WITHIN-SITE VARIATION IN LICHEN GROWTH RATES AND ITS IMPLICATIONS FOR DIRECT LICHENOMETRY

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ABSTRACT. Variation in lichen growth rates poses a significant challenge for the application of direct lichenometry, i.e. the construction of lichen dating curves from direct measurement of growth rates. To examine the magnitude and possible causes of within-site growth variation, *radial growth rates* (*RaGRs*) of thalli of the fast-growing foliose lichen *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl. and the slow-growing crustose lichen *Rhizocarpon geographicum* (L.) DC. were studied on two S-facing slate rock surfaces in north Wales, UK using digital photography and an image analysis system (Image-J). RaGRs of *M. fuliginosa* ssp. *fuliginosa* varied from 0.44 to 2.63 mm yr^{-1} and *R. geographicum* from 0.10 to 1.50 mm $yr^{-1.5}$. Analysis of variance suggested no significant variation in RaGRs with vertical or horizontal location on the rock, thallus diameter, aspect, slope, light intensity, rock porosity, rock surface texture, distance to nearest lichen neighbour or distance to vegetation on the rock surface. The frequency distribution of RaGR did not deviate from a normal distribution. It was concluded that despite considerable growth rate variation in both species studied, growth curves could be constructed with sufficient precision to be useful for direct lichenometry.

Key words: direct lichenometry, radial growth rate (RaGR), growth variation, *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl., *Rhizocarpon geographicum* (L.) DC., normal distribution

Introduction

Traditional lichenometry, i.e. indirect lichenometry, involves the dating of rock and stone surfaces from the size of lichen thalli measured on surfaces of known age (Locke *et al*. 1979; Innes 1985; Matthews 1994; Benedict 2009). By contrast, 'direct lichenometry' constructs a lichen growth curve and hence, a lichenometric dating curve, from direct measurements of lichen growth (Armstrong 1976; Bradwell and Armstrong 2007; Trenbirth and Matthews 2010) and is a potentially useful method in regions where it is not possible to establish a calibration between thallus size and age (Armstrong and Bradwell 2010a).

Relatively few studies have adopted the direct approach to lichenometry (Bradwell and Armstrong 2007; Trenbirth and Mathews 2010). Trenbirth and Matthews (2010) identified four main reasons for the neglect of the direct method: high growth rate variability; lack of ecological data concerning the effects of environmental factors on growth; small sample sizes; and the restricted number of years over which measurements were made. To address these concerns, Trenbirth and Mathews (2010) measured growth rates of the crustose lichen *Rhizocarpon geographicum* (L.) DC., at 47 sites in southern Norway over a 25-year period and assessed both between-site and temporal variations in growth. A further source of growth rate variation, identified by Trenbirth and Matthews (2010), and evident in previous growth studies (Armstrong 1973, 1975, 2005a), is 'within-site' variation, i.e. variation between thalli growing either on different rocks or boulders at a site (Armstrong 2005a) or over different parts of a rock face (Armstrong 1975). These growth variations and their possible causes have been little studied by lichenologists but also have implications in constructing a lichen growth curve for direct lichenometry.

The growth of a lichen thallus on a rock face may be influenced by many different factors, including its horizontal and vertical location (Armstrong 1978) and local differences in aspect, slope, rock porosity, and surface texture (microtopography) (Armstrong 1974), as well as variations in access to nutrients in run-off (Armstrong 1977). At Snoqualmie Pass in the Cascade mountains of Washington State, USA, for example, growth of *R. geographicum* on Miocene granodiorite boulders of a talus slope was unrelated to the slope of a boulder facet but was correlated with its

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aspect (Armstrong 2005a). In addition, growth of *Rhizocarpon* thalli varied both between and within sites in the central Brooks Range of Alaska, thalli at sites subjected to high to moderate light intensities growing approximately twice as fast as those at more shaded sites (Haworth *et al.* 1986). In addition, competition from neighbouring thalli, in which stronger competitors often overgrow the weaker, can influence growth and contribute to within-site variability (Armstrong and Welch 2007; Bradwell 2010).

