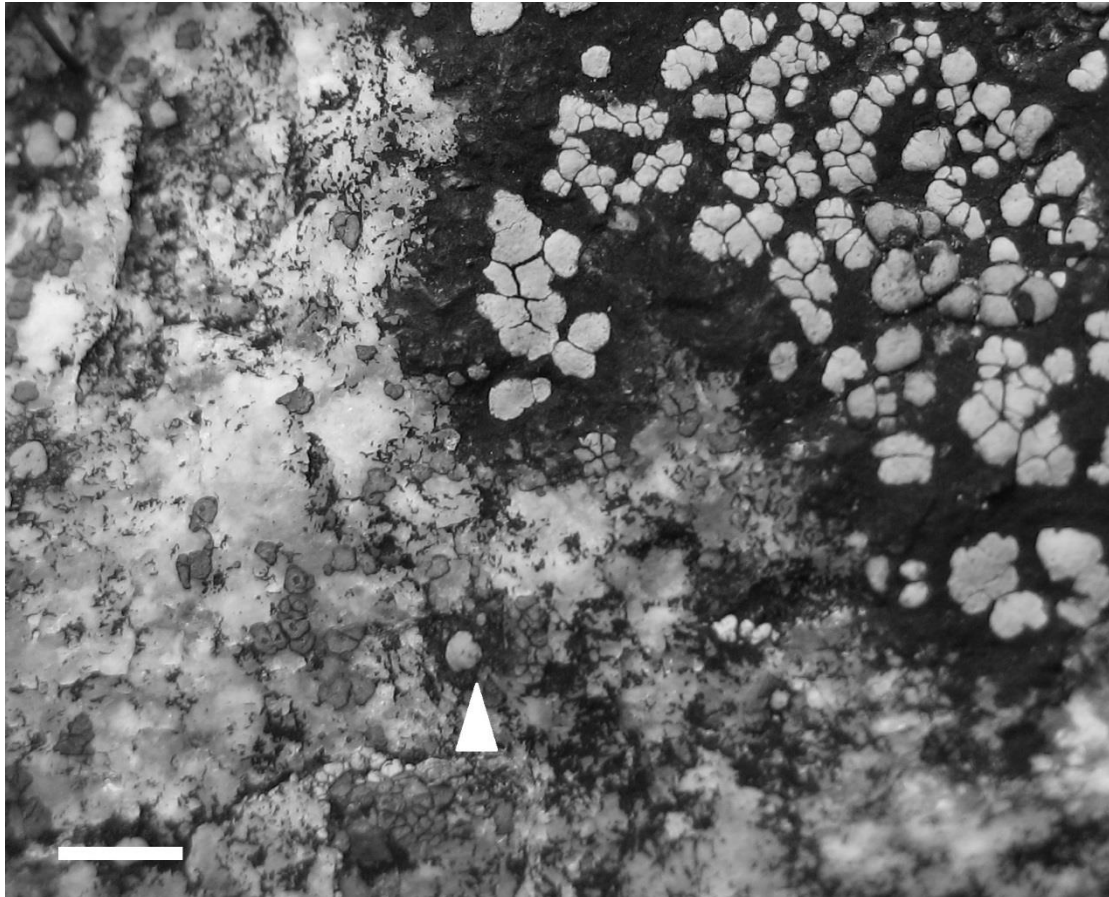
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1546   **Figure 4**. A mature thallus of *Rhizocarpon geographicum* (L.) DC. growing on

1547   quartzite in the Cascade Mountains, Pacific northwest, USA; Arrow indicates a

