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Seasonal growth of the crustose lichen *Rhizocarpon geographicum* (L.) DC. in South Gwynedd, Wales

R.A. Armstrong

Department of Vision Sciences, Aston University, Birmingham B4 7ET, United Kingdom, Tel. +44-121-204-4102, Fax. +44-121-204-4048, Email. R.A.Armstrong@aston.ac.uk

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Abstract

Seasonal growth was studied in the slow-growing crustose lichen *Rhizocarpon geographicum* (L.) DC. in an area of South Gwynedd, Wales. Radial growth rate (RGR) of a sample of 20 thalli was measured *in situ* at three-month intervals over 51 months on a southeast-facing rock surface. There were five periods of significant growth: July–September of 1993, 1994 and 1995, in January–March of 1996, and in April–June of 1997. In four of these periods, growth coincided with a mean temperature maximum (Tmax) over a three-month period exceeding 15°C and three of the maxima with greater than 450 sunshine hours. Two of the growth maxima coincided with periods of total rainfall exceeding 300 mm and one with greater than 50 rain days in a three-month period. There were no significant linear correlations between RGR and the climatic variables measured. However, there were significant non-linear relationships between RGR and Tmax, the mean temperature minimum (Tmin), the total number of air and ground frosts and the number of rain days in a growth period, the relationship with Tmax being the most significant. Hence, in south Gwynedd, maximum growth of *R. geographicum* occurs in any season although the period July–September appears to be the most favourable. Relationships between growth and climatic variables were non-linear, temperature having the most significant influence on seasonal growth.

Keywords: *Rhizocarpon geographicum*, seasonal growth, maximum temperature, curvilinear regression, multiple regression

1. Introduction

Slow growth rates and the problem of growing lichens for long periods under controlled laboratory conditions have made it difficult to study the influence of environmental factors on growth. In the absence of such studies, investigation of the seasonal pattern of growth in the field is one method of examining the affects of environmental factors (Armstrong, 1988). Significant correlations between growth and climatic variables suggest hypotheses about the causal factors limiting growth which can then be tested by more controlled physiological experiments (Armstrong, 1976; Coxon and Kershaw, 1983).

Studies suggest that the pattern of seasonal growth in foliose lichen thalli depends on geographical region. Where winters are severe, as in Poland (Rydzak, 1961), the Antarctic (Hooker, 1980), and Colorado (Benedict, 1991a,b), lichen growth tends to occur in the summer months. Where rainfall is seasonal, e.g., in autumn or winter, distinct seasonal growth patterns may be repeated in successive years (Boucher and Nash, 1990; Lawrey and Hale, 1977; Stone, 1986). More complex patterns may be observed in milder environments, where maximum growth can occur in any season (Armstrong, 1973; 1975; Moxham, 1981) and as a result, seasonal growth differs substantially from year to year (Showman, 1976). In addition, in milder climates, a single limiting factor such as temperature or rainfall may be absent and different combinations of climatic factors limit growth at different times in successive years (Armstrong, 1993).

Few studies have been carried out on the seasonal growth of crustose species as they have substantially slower radial growth rates (RGR) (Hale, 1967). The seasonal growth of two crustose species, viz., *Rhizocarpon reductum* Th. Fr. and *Lecidea tumida* Massal. (= *Porpidia tuberculosa* (Sm.) Hertel & Knoph) was studied in south Gwynedd, Wales over a single year (Armstrong, 1973). Maximum growth occurred in the period May–June but it was not possible to correlate growth with climate. The crustose lichen *Rhizocarpon geographicum* (L.) DC. has an especially low RGR with rates of less than 0.1 mm yr^{-1} (Beschel, 1961; Hooker, 1980; Haworth et al., 1986) at many sites. The slow RGR and consequent longevity of *R. geographicum* has made it one of the most important species in dating the age of exposure of substrata (lichenometry) (Beschel, 1961). However, very little is known of the environmental factors that influence the growth of this key species (Innes, 1985; Bradwell, 2001). The early growth of *R. geographicum* was studied by Asta and Letrouit-Galinou, 1995). They proposed that four processes contributed to the development of a mature thallus, viz., the formation of primary areolae, growth and division of areolae, the confluence of areolae, and the fusion of individual thalli to form larger individuals. In the present study, the RGR of *R. geographicum* thalli was measured in three-month periods over 51 months in south Gwynedd, Wales; a site where this species has a relatively high RGR (Armstrong, 1993; 2005a). The specific objectives were to determine whether: 1) *R. geographicum* exhibited a seasonal pattern of growth, 2) the seasonal pattern was consistent from year to year, and 3) the seasonal growth pattern correlated with climatic variables.