The present study assessed the degree of within-site variation in *radial growth rate* (*RaGR*) on two south-facing rock surfaces in north Wales, UK; one dominated by the relatively fast-growing foliose lichen *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl. and the other by the slow-growing crustose lichen *R. geographicum* (L.) DC. The rationale of the study was to assess the degree of growth rate variation on these surfaces, to assess its possible environmental causes, and discuss the implications for direct lichenometry.

Materials and methods

Study site

The study was carried out in an area of Ordovician slate rock in Gwynedd, north Wales, UK (National Grid Reference, SN 6196). Two approximately rectangular, steep-sided, south-facing rock surfaces, approximately 500 m apart, were chosen for the study. Each face was large enough to exhibit micro-environmental variations over the surface, one surface being dominated by *M. fuliginosa* ssp. *fuliginosa* (surface A, Fig. 1a) and the other by *R. geographicum* (surface B, Fig. 1b). The lichen flora of the two slate rock surfaces is typical of siliceous rock surfaces in the north and west of the UK (Armstrong 1974; James *et al*. 1977; Pentecost 1987). The percentage frequency of the lichen species present on each face is shown in Table 1. Vegetation, comprising mainly grasses and bryophytes, grew to the top edge of each face and also occurred in isolated patches on the face itself, and together with accompanying soil, is a potential source of nutrients in run-off (Armstrong 1977). Surface A was divided into nine approximately equal segments, each 1.65 m wide by 0.8 m high, arranged as three vertical bands (top, middle and bottom) each divided into three horizontal segments. Similarly, surface B was divided into six segments, each approximately 1.4×0.75 m, comprising two vertical bands (top, bottom) and three horizontal segments.

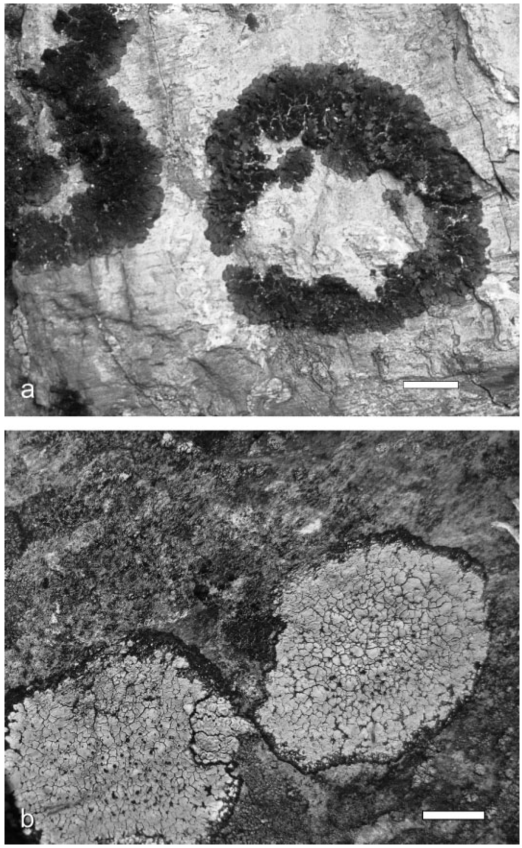

Fig. 1. Thalli of (a) *Melanelia fuliginosa* ssp. *fuliginosa* (Fr. ex Duby) Essl. on surface A; (b) *Rhizocarpon geographicum* (L.) DC. on surface B. Bar: *M. fuliginosa* ssp. *fuliginosa* = 5 mm; *R. geographicum* = 3 mm.

Selection of lichen thalli

Within each rock segment, five 10×10 cm quadrats were located at random and one thallus of either *M. fuliginosa* ssp. *fuliginosa* or *R. geographicum* selected from each quadrat for growth measurement. Thalli less than 1.5 cm in diameter were excluded as RaGRs of both species increase rapidly with size within this size range (Armstrong 1976, 1983; Aplin and Hill 1979). In addition, thalli overgrown by other lichens were excluded to reduce competition (Armstrong and Welch 2007). Many thalli, especially of *M. fuliginosa* ssp. *fuliginosa*, had fragmenting centres (Armstrong and Smith 1997), but these were not excluded since RaGR of

Table 1. Lichen flora and environmental features of the two rock surfaces studied. Data for associated lichen species represent the percentage frequency based on the occurrence of each species in 25, 10 × 10 cm quadrats randomly located over the face. Methods of measuring environmental variables are described in the text.