1548   marginal ('pioneer') areola, bar = 1 mm.
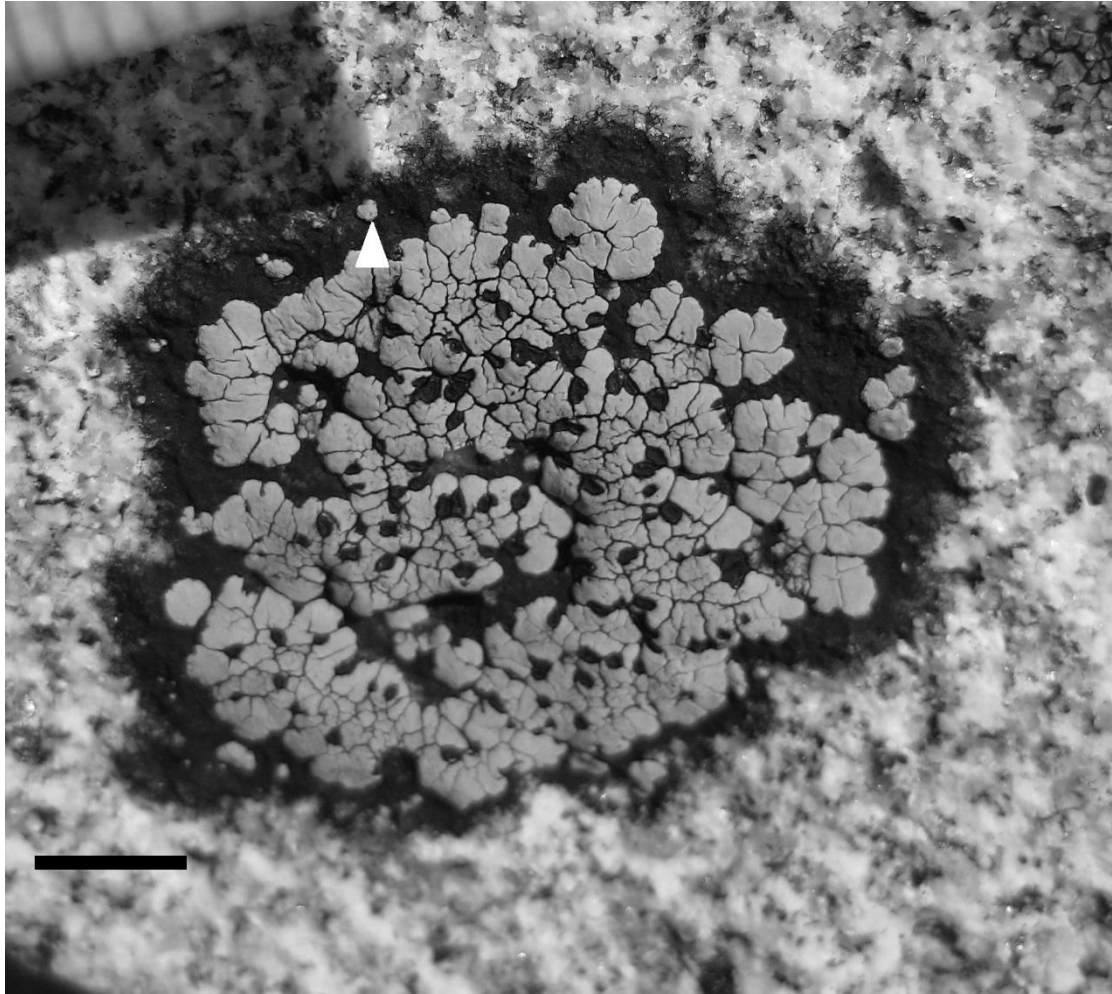
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1552   **Figure 5.** Approximate longitude and latitude of sites in the northern hemisphere
1553   where direct measurements of the growth of *Rhizocarpon geographicum* (L.) DC
1554   thalli have been made. Data opposite each point represent annual radial growth rates
1555   (RaGR) and where available, their range. (Symbols: * Corrected from diameter
1556   growth rates, ? = unclear whether diameter growth rate or RaGR measured)
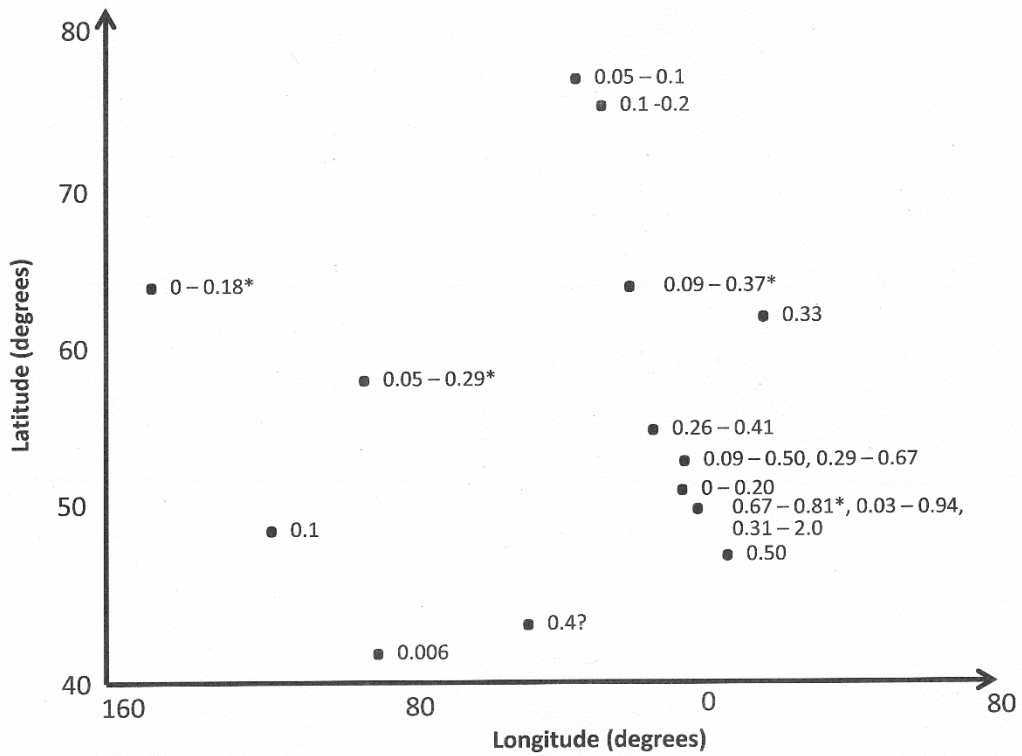
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Figure 6. Growth curve of the lichen *Rhizocarpon geographicum* (L.) DC. by direct

