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The effect of rock surface aspect on growth, size structure and competition in the lichen *Rhizocarpon geographicum*

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Abstract

Rhizocarpon geographicum is a crustose lichen found frequently on rock surfaces of southern aspect and less frequently on rock surfaces of northern aspect in Gwynedd, North Wales. This study tested the hypothesis that the radial growth of *R. geographicum* thalli predicts aspect distribution. Thalli of all sizes, however, exhibited significantly greater radial growth over 18 months on northwest compared with southeast facing surfaces. The hypothesis that a more intense competitive environment on northwest facing surfaces may explain the aspect distribution of *R. geographicum* was then tested. The size frequency distributions of thalli revealed a higher proportion of thalli in the smallest size class and a more restricted thallus size range on the northwest facing surfaces. In addition, thallus mortality appeared to be greater on northwest facing surfaces. Significantly more associated lichen species were present on rock surfaces of northern aspect at sites where *R. geographicum* was present. The mean frequency of the associated lichen species, however, was significantly lower on surfaces of northern aspect where *R. geographicum* was present. In addition, two common foliose species at these sites were demonstrated experimentally to overgrow thalli of *R. geographicum*. It is concluded that the growth of *R. geographicum* over the study period did not predict aspect distribution and that differences in the competitive environments on northwest and southeast surfaces may be an important factor determining aspect distribution. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Aspect distribution; Competition; Overgrowth; Radial growth rate; Size frequency distribution

1. Introduction

Rhizocarpon geographicum is a crustose lichen found in lichen communities on exposed siliceous rock outcrops in the UK (James et al., 1977). In an area of Gwynedd, North Wales, *R. geographicum* is most abundant on well-lit slate rock surfaces of southern aspect but the species also occurs less frequently on more shaded, north facing rocks (Armstrong, 1974).

The influence of aspect on the radial growth and distribution of foliose lichen species has been extensively studied (Armstrong, 1974, 1975, 1977; Armstrong and Smith, 1993). In most cases, lichen thalli exhibit higher radial growth rates at the sites where they are most frequent. For example, the radial growth of *Parmelia conspersa*

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(Armstrong, 1977; Armstrong and Smith, 1993) and *Physcia orbicularis* (Armstrong, 1977) was significantly greater on rock surfaces of southeast compared with northwest aspect while the radial growth of *Parmelia glabratula ssp. fuliginosa* was greater on northwest facing surfaces; growth responses which reflected the aspect preferences of the three species (Armstrong, 1974). Differences in radial growth with aspect are likely to be attributable to the contrasting microclimates of north and south facing slopes, e.g. photosynthetically active radiation (PAR) and temperature are higher for most of the year on south facing surfaces (Armstrong, 1975). Higher PAR should support higher growth rates on south facing surfaces since there is a strong correlation between growth and intercepted radiation in lichens (Palmqvist and Sundberg, 2000) but the higher temperatures could reduce the growth of some species (Armstrong, 1975). High surface temperature may have two effects on lichens. First, the thalli may dry out, resulting in the partial loss of cellular water from both symbiotic partners (Honegger, 1991). Second, since the thalli will dry out more rapidly after rain, losses of carbohydrate due to resaturation respiration (Smith and Molesworth, 1973) are less likely to be replaced readily on south facing slopes resulting in lower growth rates (Armstrong, 1976). Hence, the first objective of this study was to test the hypothesis that radial growth of *R. geographicum* on northwest and southeast facing rock surfaces reflected the aspect distribution of the lichen.

Microclimate models may not accurately predict lichen growth (Sundberg et al., 1997), e.g. microclimatic gradients may be too small to significantly affect lichen growth (Renhorn et al., 1997). Hence, in some circumstances, the growth of lichens may not predict their aspect distributions. The growth of *Parmelia saxatilis* is similar on south and north facing rock surfaces at the site in Gwynedd (Armstrong, 1977) but this species is much more frequent on north facing rock surfaces (Armstrong, 1974). In this case, physiological differences between surfaces are less likely to be the primary factor determining aspect distribution since they would be reflected in differences in growth rate. Competition between saxicolous lichens is strongly mediated by growth rate; a faster-growing species overgrowing a slower growing species (Armstrong, 1982). Hence, one possible hypothesis is that *P. saxatilis* may be eliminated by competition from faster-growing species on many south facing surfaces although growth conditions for *P. saxatilis* are at least as favourable as on north facing surfaces. Hence, the second hypothesis tested in this study is that competition may be a factor, which could account for aspect distribution of *R. geographicum*.