2. Materials and Methods

Study site

The study was carried out at a site in South Gwynedd, Wales (Grid Ref. SN 6196) in an area of Ordovician slate rock described previously (Armstrong, 1974). Slate outcrops varying in surface area from 2–30 m^2 are a common feature of the hillsides in this region. These surfaces possess a rich lichen flora characteristic of siliceous rock in the north and west of the UK (James et al., 1977) and include communities with a high proportion of crustose species (Armstrong, 1974). *Rhizocarpon geographicum* is a constituent of a number of different communities at the site, especially on south-facing rock surfaces.

Lichen species

Identification to species can be difficult in the yellow-green *Rhizocarpon* group. The lichen group most frequently used in lichenometric dating studies is *Rhizocarpon* Ram. Em. Th. Fr. subgen. *Rhizocarpon*. This subgenus is subdivided into four sections, viz., *Superficiale*, *Alpicola*, *Viridiatrum* and *Rhizocarpon* (Poelt, 1988). Thalli can be identified to section level fairly easily using the identification criteria suggested by Benedict (1988). All thalli included in the study were identified as *Rhizocarpon* section *Rhizocarpon* (L.) DC, i.e., spores greater than two-celled, epihymenium not black, medulla I+ intense blue/violet (Benedict, 1988). By contrast, identification to species level within a section is extremely difficult, especially in the *Rhizocarpon* section. Using the broadly circumscribed criteria of Purvis et al. (1992), however, the thalli included in this study were all identified as *R. geographicum* (L.) DC. These different approaches to nomenclature within the yellow-green *Rhizocarpon* group, make it difficult to compare the results of lichenometric studies with those carried out by direct measurement.

The RGR of *R. geographicum* increases with thallus size to a maximum (0.4–0.8 mm yr^{-1}) in individuals 2–5 cm in diameter after which growth declines (Armstrong, 1983; 2005a; Haworth et al., 1986; Bradwell, 2001). Hence, to maximize growth rates and reduce the degree of between thallus variability, 20 thalli of *R. geographicum* 2.0–5.0 cm in diameter were measured *in situ* on a single rock surface. The rock surface was steep-sided and of southeast aspect (315°). All thalli chosen for measurement were relatively symmetrical, without disintegrating centres, and were located at least 1 cm from their nearest competitor.

Climatic records

Climatic data were obtained from the Welsh Plant Breeding Station, Plas Gogerddan, near Aberystwyth, approx. 8 miles to the south and at the same altitude as the sample site. Previous studies have suggested that a number of climatic variables could influence the seasonal growth of lichens (Armstrong, 1973, 1993). Hence, the following variables were included in the study: 1) total rainfall over each three-month period (Armstrong, 1973; Armstrong, 1976; Fisher and Proctor, 1978; Lawrey and Hale, 1977), 2) the total number of rain days (Armstrong, 1976), 3) maximum (Tmax) and minimum (Tmin) temperature recorded on each day and averaged for each three-month period (Fisher and Proctor, 1978; Lawrey and Hale, 1977), 4) the total number of air and ground frosts, 5) the total number of sunshine hours (Armstrong, 1973; Lawrey and Hale, 1977), and average daily wind speed (Armstrong 1975). The frequency of cloudy days may also be important (Hausmann, 1948; Rydzak, 1961; Lawrey and Hale, 1977) but these data were not available for the period under study. A limitation of this type of study is that growth at the site is related to climatic records compiled from some distance away (Armstrong, 1991; Lawrey and Hale, 1977) and such data should not be used without corroborating measurements (Lawrey and Hale, 1977). Hence, total rainfall and temperature measurements were also made adjacent to the lichens on a sample of days and these data correlated well with daily records from Plas Gogerddan (Pearson's 'r'>0.80).