1559   measurement: a plot of radial growth rate [RaGR] versus thallus diameter on rock

1560   surfaces in north Wales. Three phases of growth were identified: (1) an early growth

1561   phase in which RaGR increased to a maximum, (2) a short phase in thalli 30 – 40 mm

1562   in diameter at which RaGR was maximal, and (3) a phase in which RaGR declined in

1563   thalli greater than approximately 50 mm in diameter (data from Armstrong 2012)

1564   (Data from Armstrong 2005b).
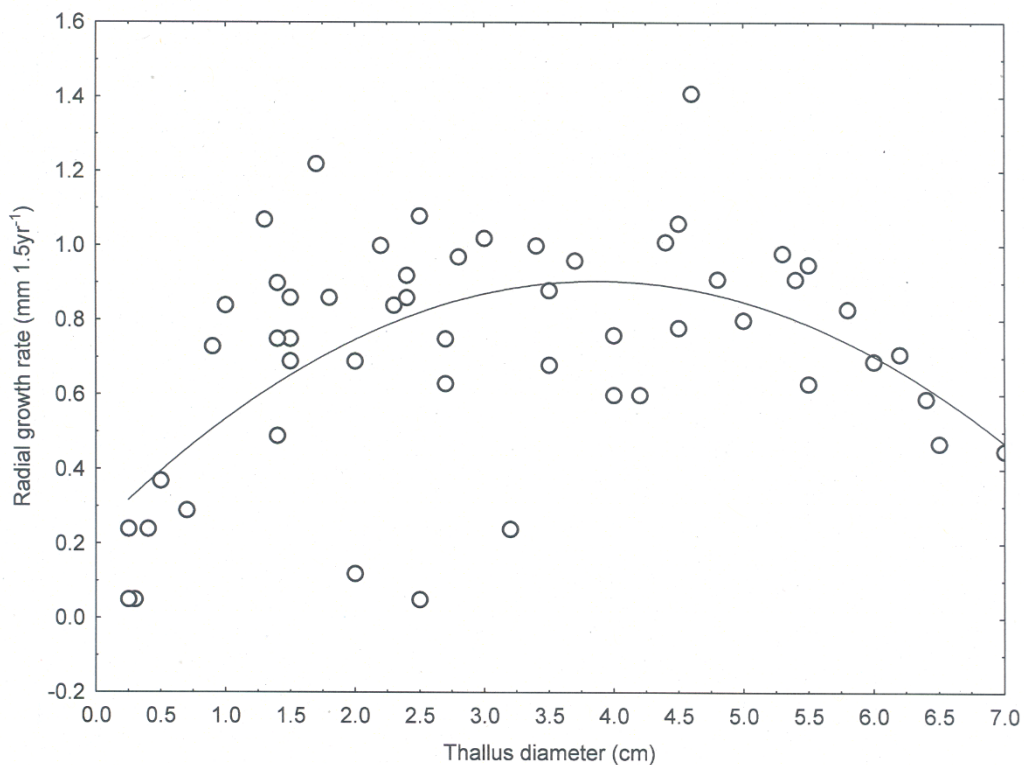
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1568   **Figure 7**. Fusion of adjacent thalli (arrows) of the lichen *Rhizocarpon geographicum*