2. Materials and methods

2.1. Site

The study was conducted in the field in an area of Ordovician slate rock in Gwynedd, North Wales, UK (Nat. Grid Ref. SN 6196) (Armstrong, 1974). Populations of yellow–green *Rhizocarpon* species are frequent at this site in a variety of lichen communities (James et al., 1977). Identification to species can be difficult in the *Rhizocarpon* group and thalli are often identified to the section level using the criteria of Poelt (1988). Using the broadly circumscribed criteria of Purvis et al. (1992), however, all populations included in this study were identified as *R. geographicum* (L.) DC.

2.2. Distribution of R. geographicum

The distribution of *R. geographicum* at the site was investigated on 48 individual rock outcrops of Ordovician slate. The presence/absence of *R. geographicum* was recorded in 25, randomly located, 30×30 cm quadrats placed on each rock surface. Several aspects of the rock surface environment were also measured using previously described methods (Armstrong, 1974), viz. aspect (Armstrong, 1975), slope (Link and Nash, 1984), rock hardness (Pentecost, 1980), and surface texture (James et al., 1977; Pentecost, 1980; Benedict and Nash, 1990). The percentage frequency of *R. geographicum* on each rock surface was plotted in relation to slope and aspect on a polar graph using the method described by Pentecost (1979).

2.3. Growth of R. geographicum

Four steep-sided rock surfaces, all within 5 m of each other, and each with a population of *R. geographicum*, were chosen for study. Two of the rock surfaces were approximately northwest facing (aspect 135°) and the other two southeast facing (aspect 315°). The radial growth of a total of 19 thalli from the northwest facing surfaces and 24 thalli from the southeast facing surfaces was measured *in situ* at 6-month intervals from 1 June 1996 until 1 January 1998. All thalli chosen for measurement were relatively symmetrical, without disintegrating centres, and were located at least 1 cm from the nearest potential competitor. Radial growth was measured at five randomly located positions around each thallus using the methods described previously (Armstrong, 1975) and averaged for each individual. Essentially, the advance of the thallus margin was measured with reference to fixed points marked on the substratum using a hand lens incorporating a micrometer scale. No significant differences in the pattern of growth were observed between the two rock surfaces at each aspect and the data were combined for analysis. Thalli were divided into five size classes and the data analysed by a two-factor, split-plot analysis of variance (ANOVA) (SuperANOVA software, Abacus Concepts Inc., Berkeley, CA, USA) in an unbalanced design to determine whether aspect, thallus size, or interaction significantly influenced radial growth.

2.4. Size class frequency distributions

To determine whether there were aspect differences in the pattern of colonisation and thallus mortality, the size frequency distribution of the *R. geographicum* thalli (Farrar, 1974) was studied on each of the surfaces used for the growth measurements. The greatest diameter of all *R. geographicum* thalli was measured in 25, 10×10 cm quadrats located at random on each surface. Whether each thallus was entire or exhibited disintegration of the central regions was recorded. Disintegration of the centre is often a sign of thallus degeneration and hence, the frequency of such thalli may indicate potential mortality in a population (Armstrong and Smith, 1997). The size distributions were totalled for the two surfaces at each aspect and aspect differences compared using a χ^2 contingency table test. In addition, for each population, the relationship between the percent thalli, which exhibited evidence of disintegration and the mid-point of thallus size class, was fitted by a first, second or third-order polynomial. A higher order function was accepted when a significant reduction in the sums of squares was achieved relative to a linear fit (Snedecor and Cochran, 1980). The size class at which 50% of the thalli exhibited disintegration of the centre was then estimated from the fitted curve.

2.5. Influence of rock surface competition

To determine the possible effects of competition in determining the aspect distribution of *R. geographicum*, the number of associated lichen species and their mean frequency was measured on 16 rock surfaces of northern aspect (90–150°) and 23 rock surfaces of southern aspect (230–359°). On each surface, the presence and absence of all lichen species was recorded in 25 randomly located 30×30 cm quadrats. The mean number of associated species and the mean frequency of the associated species were compared between rock surfaces of northern and southern aspect where *R. geographicum* was present or absent using a two-factor ANOVA in an unbalanced design. In addition, differences in rock hardness and surface texture between the four types of surface were tested. Rock hardness was measured using previously described methods (Armstrong, 1974) by determining the time taken for a rock sample collected from the surface centimetre of the rock to dry to a constant weight; softer rocks absorbing more water and therefore, taking longer to dry out.