Species	Surface A	Surface B
Xanthoparmelia conspersa	25	0
Melanelia fuliginosa ssp. fuliginosa	100	47
Phaeophyscia orbicularis	0	100
Lecanora polytropa	17	50
Lecanora campestris	25	33
Rhizocarpon geographicum	0	100
R. reductum	8	63
Porpidia tuberculosa	0	17
Lecanora sulphurea	8	17
Acarospora smaragdula	0	56
Candelariella vitellina	100	100
Ochrolechia parella	0	86
Pertusaria lactea	8	0
Scolciosporum umbrina	33	0
Polysporina simplex	67	50
Buellia aethalia	92	0
Catillaria chalybeia	25	0
Environment		
Dimension (m, width × height)	5 × 2.4	4.3 × 1.5
Aspect (mean, range)	178° (170–184°)	181° (169–185°)
Slope (mean, range)	69° (45–90°)	67° (56–90°)
Light intensity (lux, mean, range)	1488 (1320–1580)	1520 (1432–1651)
Rock porosity (mean, range)	1.8% (1–5%)	1.9% (1–5%)
Rock texture (median, range)	2 (1–5)	3 (1–5)
Distance to nearest lichen (mm, mean, range)	5.15 (0–11)	4.95 (0–13)
Distance to nearest vegetation (m, mean, range)	1.17 (0.06–2.3)	0.85 (0.2–2.6)

this species is unaffected by degeneration of the thallus centre (Armstrong 1974). Each thallus was photographed in its entirety using a Canon IXUS-70 digital camera, which incorporates a ×12 zoom lens (Armstrong and Bradwell 2010b). A scale measure was located next to each thallus.

Measurement of growth

Various measures of growth could be used, including linear growth [mm], RaGR [mm yr^{-1}] and *relative growth rate* (*RGR*) [e.g. cm^2, cm^{-2}, yr^{-1}) and it is not clear which would be the best method for direct lichenometry. RaGR was chosen in this study as there are a greater number of studies of lichen growth which have employed this measure. To measure RaGR of each thallus, the advance of the marginal lobes of *M. fuliginosa* ssp. *fuliginosa* (Armstrong 1975) or hypothallus of *R. geographicum* (Armstrong and Smith 1987) was measured in relation to fixed points marked on the rock located at 1 mm intervals from the edge of the thalli (Hale 1970; Armstrong 1973, 1975). Between eight and ten randomly chosen locations were measured around each thallus for a total of 12 and 18 months for *M. fuliginosa* ssp. *fuliginosa* and *R. geographicum* respectively. Growth increments were measured using 'Image J' software developed by the National Institute of Health (Bethesda, MD, USA) (Syed *et al*. 2000; Girish and Vijayalakshmi 2004; Armstrong and Bradwell 2010b; Armstrong 2013) and available as a free download. Each lichen image was magnified to clearly reveal the fixed markers and the scale measure. The image was then calibrated using the scale measure and the distance from the tip of the lobe or hypothallus to the fixed marker measured. Subsequent measurements of these distances were made from sequential photographs, taken over the growth periods 1 or 3 months apart for *M. fuliginosa* ssp. *fuliginosa* and *R. geographicum* respectively. Growth increments were totalled over growth periods and averaged to give a RaGR [mm yr^{-1} for *M. fuliginosa* ssp. *fuliginosa* or mm $yr^{-1.5}$ for *R. geographicum*] for each thallus.

Measurement of environmental factors

Several environmental measurements were made adjacent to each lichen thallus. First, light intensity (lux) was measured using an OS1301 pocket light

Table 2. The degree of variability in RaGR (mm yr^{-1}) of *Melanelia fuliginosa* ssp. *fuliginosa* and *Rhizocarpon geographicum* over south-facing slate rock surfaces in north Wales, UK.