Measurement of radial growth

R. geographicum comprises discreet areolae containing the alga *Trebouxia* on a black fungal hypothallus that extends beyond the areolae to form a marginal ring 2–3 mm in width (Armstrong and Bradwell, 2001). The marginal hypothallus grows particularly slowly and depends on transport of carbohydrates from adjacent areolae (Armstrong and Smith, 1987). The radial growth of the hypothallus (Armstrong and Smith, 1987) was measured at between eight and ten randomly chosen locations around each thallus at three-month intervals from April 1993 to

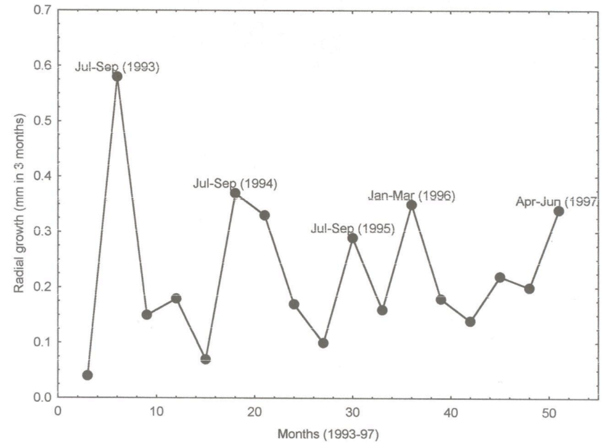

Figure 1. Mean radial growth of thalli of *Rhizocarpon geographicum* measured in 17 three-month periods from 1993 to 1997 in south Gwynedd, Wales, UK. Analysis of variance (two-way), between thalli, F=0.03 (P>0.05), between growth periods, F=3.86 (P<0.001).

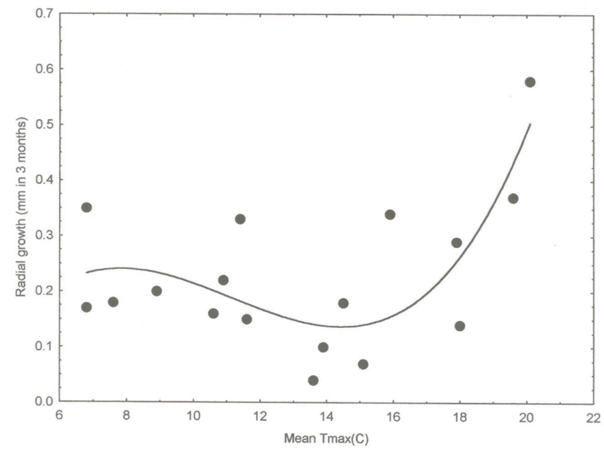

Figure 2. Relationship between radial growth of *Rhizocarpon geographicum* in each three-month growth period and mean maximum temperature (Tmax). Curve fit: cubic polynomial r=0.75 (P<0.01).

June 1997 using the method described by Armstrong (1973, 1975). Essentially, the advance of the hypothallus, using a micrometer scale, is measured in relation to fixed markers on the substratum. Radial growth in each period was averaged for each thallus and then over the 20 thalli to examine the pattern of seasonal growth.