Of the associated lichen species, four foliose species, viz. *P. conspersa* (Ehrh. ex Ach.)Ach., *P. glabratula ssp. fuliginosa* (Fr. ex. Duby)Laund., *P. saxatilis* (L.)Ach. and *P. orbicularis* (Neck.)Poetsch were the most likely species to compete with *R. geographicum*, being the most frequent species present and having the highest radial growth rates (Armstrong, 1977). The radial

Table 1
Radial growth (mm per year) of four foliose saxicolous lichens on southeast and northwest facing rock surfaces in Gwynedd, North Wales (data from Armstrong, 1977)

Species	Rock surface aspect	
	Southeast facing	Northwest facing
P. conspersa	2.58	1.66
P. glabratula ssp. fuliginosa	1.08	1.42
P. saxatilis	1.68	0.38
P. orbicularis	2.70	1.42

growth rates of samples of thalli of these four species on northwest and southeast rock surfaces at the site are shown in Table 1.

2.6. Growth of foliose lichens adjacent to R. geographicum

The objective of this experiment was to determine whether foliose species could overgrow and therefore, outcompete thalli of *R. geographicum*. Six thalli of *R. geographicum*, 3–7.5 cm in diameter were collected on thin pieces of slate and placed on horizontal boards in the field. Fragments of two foliose species, viz. *P. conspersa* and *P. glabratula ssp. fuliginosa* were cut from the perimeters of large thalli and glued (Bostik No. 1 clear adhesive) (Armstrong, 1982) adjacent to thalli of *R. geographicum*. Thallus fragments were glued with the tips of the lobes touching the edge of the hypothalli. Fragments were also glued at least 20 cm away from the *R. geographicum* thalli in an area of slate without lichen thalli as a control. The radial growth of the lichen fragments as they advanced over the hypothalli and areolae of *R. geographicum* thalli was measured at 2-month intervals from 1 September 1998 until 1 September 1999) and the data analysed by a two-factor split-plot ANOVA.

3. Results

The presence and absence of *R. geographicum* on 48 rock outcrops in Gwynedd, North Wales in

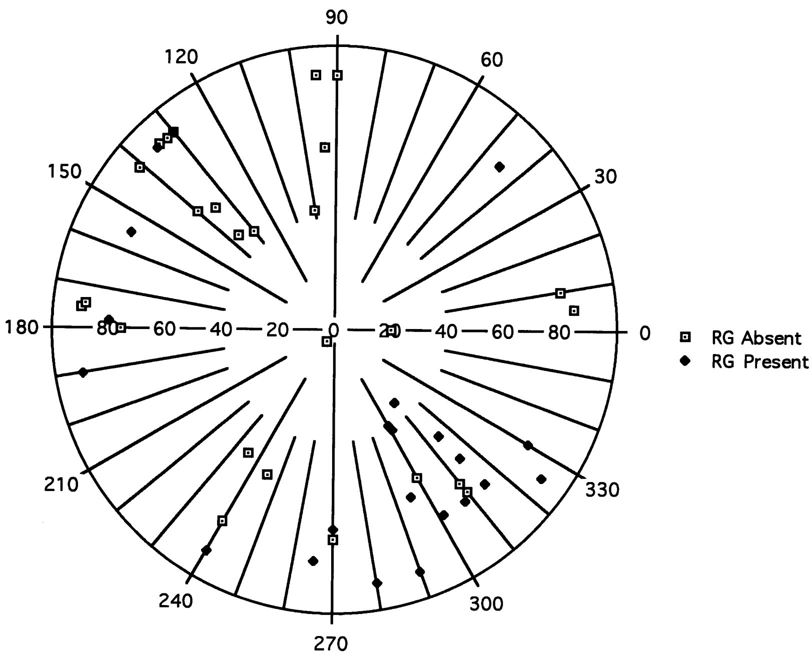

Fig. 1. Polar graph showing the presence and absence of *R. geographicum* (RG) on 48 rock surfaces in relation to aspect (distance around circle) and slope (distance along radius) in Gwynedd, North Wales.