Species	RaGR			CV	Skew	Kurtosis
	Mean	SD	Range			
M. fuliginosa ssp. *fuliginosa*	1.66	0.48	0.44–2.63	28.9	–0.14 ns	–0.20 ns
R. geographicum	0.78	0.34	0.10–1.50	43.6	–0.36 ns	–0.30 ns

CV, coefficient of variation (%); ns, not significant; radial RaGR, radial growth rate; SD, standard deviation.

meter. The device had a silicon diode sensor and a 1 m connective cable. Measurements were made three times during the day (8 am, 12 midday, 6 pm) on a single day, selected at random, from each growth period. Second, variation in aspect and slope of the rock were measured using compass and clinometer respectively. Third, lower growth rates could occur on older parts of the surface as a result of reduced nutrient supply following chemical or biological weathering (McCarroll 1990; McCarroll and Viles 1995; Owen *et al*. 2007; Matthews and Owen 2008) and these parts of the surface often exhibit increased porosity (Armstrong 1974). Hence, porosity of the surface layers of the rock was measured using a water saturation method (Dullien 1992). A small sample of the surface cm of the rock was collected from within 1 cm of each thallus and weighed both in water and in air to estimate the volume of the rock. Rock samples were then dried and weighed again in air, water weight loss estimating pore space. Porosity was then expressed as the ratio of pore space to volume. Fourth, the texture ('roughness' or 'microtopography') of the rock surface adjacent to the growing margin was assessed from the images on a five-point scale from 1 (smooth) to 5 (rough) (Armstrong 1974). Fifth, distance of each thallus to its nearest lichen neighbour, and to the nearest patch of vegetation was measured. Mean, or median, and range of values for each environmental variable are shown in Table 1.

Data analysis

Statistical analysis was carried out using STATISTICA Software (Statsoft Inc., Tulsa, OK, USA). First, to determine whether there were systematic variations in RaGRs with horizontal or vertical location on each face, mean RaGRs from each segment were compared using two-factor analysis of variance. Second, correlations between RaGR and environmental factors were tested using Pearson's correlation coefficient (r). For rock texture, which was measured on an ordinal scale, Spearmans's non-parametric rank correlation coefficient (r_s) was used. For light intensity measures, correlations were calculated using the average of all measurements taken in each growth period. Third, the normal distribution was fitted to the frequency distribution of RaGRs for each species and goodness of fit tested using χ^2, Kolmogorov–Smirnov and Lilliefors tests (Snedecor and Cochran 1980). For comparative purposes, a normal distribution was also fitted to data from three previously published lichen growth studies, namely, *Xanthoparmelia conspersa* (Ehrh. ex Ach.) Hale and *M. fuliginosa* ssp. *fuliginosa* from north Wales growing in full sun on horizontal boards in the field (Armstrong 1976; Armstrong and Smith 1996), and a population of *R. geographicum* growing on a SW-facing talus slope located at an altitude of approximately 940 m a.s.l. in the Cascade Range at Snoqualmie Pass, Washington State, USA (Armstrong 2005a).

Results

The degree of variation in RaGRs between thalli of *M. fuliginosa* ssp. *fuliginosa* and *R. geographicum* over the two faces studied is shown in Table 2. On surface A, RaGRs of *M. fuliginosa* ssp. *fuliginosa* varied from 0.44 to 2.63 [mm yr^{-1}] (mean = 1.66; SD = 0.48) and on surface B, RaGRs of *R. geographicum* varied from 0.10 to 1.50 [mm $yr^{-1.5}$] (mean = 0.78; SD = 0.34). The *coefficients of variation* (*CV*), which correct for differences between the means, suggest that growth of *R. geographicum* was more variable than *M. fuliginosa* ssp. *fuliginosa*. Neither sample of measurements exhibited significant skew or kurtosis.