1569   (L.) DC. growing in north Wales with bands of prothalli marking the original thalli,
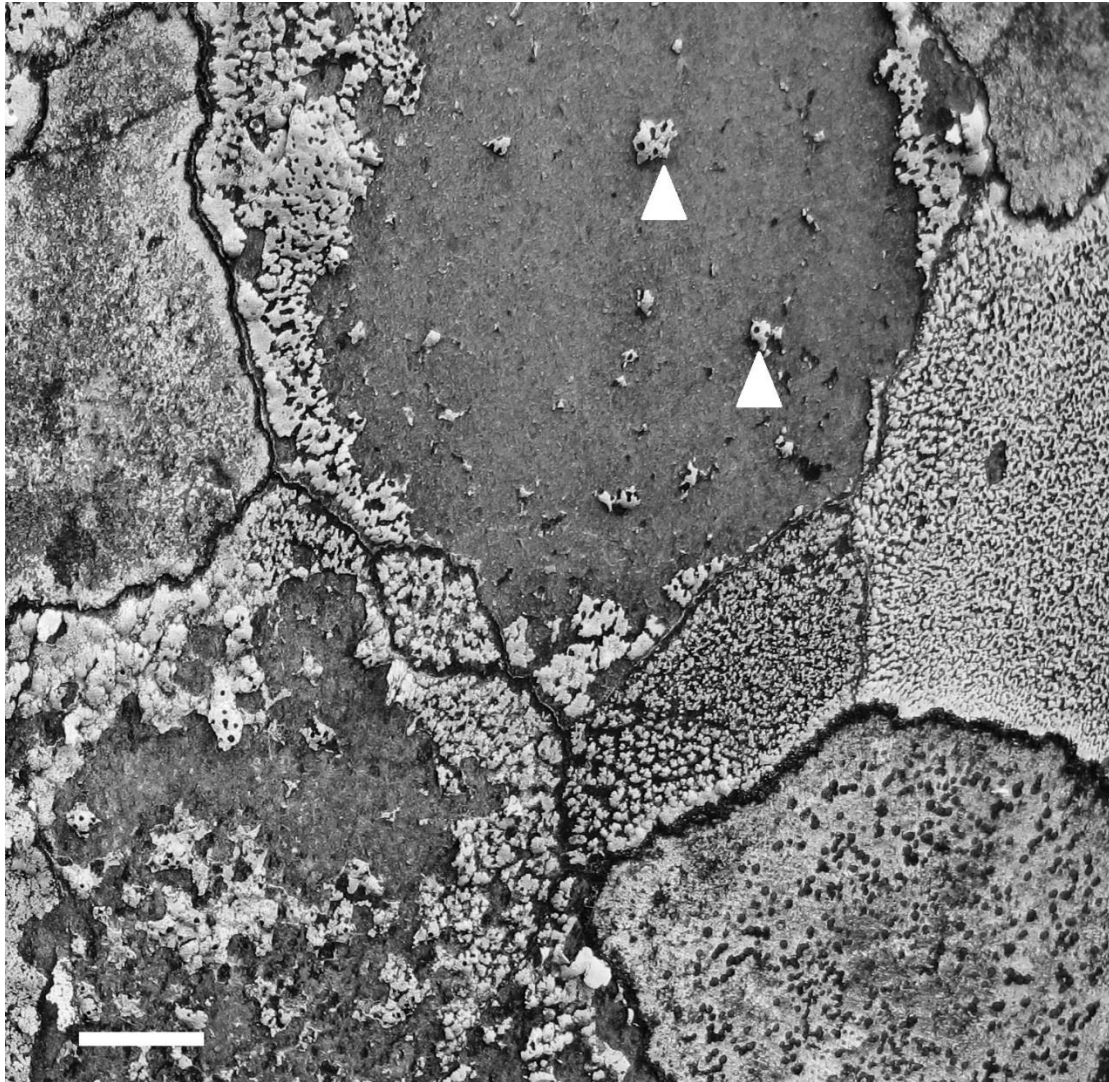
1570   bar = 5 mm.
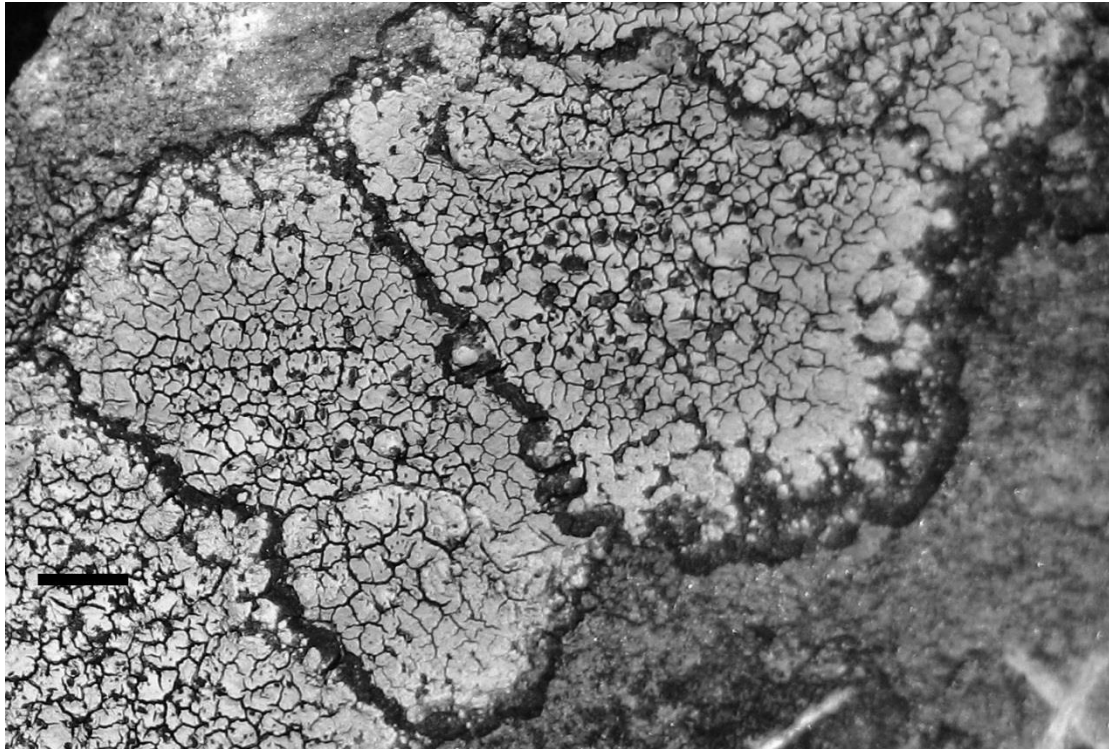
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1574   **Figure 8.** An older thallus of *Rhizocarpon geographicum* with degenerating centre.

