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Radial Growth of *Rhizocarpon* Section *Rhizocarpon* Lichen Thalli over Six Years at Snoqualmie Pass in the Cascade Range, Washington State

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Abstract

This article describes a 6-yr study of the radial growth rates (RGR, mm yr^{-1}) of *Rhizocarpon* section *Rhizocarpon* thalli on a talus slope at Snoqualmie Pass in the Cascade Range, Washington State, United States (47°27′N; 121°26′W). At the end of the growth period, 32 of a total of 39 thalli had exhibited a positive RGR, and 7 of a total of 39 thalli showed no measurable growth. Mean RGR of all thalli was 0.07 mm yr^{-1} (range, 0–0.19 mm, SD = 0.06). Analysis of variance suggested no significant variation in RGR in successive growth periods, but significant differences were present both within and between thalli. The slope of a boulder facet did not influence RGR, but growth was affected by aspect, the least growth being observed on north-northwest facets. A plot of RGR against thallus diameter revealed a wide scatter of data points with little evidence for a significant change in growth with thallus size. Hence, the study showed that the RGR of *Rhizocarpon* thalli at Snoqualmie is extremely slow and highly variable and significantly less than estimates based on lichenometry. To determine the growth curve of a yellow-green *Rhizocarpon* by direct measurement at such a site would require a large sample of thalli and careful standardization of the species studied, the aspect conditions under which the thalli were measured, and the initial hypothallus width of the thalli.

Introduction

The yellow-green species of the crustose lichen genus *Rhizocarpon* comprise discrete areolae, which contain the alga *Trebouxia*, located on a black prothallus or hypothallus composed of fungal hyphae. This hypothallus extends beyond the areolae to form a marginal ring of varying width but normally less than 2 mm. The marginal hypothallus grows particularly slowly, with annual rates of radial extension of the margin (RGR) that range from 0.02 to 2 mm yr^{-1} (Hale, 1983; Armstrong, 1983; Innes, 1985; Matthews, 1994).

The slow growth and longevity of the yellow-green *Rhizocarpon* species have made them especially valuable in lichenometric studies (Innes, 1985). In relatively dry areas, where growth rates are very low and *Rhizocarpon* is commonly assumed to grow at uniform rates for many centuries, the temporal range of lichenometric dating may exceed 9,000 yr (Miller and Andrews, 1972). Growth curves of *Rhizocarpon* species derived from lichenometric studies, i.e., where RGR is calculated from a graph of the diameter of the largest thallus vs. substratum age, are well established (Porter, 1981). Various growth phases are likely to be present, including establishment, juvenile, maturation, and senescence (Armstrong, 1983), and the duration of the various phases may influence the accuracy of the dating method. Most lichenometric studies suggest an initial "lag" phase leading to a phase of accelerating growth up to a maximum growth rate that is then followed by a phase of declining growth in which large thalli continue growing at a slower, more constant rate (Beschel, 1961; Mottershead and White, 1972; Miller, 1973; Innes, 1988). However, modern growth rates for *Rhizocarpon* species determined by direct measurement and averaged over several years can potentially provide close estimates of lichen age (McCarthy, 2003).

Relatively few studies have attempted to determine the growth curve of the yellow-green *Rhizocarpon* species by direct measurement especially in arctic and alpine environments. In particular, there is a scarcity of data relating to the final phase of growth in which there may be a decline in RGR (Armstrong, 1983). In most studies, the variability in RGR between individual thalli has been too great to establish the different growth phases with any certainty (Proctor, 1983; Haworth et al., 1986; Matthews, 1994; McCarthy, 2003). The present study measured the RGR of thalli of *Rhizocarpon* section *Rhizocarpon* over 6 yr on boulders of a talus slope at Snoqualmie Pass, Washington State, United States. The principal objectives were (1) to determine the overall RGR of *Rhizocarpon* at the site, (2) to study the variation in growth from year to year and between and within thalli, (3) to determine whether slope or aspect of the substratum influenced growth, and (4) to investigate the relationship between RGR and thallus size.

Materials and Methods

SITE

The study was conducted in the Cascade Range at Snoqualmie Pass, Washington State, United States, an area with a moist, maritime climate (mean temperature, 3.4°C; mean annual precipitation, 152 cm). The study site was a southwest-facing talus slope located at an altitude of ~940 m on the Snow Lake trail, at a distance of 0.8 km northwest of the Alpental Ski Area (121°26′W; 47°27′N). The talus slope comprised boulders of Miocene granodiorite of the Snoqualmie batholith (McKee, 1972). Average annual snowfall at Alpental is 1056 cm; the maximum recorded was 1987 cm (Northwest Weather and Avalanche Centre data). Yellow-green species of *Rhizocarpon* are among the most common crustose lichens on rock surfaces between 1000 and 2000 m in the Cascades (Porter, 1981) and the first species to establish on recently stabilized moraines and talus slopes.