The mean and range of RaGRs within each segment of rock surfaces A and B are shown in Table 3. Both datasets reveal considerable variation in RaGRs even within individual segments on the face. In neither *M. fuliginosa* ssp. *fuliginosa* nor *R. geographicum*, however, were there significant

Table 3. Mean annual RaGRs (mm yr^{-1}) of the lichens *Melanelia fuliginosa* ssp. *fuliginosa* and *Rhizocarpon geographicum* (range in parentheses) growing in each vertical and horizontal segment of south-facing slate rock surfaces (surface A) in north Wales, UK.

Species	Vertical segments	Horizontal segments		
		1	2	3
M. fuliginosa ssp. *fuliginosa*	Top	1.71 (1.26–2.33)	1.94 (1.67–2.20)	1.50 (0.94–2.14)
	Middle	1.46 (1.07–1.95)	1.53 (0.74–2.48)	1.31 (0.44–1.87)
	Bottom	1.50 (1.26–1.97)	2.04 (1.31–2.42)	1.92 (1.33–2.63)
R. geographicum	Top	0.63 (0.10–1.07)	1.03 (0.70–1.50)	0.79 (0.42–1.08)
	Bottom	0.62 (0.10–1.07)	0.84 (0.55–1.07)	0.71 (0.34–1.22)

Analysis of variance (two-factor): *M. fuliginosa* ssp. *fuliginosa* vertical position $F = 2.93$ ($P > 0.05$), horizontal position $F = 1.78$ ($P > 0.05$), interaction $F = 0.83$ ($P > 0.05$); *R. geographicum* vertical position $F = 0.49$ ($P > 0.05$), horizontal position $F = 1.99$ ($P > 0.05$), interaction $F = 0.20$ ($P > 0.05$). RaGR, radial growth rate.

Table 4. Correlations (Pearson's 'r' or *Spearman's 'r_s') between radial growth rate of *Melanelia fuliginosa* ssp. *fuliginosa* and *Rhizocarpon geographicum*, thallus diameter, and environmental variables.

Variable	*R. geographicum*	*M. fuliginosa* ssp. *fuliginosa*
Thallus diameter	0.31 ($P > 0.05$)	–0.04 ($P > 0.05$)
Aspect	–0.06 ($P > 0.05$)	0.03 ($P > 0.05$)
Light intensity	–0.05 ($P > 0.05$)	–0.01 ($P > 0.05$)
Rock permeability	0.13 ($P > 0.05$)	0.11 ($P > 0.05$)
Slope angle	–0.24 ($P > 0.05$)	–0.18 ($P > 0.05$)
Rock texture*	0.01 ($P > 0.05$)	0.001 ($P > 0.05$)
Distance to nearest lichen	–0.09 ($P > 0.05$)	0.15 ($P > 0.05$)
Distance to nearest vegetation	0.15 ($P > 0.05$)	0.17 ($P > 0.05$)

differences in growth associated with horizontal or vertical location of the segment. The effect closest to statistical significance was that of vertical location on growth of *M. fuliginosa* ssp. *fuliginosa* ($F = 2.93$, $P > 0.05$), suggesting that growth may be greater in the upper and lower segments compared with those in the centre of the face.

Correlations (Pearson's r, Spearman's r_s) between RaGR, thallus diameter and environmental factors are shown in Table 4. There were no significant correlations between RaGR of either species and thallus diameter, aspect, slope, light intensity, rock porosity, rock texture, distance to nearest lichen, or distance to nearest patch of vegetation.

The results of fitting the normal distribution to the data for *M. fuliginosa* ssp. *fuliginosa* and *R. geographicum*, together with data from three additional populations studied previously, are shown in Table 5. In none of these populations did the frequency distribution of RaGRs deviate significantly from normality on any measure of goodness of fit.

Discussion

Within-site variation

Several sources of variation in lichen growth rates have now been identified, including variation in time (Phillips 1969; Trenbirth and Mathews 2010), between geographical sites (Trenbirth and Mathews 2010), between different rocks at a site (Haworth *et al*. 1986; Armstrong 2005a), and between different facets of a boulder (Armstrong 2005a). The present data, obtained from relatively uniform slate rock surfaces in north Wales, reveal a surprising degree of variation in RaGR over a single face, representing a 15-fold difference in RaGRs in *R. geographicum* measured over 18 months and a six-fold difference in annual RaGRs in *M. fuliginosa* ssp. *fuliginosa*. At Snoqualmie Pass, average growth variation of *R. geographicum* was even greater (mean of 39 thalli = 0.07, range 0–0.19) but these data included measurements of thalli on different boulder facets which varied significantly in aspect (Armstrong 2005a). Within-site variation in RaGRs was also observed by Rogerson *et al*. (1986), Winchester and Chaujer (2002), and McCarthy (2003). This degree of variation has significant implications for constructing a lichen growth curve at a single site in north Wales.