1575   Arrows indicate surviving fragments which may develop into new individuals, bar =
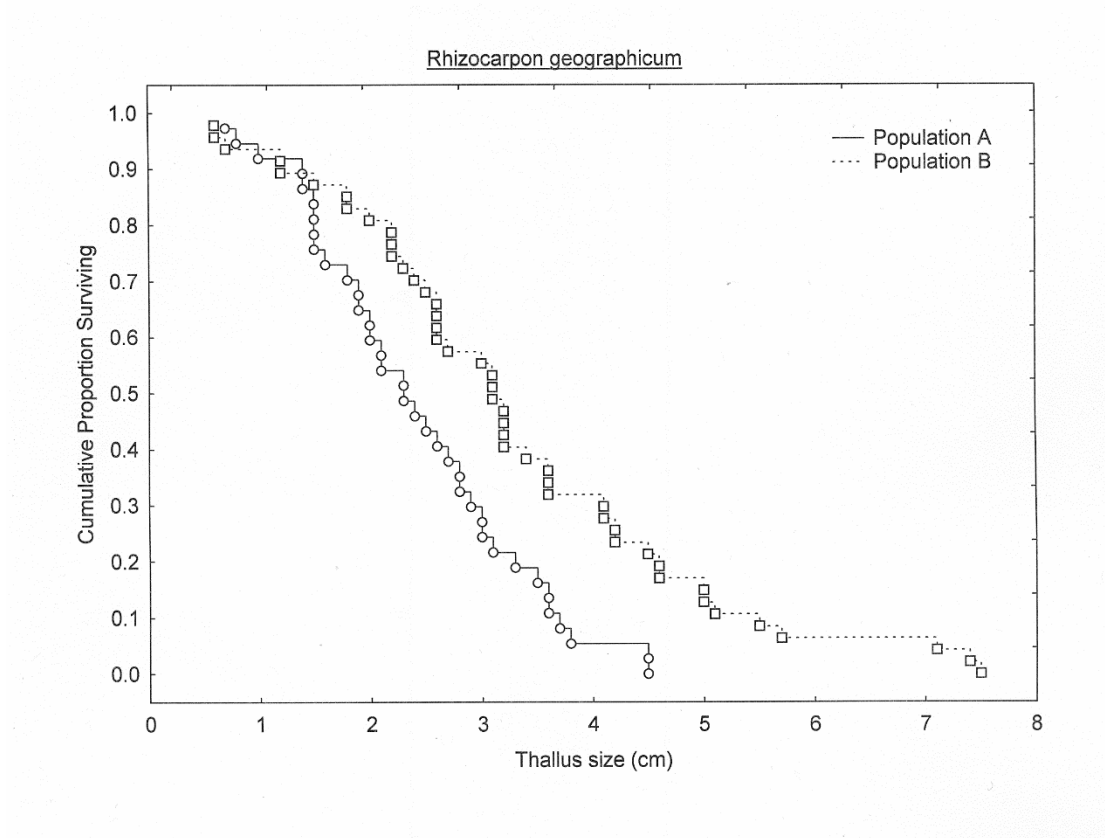
1576   10 mm.