Statistical analysis

Data analysis was carried out using SuperANOVA (Abacus Concepts Inc., Berkeley, CA 94704, USA) and STATISTICA (Statsoft Inc., 2300 East 14th St, Tulsa, OK 74104, USA) software. First, the data were analysed by a two-way (thalli and growth periods) analysis of variance (ANOVA) and subsequent comparisons between the growth means were made using Fishers protected least significant difference (PLSD). Second, the linear correlation between RGR in a growth period and the climatic variables was tested using Pearson's correlation coefficient ('r'). Third, a multiple regression and a forward (stepwise) multiple regression (Lawrey and Hale, 1977; Snedecor and Cochran, 1980) was carried out with RGR as the dependent variable. This analysis selects the climatic variables that may significantly influence growth in order of importance (Armstrong, 1991). Curves were also fitted to the relationship between RGR and each climatic variable using a polynomial curve-fitting program. A more complex curve was accepted as a better fit if it resulted in a significant reduction in the error sums of squares and an increase in Pearson's correlation coefficient ('r') compared with the preceding curves (Snedecor and Cochran, 1980).

3. Results

Mean RGR of *R. geographicum* in each three-month growth period over 51 months is shown in Fig. 1. Analysis of variance of the data suggested significant variation in RGR between growth periods (F=3.86, P<0.001) with five periods of notable growth, viz., in July–September during 1993, 1994 and 1995, in January–March of 1996, and April–June of 1997. The most significant period of growth during the study was in July–September 1993.

A summary of the relationships between the periods of significant growth and the climatic variables studied is shown in Table 1. Of the five growth maxima, four coincided with a mean Tmax over a three-month growth period exceeding 15°C and three with greater than 450 sunshine hours. Two of the growth maxima corresponded to periods of maximum rainfall of greater than 300 mm and one with more than 50 rain days. The remaining growth maximum, viz. January–March 1996, did not coincide with a period of either higher temperature or rainfall.

The results of the regression analyses are shown in Table 2. There were no significant linear relationships between RGR and any of the climatic variables analysed. In addition, in a multiple regression analysis, none of the regression coefficients (β) were significant and a stepwise multiple regression selected no significant variables. Nevertheless, a number of non-linear relationships were observed between RGR and the climatic variables. First, the relationship between RGR and the total number of rain days was fitted by a fourth-order (quartic) polynomial (r=0.69, P<0.05). RGR increased with increasing rain days to a peak between 30–40 rain days per three-month period and then declined with slightly increased growth between 60–70 rain days. Second, the relationship between Tmax and RGR was fitted by a third-order (cubic) polynomial (r=0.75, P<0.01), RGR increasing steeply after a mean Tmax of 17°C (Fig. 2). Third, the relationship between RGR and Tmin was fitted by a second-order (quadratic) polynomial curve (r=0.53, P<0.05), RGR increasing after a Tmin of 7°C. Fourth, the

Table 1. Distribution of the growth maxima of *Rhizocarpon geographicum* (Max RGR) during the 17 successive three-month growth periods and critical maxima and minima of the climatic variables.

Growth period	Climatic variables								
	Max RGR	RF >300 mm	RD >50	Tmax >15°C	Tmin <5°C	AF >15	GF >30	SH >450 hrs	WS >10 m s^{-1}
April–June (1993)			+						
July–September	+	+		+			+	+	
October–December		+					+		+
January–March (1994)			+		+	+	+		+
April–June				+				+	
July–September	+			+				+	
October–December		+	+						
January–March (1995)					+	+	+		
April–June								+	+
July–September	+	+	+	+					+
October–December		+	+		+	+			
January–March (1996)	+				+	+	+		
April–June								+	
July–September				+				+	
October–December		+	+		+	+			
January–March (1997)		+	+		+	+			+
April–June	+			+				+	

RGR = radial growth rate, RF = total rainfall (mm), RD = total number of rain days, Tmax = mean maximum temperature, Tmin = mean minimum temperature, AF = total number of air frosts, GF = total number of ground frosts, SH = total sunshine hours, WS = mean wind speed (m sec^{-1}).