Table 5. Fitting the normal distribution to within-site variation in radial growth rates of foliose and crustose lichens.

Site	Species	N	Goodness-of-fit tests		
			χ^2	KS	Lilliefors
South-facing rock surface (NW)	*M. fuliginosa* ssp. *fuliginosa*	45	3.71 ($P = 0.29$)	0.08 ($P > 0.05$)	$P > 0.05$
South-facing rock surface (NW)	*R. geographicum*	30	1.70 ($P = 0.19$)	0.09 ($P > 0.05$)	$P > 0.05$
Horizontal board (NW)*	*Xanthoparmelia conspersa*	54	2.28 (P = 0.51)	0.10 (P > 0.05)	$P > 0.05$
Horizontal board (NW)*	*M. fuliginosa* ssp. *fuliginosa*	45	0.71 ($P = 0.87$)	0.03 ($P > 0.05$)	$P > 0.05$
Talus slope (SNO)*	*R. geographicum*	32	4.19 ($P = 0.12$)	0.09 ($P > 0.05$)	$P > 0.05$

*Previously published data.
KS, Kolmogorov–Smirnov; N, number of thalli in sample; NW, North Wales; SNO, Snoqualmie Pass in the Cascade Range, Washington State, USA.

Errors in measuring growth

Errors of measurement could have contributed to the observed variation in RaGRs (TenBrink 1973; Innes 1985; Armstrong 2005a; Benedict 2008; Trenbirth and Mathews 2010). The present method of measuring growth is based on that of Hale (1970) and involves measuring the advance of the thallus perimeter, either the tip of the lobe or edge of the hypothallus, with reference to fixed markers on the rock and employs digital photography (Hooker 1980; Proctor 1983) and an image analysis system. This method enables measurements to be made over small time scales, namely, one month for faster-growing and three months for slower-growing species in north Wales, thus potentially reducing the time necessary to obtain a growth curve. Nevertheless, errors of measurement are likely to be present; for example, both the markers on the rocks and the calibration scale rule have thickness, necessitating a degree of subjectivity in measuring distances on magnified images. Hence, improvements in methodology could potentially reduce growth variability. For example, a new photographic method of measuring growth applied to *R. geographicum* suggested that repeat measurements could be taken over months rather than years (McCarthy and Henry 2012).

Effect of thallus size

It is well established that RaGR is related to thallus size in both *M. fuliginosa* ssp. *fuliginosa* (Armstrong 1976) and *R. geographicum* (Trenbirth and Mathews 2010; Armstrong and Bradwell 2011; Armstrong 2011). In foliose lichens, RaGR increases in smaller diameter thalli becoming linear or asymptotic in individuals larger than about 1.5 cm (Armstrong 1974; Aplin and Hill 1979; Armstrong and Smith 1996). Since thalli smaller than 1.5 cm were excluded, size is not a source of variability in *M. fuliginosa* ssp. *fuliginosa*. The shape of the growth curve of *R. geographicum*, however, is more controversial and the data suggest some effect of size on RaGR in this species, the correlation coefficient being the largest of those recorded. A parabolic growth curve has been identified in some studies (Armstrong 1983; Armstrong 2005b; Bradwell and Armstrong 2007) describing an initial phase in which RaGR increased with size to a maximum; a short phase in which RaGR was maximal; and a declining phase in which RaGR fell in thalli greater than 50 mm in diameter, the overall shape of the growth curve being parabolic. Trenbirth and Matthews (2010), however, reported several different curves for *R. geographicum* growth in southern Norway. At many of their sites, annual growth rates remained relatively constant or increased with size up to 12 cm, the growth 'curve' being linear rather than parabolic or asymptotic, raising the prospect that the growth curve of *R. geographicum* could vary at different sites or even within the same site in different years. These data emphasize that a lichen growth curve obtained at a location is unlikely to be applicable to other sites.