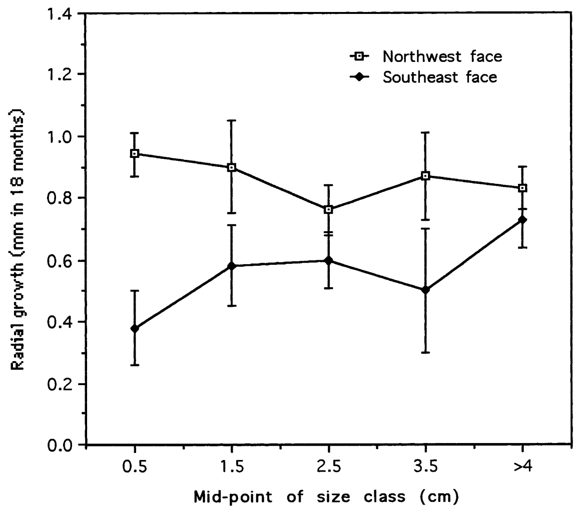

Fig. 2. Radial growth (mm in 1.5 year) of *R. geographicum* thalli of different size on two northwest and two southeast facing rock surfaces. (ANOVA: aspect $F = 8.38$ ($P < 0.01$), size class $F = 0.19$ ($P > 0.05$), interaction $F = 0.64$ ($P > 0.05$).)

relation to aspect and slope is shown in Fig. 1. The species is present mainly on surfaces of southern aspect and especially on south to southeast facing surfaces with slopes varying from 30 to 90°. In addition, *R. geographicum* is present on a small number of steep-sided rock surfaces of northern aspect.

The radial growth (mm in 18 months) of a sample of *R. geographicum* on northwest and southeast facing surfaces is shown in Fig. 2. The ANOVA suggests significantly greater growth on the northwest facing surfaces ($F = 8.38$, $P < 0.01$). The interaction between aspect and size class of thalli was not significant ($F = 0.64$, $P > 0.05$) suggesting that differences in growth between aspects affected all sizes of thalli. The standard errors of the mean suggest, however, that the growth difference with aspect may be less evident in the larger thalli.

The size class frequency distribution of *R. geographicum* thalli on the northwest and southeast facing rock surfaces is shown in Fig. 3. The χ^2-test suggested that the size distributions were significantly different (9 DF, $\chi^2 = 125.34$, $P < 0.001$) suggesting differences in the proportions of the thalli in the various size classes. Two major differences between the two populations were apparent: (1) there was a higher proportion of the total thalli in the smallest size class on the northwest surfaces; and (2) there was a more restricted thallus size range on the northwest surfaces. In addition, the mid-point of the size class in which 50% of the thalli showed signs of disintegration (Fig. 4) varied with aspect, being 17.5 cm for the northwest surfaces and 22 cm for the southeast surfaces.

The mean number of associated lichen species and their mean frequency on a sample of northern

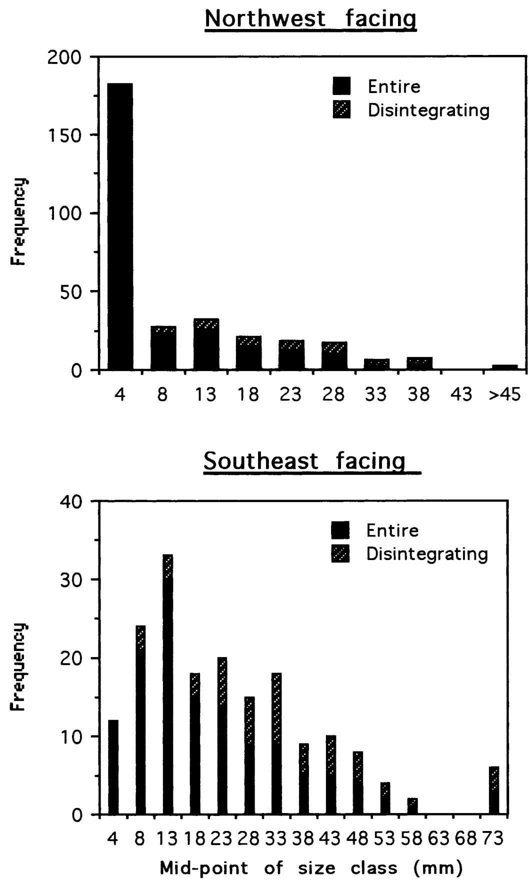

Fig. 3. Size class frequency distribution of *R. geographicum* thalli on northwest and southeast facing rock surface. (Comparison between surfaces $\chi^2 = 125.34$ (9DF, $P < 0.001$).)