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1580   **Figure 9.** Survival curves of two *Rhizocarpon geographicum* populations (A,B)

1581   growing on slate rock surfaces in north Wales, based on the Kaplan-Meier estimator

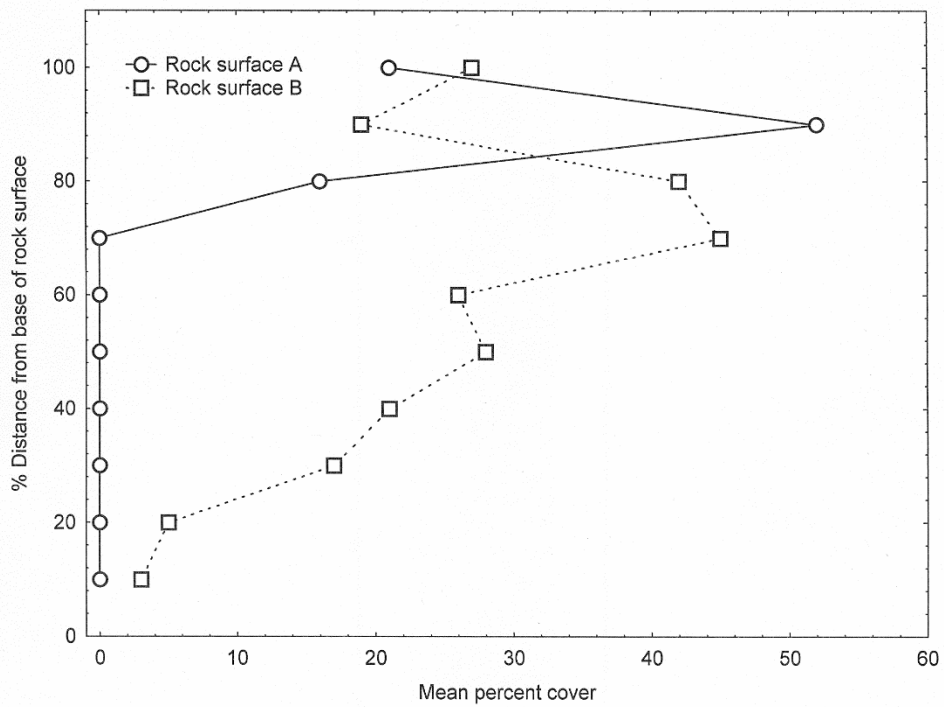1582   (R.A. Armstrong, unpublished data).