Table 2. Correlations between the radial growth of *Rhizocarpon geographicum* in a three-month growth period and climatic variables at a site in south Gwynedd, Wales.

Variable	Linear analysis			Curvilinear analysis	
	'r'	β	't'	Type of curve	'r'
Total rainfall	0.26	0.62	1.10	–	NS
Number of raindays	0.10	0.47	0.57	Quartic	0.69*
Mean Tmax	0.31	1.75	0.46	Cubic	0.75**
Mean Tmin	0.30	1.43	0.45	Quadratic	0.53*
Total air frosts	0.11	0.68	1.11	Cubic	0.62*
Total ground frosts	0.27	–0.79	0.50	Quadratic	0.52*
Total sunshine hours	0.18	–0.40	0.27	–	NS
Average wind speed	0.22	0.08	0.18	–	NS

Abbreviations: Tmax and Tmin = maximum and minimum temperature, r = Pearson's correlation coefficient, β = regression coefficient, t = Student's t, NS = no significant relationship, ** $P<0.01$, * $P<0.05$.

total number of air and ground frosts was fitted by a third-order ($r=0.62$, $P<0.05$) and a second-order ($r=0.52$, $P<0.05$) polynomial respectively, in both cases RGR declining with increasing frequency of frost. The relationships between RGR and total rainfall, total number of sunshine hours, and average wind speed were not fitted successfully by any polynomial curve up to and including the fourth-order.

4. Discussion

The first objective was to determine whether *R. geographicum* exhibited a pattern of seasonal growth (Armstrong, 1993) and whether seasonal growth was consistent from year to year. The data suggest that *R. geographicum* does exhibit seasonal growth with periods of significant growth at distinct times of the year.

In addition, significant growth of *R. geographicum* occurred in different periods. In the first three years, maximum growth occurred in July–September, in the fourth year in January–March, and in the fifth year in April–June. In south Gwynedd (Armstrong, 1973), growth of *R. reductum* and *Lecidea tumida* was maximal in May–June with lower growth in November–January and particularly slow growth in August–October. In foliose species at the same site, periods of maximum growth are highly variable

(Armstrong, 1993). In *Parmelia* (=*Xanthoparmelia*) *conspersa*, a growth maximum occurred in the June of one year, September of the following year, and January of the third year (Armstrong, 1993). These patterns of growth contrast with those locations in which consistently severe winters (Benedict, 1991a;b; Hooker, 1980; Rydzak, 1961) or more stable patterns of rainfall (Boucher and Nash, 1990; Hale, 1970; Stone, 1986) result in similar seasonal patterns of growth from year to year.