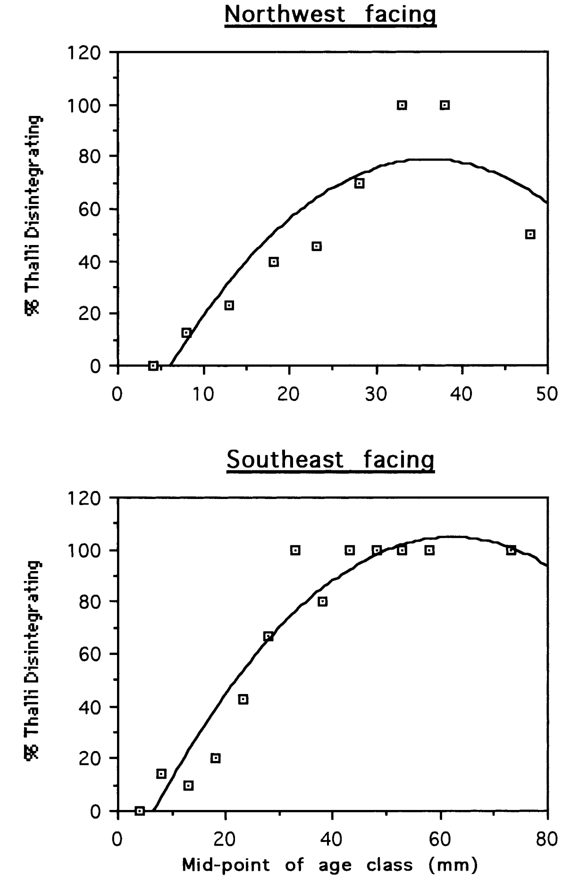

Fig. 4. The percentage of thalli of *R. geographicum* in each size class exhibiting disintegration of the thallus centre on northwest and southeast facing rock surfaces. (Curve fitting: NW surface $Y = -36.28 + 27.95x - 1.72x^2$, $r = 0.88$, $P < 0.001$; SE surface $Y = -26.6 + 4.24X - 0.03X^2$, $r = 0.96$, $P < 0.001$.)

and southern facing rock surfaces where *R. geographicum* was either present or absent is shown in Fig. 5. Significantly more lichen species were present on the northern rock surfaces where *R. geographicum* was present. In addition, the mean frequency of the associated species was significantly lower on the northern surfaces ($F = 13.96$, $P < 0.001$) at sites where *R. geographicum* was present. There were no significant differences in surface hardness or texture between the four types of site.

The growth of fragments of *P. conspersa* and *P. glabratula ssp. fuliginosa* adjacent to thalli of *R. geographicum* is shown in Table 2. The ANOVA suggests that both species were able to overgrow the hypothallus and areolae of *R. geographicum* but also suggests that radial growth was reduced in some growth periods compared with control thallus fragments. In addition, two of the thalli of *P. glabratula ssp. fuliginosa* became discoloured during the March/April growth period although growth continued until the end of the experiment.

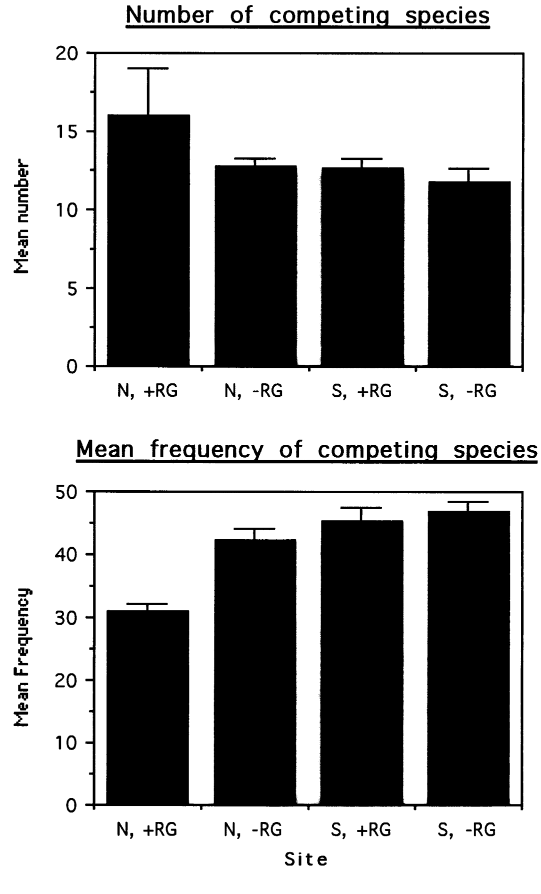

Fig. 5. The number of associated lichen species and the mean frequency of the associated species on northern (N) and southern (S) facing rock surfaces where *R. geographicum* (RG) was either present (+) or absent (−). (ANOVA: number of species, aspect $F = 4.56$ ($P < 0.05$), presence of RG $F = 3.83$ ($P < 0.05$), interaction $F = 0.26$ ($P > 0.05$); frequency of species aspect $F = 13.96$ ($P < 0.001$), presence of RG $F = 6.48$ ($P < 0.01$), interaction $F = 3.45$ ($P < 0.01$).)