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1586   **Figure 10.** Changes in the abundance (% cover) of the lichen *Rhizocarpon*

1587   *geographicum* (L.) DC. with vertical distance down the face on two southeast-facing

1588   rock surfaces (A,B), 50 m apart, in north Wales, UK. (R.A. Armstrong, unpublished
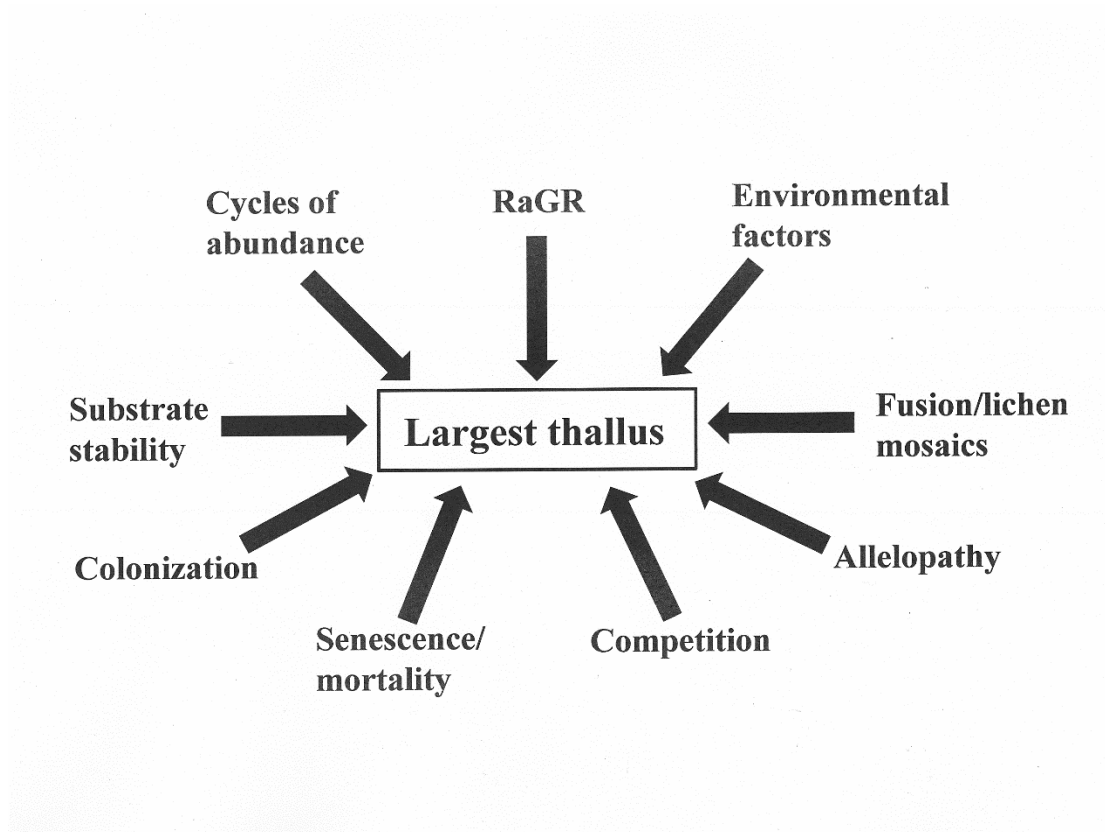
1589   data).

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1593   **Figure 11**. Variables influencing the size of largest thallus achieved on a rock surface

1594   (RaGR = Radial growth rate).

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