LICHEN THALLI

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*,

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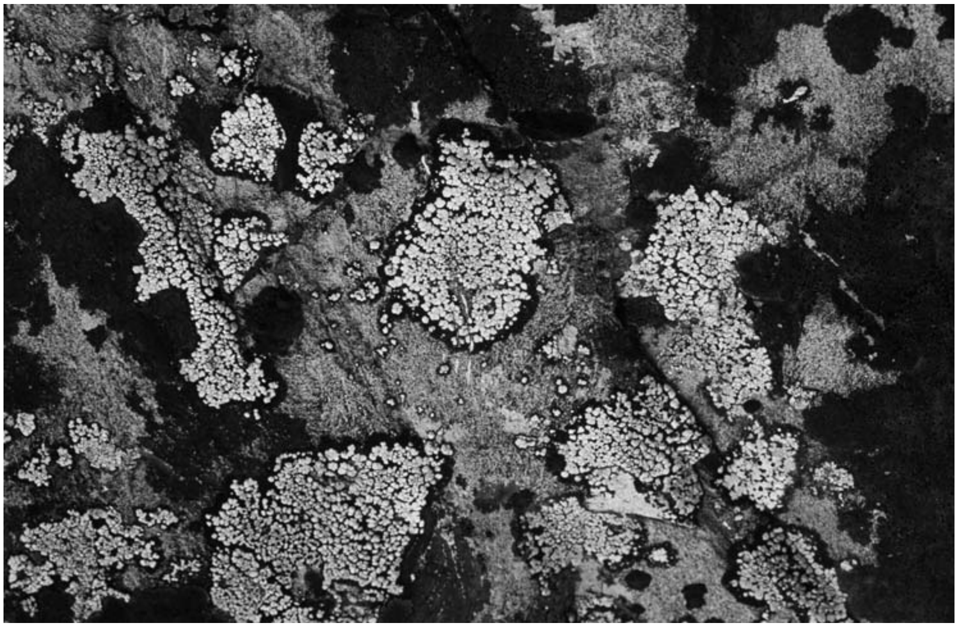

FIGURE 1. A boulder facet showing thalli of *Rhizocarpon* section *Rhizocarpon* at Snoqualmie Pass, Washington State. Image is courtesy of Dr. K. M. Wade.

Viridiatrum, and *Rhizocarpon* (Poelt, 1988). Thalli can be identified to section level fairly easily by 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, and was not attempted in the present study.

GROWTH MEASUREMENTS

The growth of a sample of 39 thalli of *Rhizocarpon* section *Rhizocarpon* (Fig. 1), 3–102 mm in diameter (the maximum size observed), was measured on 12 stable boulders at the site. A single, relatively smooth facet was selected from each boulder and between two and six thalli chosen for measurement from each facet. Each thallus was relatively symmetrical in shape, without evidence of thallus disintegration (Armstrong and Smith, 1997), had a distinct marginal hypothallus at least 1 mm in width, and was located at a minimum distance of 1 cm from the nearest lichen thallus to avoid competition (Armstrong, 1982). The aspect and slope of each facet was determined by compass and clinometer, respectively, as described previously (Armstrong, 1974).

The RGR of a *Rhizocarpon* thallus can vary at different locations around the thallus perimeter (Armstrong and Bradwell, 2001). Hence, four locations were selected at random around each thallus, and the RGR of the hypothallus was measured by using previously described methods (Armstrong, 1973, 1975). Essentially, the advance of the hypothallus was measured along guidelines marked on the boulder surface. Measurements of growth increments were made with a Beck Kassal CBS lens with a ×8 magnification incorporating a 1-cm micrometer scale divided into 100 divisions. Growth measurements were made on dry days during the month of August from 1988 until August 1994. Initially, measurements were made each year until 1990 and then, as a consequence of the very low growth rates recorded, at 2-yr intervals until 1994.

DATA ANALYSIS

Variations in RGR within thalli, between thalli, and between growth periods were analyzed by analysis of variance (ANOVA). The total variance was partitioned into components, i.e., the proportion of the total variance attributable to different locations within a thallus, between thalli, and between growth periods. The growth data from the first 2 yr and the final 4 yr were analyzed separately. The correlation between RGR of each thallus and slope of the facet was tested by using Pearson's correlation coefficient r. To determine whether aspect influenced growth, boulder facets were divided into six groups, viz., those facing east, east-southeast, south-southeast, south, southeast, and west-northwest. Growth rates were averaged for each thallus and compared between facets by using a one-way ANOVA. Subsequent comparisons between the different aspects were made by using Fisher's protected least-significant-difference (LSD) posthoc test. Relationships between thallus diameter and RGR were studied by using correlation and regression methods.