Table 2
Radial growth of thallus fragments of *P. conspersa* and *P. glabratula ssp. fuliginosa* glued to pieces of slate adjacent to and 20 cm away from thalli of *R. geographicum* (control)

Growth period	*P. conspersa*		*P. glabratula ssp. fuliginosa*	
	Adjacent	Control	Adjacent	Control
September–October	0.06	0.25	0.29	0.15
November–December	0.70	0.48	0.25	0.20
January–February	0.13	0.16	0	0.13
March–April	0.33	0.66	0.04	0.21
May–June	0.19	0.25	0.06	0.03
July–August	0.33	0.34	0.09	0.19

ANOVA: *P. conspersa*, location of fragment $F = 5.18$ ($P < 0.01$), growth period $F = 3.22$ ($P < 0.05$), interaction $F = 0.76$ ($P > 0.05$); *P. glabratula ssp. fuliginosa*, location of fragment $F = 4.38$ ($P < 0.5$), growth period $F = 2.25$ ($P > 0.05$), interaction $F = 1.73$ ($P > 0.05$).

4. Discussion

The first objective of this study was to test the hypothesis that the growth of *R. geographicum* thalli on northwest and southeast facing rock surfaces predicted aspect distribution. The growth data, however, suggested that the radial growth of the thalli on northwest facing surfaces was significantly greater compared with the southeast facing surfaces. It is possible that the growth data obtained over 18 months were atypical of growth over longer periods. For example, Zotz and Winter (1994) in a study of *Leptogium azureum* demonstrated a negative carbon balance over a year, as measured by CO_2 exchange, although this species occurred frequently at the study site. Against this, McCarthy (1997) found greater lichen growth on more shaded steep or overhanging facets on glacial moraines. In addition, a study of the radial growth of *R. geographicum* on boulders of different aspect in the North Cascade mountains, Washington State also suggest greater growth on north facing surfaces (R.A. Armstrong, unpublished data). Hence, the present growth data suggest that the radial growth of *R. geographicum* may not predict its aspect distribution and raise the question of the exclusion of this species from many northern surfaces in South Gwynedd despite growth conditions being potentially favourable at these sites.

The second hypothesis tested in this study was that differences in the intensity of competition could explain the aspect distribution of *R. geographicum*. The size frequency data suggest a much higher rate of mortality of thalli on northern surfaces. Size frequency distributions of yellow–green *Rhizocarpon* species have also been studied in Northern Iceland and show frequent disruption and high mortality (Caseldine and Baker, 1998), the authors attributing the high mortality to either environmental changes or to competition. Examination of macroclimatic records for the north Wales site over the last 10 years, however, failed to provide data, which could explain the variations in colonisation or mortality. In addition, the degree of rock hardness and texture may be important rock surface variables influencing lichen growth (Armstrong, 1974; James et al., 1977; Pentecost, 1980). The present study suggested, however, that the absence of *R. geographicum* on many north facing surfaces at the site could not be attributable to differences in the texture or porosity of the rock surface.

Several aspects of the data are consistent with this hypothesis that differences in the competitive environments on northwest and southeast facing surfaces could be a factor determining the aspect distribution of *R. geographicum*. First, there are four common foliose lichen species present at these sites with significantly higher growth rates than *R. geographicum* (Armstrong, 1977), which could be potential competitors. Second, two of these species were able to overgrow thalli of *R.*

geographicum. Third, there are significantly more potential competitors on northern surfaces on the outcrops where *R. geographicum* thalli were present. The mean frequency of the associated species, however, was significantly lower on the northern surfaces where *R. geographicum* was present. This suggests that *R. geographicum* may survive on certain north facing surfaces where there are large numbers of species present but at low mean frequency. An experimental study of the competitive interactions between four foliose lichen species on north and south facing rock surfaces in Gwynedd (Armstrong, 1991) suggested that the effect of a particularly strong competitor in two-species mixture was significantly reduced in three and four-species mixtures. Hence, with many more species present, a 'competitive equilibrium' could be established allowing a weaker competitor to coexist (Lawrey, 1981).

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