Effect of environmental factors

Growth variation could be attributable to systematic differences in microclimate across or down a rock surface, for example, light intensity decreased down the faces studied. Apart from a possible but non-significant vertical effect on RaGR of *M. fuliginosa* ssp. *fuliginosa*, which could be related to light, the data do not suggest that horizontal or vertical location on the face significantly affected growth. In a previous study in north Wales (Armstrong 1978), a gradual decrease in mean size of foliose thalli with distance down a rock face was observed, but RaGR was unrelated to height on the face. More substantial microclimatic gradients could be present on larger rock faces and this aspect of growth variation warrants further study. In addition, none of the environmental factors measured were significantly correlated with RaGR on either face. At Snoqualmie Pass, RaGR of *R. geographicum* was correlated with aspect of the surface (Armstrong 2005a) but larger variations in aspect were present than at the present site. Although not reaching statistical significance, slope angle exhibited a degree of negative correlation with RaGR, which would be expected if steeper portions of rock were more rapidly drained, and should be investigated further. Some variables which could influence RaGR were not measured, e.g. the chemical content of the rock (Armstrong 1997) and concentration of ions in run-off (Armstrong 1977). However, there was no evidence from previous studies that these variables substantially influence RaGR (Armstrong 1997). In addition, light intensity varies through the day, from day to day, and through the year, and measurements were not made frequently enough to demonstrate an effect on growth. The competition measures may also have been inadequate, as competition may only be relevant when thalli come into contact with each other (Armstrong and Welch 2007). In addition, distance to nearest vegetation may have little relevance unless thalli are overgrown apart from the possibility that patches of vegetation on the face are a source of nutrients. The study also raises the question of whether variation in RaGR is genetically determined or a consequence of unmeasured environmental variables? The present data suggest that environmental fluctuations on a rock face may have relatively little effect on RaGR variability, thus making it easier to construct a suitable growth curve for direct lichenometry. The data may also have implications for indirect lichenometry in that the size of the largest thallus on the face may not be dependent on variation in local environmental factors.

Fit to normal distribution

In neither *M. fuliginosa* ssp. *fuliginosa* nor *R. geographicum* did the frequency distribution of RaGR deviate from a normal distribution. However, the conclusion that variation in RaGR over a rock face is normally distributed should be regarded as tentative as only two surfaces were studied and sample sizes were small. Nevertheless, previously published data from three further lichen populations grown either on rock fragments placed on horizontal boards in north Wales (Armstrong and Smith 1996) or boulders at Snoqualmie Pass (Armstrong 2005a) did not deviate from normality, supporting the conclusion that on a single face, where environmental variations are more limited, RaGR is a normally distributed variable. If growth variation over a face is normally distributed it would have several important implications: that RaGR is determined by many relatively ‘weak’ variables; no single factor has an overriding effect on growth; each variable acts independently; and the overall effect of the variables is additive (Armstrong and Hilton 2011). This result could also explain why no individual variable was strongly correlated with growth on either rock surface studied.