The second objective was to determine whether variations in growth of *R. geographicum* could be related to climate. The most consistent relationship was with temperature. First, of the five periods of significant growth, four coincided with values of mean Tmax of greater than 15°C. Second, the strongest correlation was observed between RGR and Tmax, radial growth increasing steeply after a Tmax of 17°C. Third, RGR was also significantly correlated with Tmin and with the number of air and ground frosts, with lower growth at temperatures less than 7°C. These results contrast with those reported for foliose species at the site (Armstrong 1973, 1993) and at other locations (Boucher and Nash, 1990; Fisher and Proctor, 1978; Hale, 1970; Karenlampi, 1971; Lawrey and Hale, 1977) in which rainfall was reported as the most influential variable. Some previous studies have suggested that temperature could influence seasonal growth. In the foliose species *Physcia orbicularis* in south Gwynedd, RGR per month was positively correlated with mean daily Tmax and Tmin (Armstrong, 1993). In addition, a weak positive correlation between two foliose species *Parmelia* (=*Flavoparmelia*) *caperata* and *P. sulcata* and temperature was found in south Devon (Fisher and Proctor, 1978) while a Tmax of 25–30°C was found to be optimal for growth of *Pseudoparmelia baltimorensis* in Maryland, USA (Lawrey and Hale, 1977). Epilithic lichens are subject to much greater extremes of temperature than foliose species growing on the same substratum (Bradwell, 2001) and they must therefore, be able to tolerate very high and subfreezing temperatures. Studies suggest that *Rhizocarpon* species are tolerant of high surface temperatures. In the study of Coxon and Kershaw (1983), *R. superficiale* showed a broad response to temperature and a high resistance to heat stress characteristic of boundary layer habitats. However, radial growth of *R. geographicum* appears to be restricted at lower temperatures (Innes, 1985). Sensitivity to lower temperatures was also apparent in the study of Hooker (1980) who measured peripheral concentric growth rings in crustose species of *Buellia* and *Caloplaca* in Antarctica and showed that the zonation effect correlated with an unusually severe winter. The sensitivity of *R. geographicum* to low temperatures together with aridity may explain the extremely low growth rates of this species reported from Arctic and Alpine environments (Beschel, 1961; Armstrong, 2005b).

The data also suggest a relationship between seasonal growth of *R. geographicum* and rainfall. Two of the five periods of significant growth coincided with periods of maximum total rainfall suggesting that increased moisture is necessary for growth of this species. However, radial growth was optimal in periods with 30–40 rain days per three-month period and declined as the number of rain days increased. With increasing rain days, thalli are subjected to more wetting and drying cycles and may be vulnerable to losses of carbon by leaching and resaturation respiration (Smith and Molesworth, 1973; Armstrong, 1976). It is possible that carbohydrates are readily leached from the areolae of *R. geographicum* thalli making it especially vulnerable to increasing frequency of rain events.

A feature of the seasonal pattern of growth of foliose species in south Gwynedd is that periods of maximum growth can occur virtually in any season and depend on first, the distribution of periods of high total rainfall, and second, whether or not these periods coincide with periods of maximum sunlight (Armstrong, 1993). During the present study, maximum RGR over 51 months was observed in July–September 1993, an interval coinciding with a particularly favourable combination of temperature, moisture and sunshine hours. This observation suggests that as in foliose species, it is the interaction of variables in particular seasons that determine the seasonal growth of *R. geographicum*.

The growth peak in January–March 1996, did not coincide with a high Tmax or high rainfall but with low temperatures accompanied by frequent air and ground frosts. Stone (1986) found that the growth of *Ramalina farinacea* in western Oregon could not be predicted using climatic data alone and suggested that this could be due to growth of the lichen reflecting the environmental conditions of a previous season. In addition, there were no seasonal changes in photosynthetic capacity in *R. superficiale* suggesting differences in allocation or transport of carbohydrates in different seasons (Coxon and Kershaw, 1983). Hence, carbohydrates may be accumulated by lichen thalli in the summer months and not allocated for growth until later in the year. Such effects could explain the poor correlations between monthly growth measurements and climatic factors in a number of studies (Armstrong, 1988; Boucher and Nash, 1990; Lawrey and Hale, 1977). In the present study, the growth maximum in January–March was preceded by 6 months of higher than average rainfall. Carbohydrate may have accumulated in the areolae during this period but not released and transported to the hypothallus until early the following year. Hence, the seasonal pattern of growth of a symbiotic organism may be determined not only by the differential response of the symbionts to climate but also by environmental conditions that influence the physiological interactions between the partners.

In conclusion, in south Gwynedd, maximum growth of *R. geographicum* can occur in any season although the period July–September appears to be the most favourable. Significant radial growth is dependent on the interaction of a number of variables but the most important appears to be temperature. The growth of *R. geographicum* is encouraged by higher temperatures and inhibited by lower temperatures. The study also emphasizes the value of a non-linear statistical analysis in establishing the relationships between growth and environmental factors.

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