Implications for direct lichenometry

These results add a further limitation to studies of direct lichenometry, i.e. within-site growth variation may be so large as to make it especially difficult to establish a lichen growth curve of sufficient accuracy to be useful in dating. Construction of a lichen growth curve usually involves dividing up the range of thallus size into suitable size classes (Armstrong 1976). Hence, classes of 1 cm were used to construct growth curves of *X. conspersa* (Armstrong and Smith 1996), *M. fuliginosa* ssp. *fuliginosa* (Armstrong 1976) and *R. geographicum* (Armstrong 1983). RaGR of a sample of thalli is then measured within each size class and RaGR plotted against thallus size to obtain the growth curve. The estimated age of a thallus of a diameter d cm is then obtained by fitting a growth curve to the data and calculating the time taken to grow each centimetre. A calibration of diameter against estimated age can then be constructed based on measured growth rates (Armstrong 1976). However, the within-site variation in RaGR will result in large confidence intervals for estimated ages which markedly increase with thallus size. Nevertheless, if variation in RaGR on a single face is normally distributed, it is possible to estimate the number of thalli that should be measured in each size class to estimate RaGR within defined limits. First, decide on how big an error (±*L*) is tolerable in estimating RaGR and hence thallus age. Second, the number of thalli required to estimate RaGR with this level of accuracy is given by the formula $4S^2/L^2$ where *S* is the standard deviation of growth measurements (Snedecor and Cochran 1980). To apply this method it would be necessary to obtain an estimate of the growth variability on the face from a pilot study or to use published data from comparable sites to provide a likely estimate. For example, in *M. fuliginosa* ssp. *fuliginosa*, to determine sample size to estimate RaGR with a high probability of not exceeding an error of 0.2 mm in the linear growth phase with $S = 0.48$ (Table 2), would require $4 \times 0.48^2/0.2^2 = 23$ thalli. However, samples of thalli would also be necessary to define the earlier increasing growth phases in which RaGR increases with size (Armstrong 1976; Armstrong and Bradwell 2011). For *R. geographicum*, to estimate RaGR with a high probability of not exceeding an error of 0.2 mm in the growth phase in thalli greater than 2 cm in diameter with $S = 0.34$ (Table 2) would require a sample of 12 thalli. However, RaGR variation is significantly greater in smaller thalli with an estimated SD = 0.70 (Armstrong 1983). This would require a sample of 49 thalli to define this phase of growth, giving a total of approximately 60 thalli to define the growth rate–size curve.

Controlling growth rate variation

This study failed to detect any environmental factor whose variation could be used to control within-site variation in RaGR. Nevertheless, previous studies suggest that if large differences in aspect are present over the face, then this variable should be taken into account (Armstrong 2005a). In addition, further research may yet reveal that vertical location on a face influences growth (Armstrong, 1978).

Within-site growth rate variation could also be reduced by averaging annual growth measurements collected over a longer period of time. Direct studies of foliose lichen growth have usually been made over a year, but year to year variation in annual growth rates (Phillips 1969) suggests a period of at least three years may be appropriate for faster-growing foliose species and at least five years for slower-growing crustose species (Innes 1985). For example, Phillips (1969) measured the growth of *Menegazzia terebrata* (Hoffm.) Massal. thalli over three successive years, the magnitude of CV being 47%, 34% and 51% respectively. However, the average of the three years' data yielded a CV of 32%, thus significantly reducing growth variation in at least two of the individual years. Similarly, data from Armstrong (2005a) from Snoqualmie Pass suggest considerable within-site variation in RaGR for *R. geographicum* (CV = 87–146%). Nevertheless, mean RaGR over three years had a CV = 79%, substantially less than present in some years.

A further method of potentially reducing growth rate variation in *R. geographicum* is to take into account hypothallus width. Previous studies suggest that RaGR may be related to variation in the width of the peripheral hypothallus (Proctor 1983; Armstrong and Bradwell 2001), i.e. faster-growing thalli and faster-growing regions of individual thalli being identified by their wider hypothalli. Hence, measuring a sample of *R. geographicum* thalli with similar hypothallus widths could reduce within-site growth variability.

Conclusion

The data suggest considerable variation in RaGR of *M. fuliginosa* ssp. *fuliginosa* and *R. geographicum* over two south-facing rock surfaces in north Wales, UK. No single environmental variable could account for this variation, suggesting that such environmental fluctuations may have little influence on RaGR variation over a single rock face. In addition, growth variation over a face may be normally distributed, and therefore, in studies of direct lichenometry, the normal distribution could be used to estimate the number of thalli needed to construct a growth curve within specified limits of accuracy. Measurement of RaGR over a number of years and in *R. Geographicum*, standardizing thalli according to prothallus width, may also reduce growth variability. Hence, despite considerable growth rate variation in both species, growth curves could be constructed with sufficient precision to be useful for direct lichenometry.

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