Results

Total radial growth of each thallus over the 6 yr is shown in Table 1. At the end of the 6-yr growth period, 32 out of 39 (82%) thalli had exhibited a positive RGR and 7 out of 39 (18%) thalli showed no measurable growth. In the latter group, 6 out of 7 thalli also showed evidence of disintegration of the areolae, and in one thallus the marginal hypothallus had retreated from its starting position. Mean RGR, averaged over the 6 yr, was 0.07 mm yr^{-1} (range 0–0.19 mm yr^{-1}, SD = 0.06). No significant correlation was observed between growth over 6 yr and the slope of the facet ($r = -0.15$, $P > 0.05$). The data suggest that greatest growth occurred on south-southeast facets and lowest growth on west-northwest facets; Fishers LSD *posthoc* tests suggested significantly slower growth on west-northwest facets compared with the east-southeast and south-southeast facets.

The ANOVA of the within- and between-thallus variation and variation between growth periods is shown in Table 2. The ANOVA of the first 2-yr and the last 4-yr growth suggested no significant variation in RGR associated with the different pairs of growth periods. By contrast, significant variation was present between thalli and within individual thalli, the variance within thalli being the greater source of variation.

A plot of RGR against thallus diameter for all thalli is shown in Figure 2. A wide scatter of data points is evident and, excluding thalli exhibiting zero growth, there was no significant relationship between

TABLE 1

Total radial growth (millimeters in 6 yr with standard deviation in parentheses) of 39 thalli of the lichen *Rhizocarpon* section *Rhizocarpon* on boulder facets on a talus slope at Snoqualmie Pass, Washington State. Superscripts: "F" indicates disintegration of areolae, "R" indicates retreat or shrinkage of the hypothallus. Correlation between radial growth and slope of facet: $r = -0.15$, $P > 0.05$. Effect of aspect analyzed by one-way analysis of variance (ANOVA) yielded significant differences between aspects (Fishers PLSD) for ESE vs. WNW and for SSE vs. WNW.

			Thallus					
Facet	Aspect	Slope	1	2	3	4	5	6
A	SSE	50°	0.43 (0.55)	0.10 (0)	—	—	—	—
B	ESE	46°	0.13 (0.12)	0.93 (0.06)	0.17 (0.05)	0.23 (0.40)	—	—
C	ESE	45°	1.13 (0.15)	1.00 (0)	0.03 (0.07)	1.10 (0.17)	—	—
D	S	80°	0.39 (0.06)	0.57 (0.46)	—	—	—	—
E	ESE	30°	0.30 (0.36)	0^{F}	0.77 (0.68)	—	—	—
F	ESE	45°	0^{F}	0.89 (0.43)	0.57 (0.12)	0.30 (0.43)	0.30 (0.44)	—
G	SSE	70°	0.86 (0.23)	1.00 (0.50)	0.82 (0.29)	0.67 (0.49)	—	—
H	N	35°	0^{F}	0^{F}	—	—	—	—
I	SE	75°	0.40 (0.52)	0^{F}	—	—	—	—
J	E	90°	0.70 (0.58)	0.27 (0.31)	0.10 (0)	—	—	—
K	WNW	80°	0.25 (0.25)	0^{F}	0^{FR}	0.17 (0.29)	0.15 (0.07)	0.25 (0.98)
L	ESE	45°	0.45 (0.64)	0.83 (0.21)	—	—	—	—

diameter and growth rate ($r = 0.21$, $P > 0.05$), suggesting little significant change in growth rate with thallus size.

Discussion

GROWTH RATE OF RHIZOCARPON

The very low growth rate of thalli *Rhizocarpon* section *Rhizocarpon* over 6 yr is a notable feature of the Snoqualmie site. Comparisons with other sites should take into account the number of thalli measured, the range of size, the mode of measurement, and the general microclimatic conditions at the site. For example, Matthews (1994) measured the long axes of 63 thalli as much as 600 mm in diameter at a site of apparently optimal growth on an outer moraine. By contrast, Proctor (1983) used a photographic method to measure 22 thalli 1–18 mm in diameter at an alpine site in Switzerland. The mean RGR of ~0.07 mm yr^{-1} observed in the present study is significantly less than that reported by most previous studies, e.g., 0.4 mm yr^{-1} at a mountain summit in New Hampshire (Hausman, 1948), 0.48 mm yr^{-1} from Switzerland (Proctor, 1983), and 0.66 mm yr^{-1} in south Norway (Matthews, 1994). By contrast, the data are more consistent with a growth rate of 0.05 mm^{-1} in West Greenland reported by Beschel (1958, 1961) and 0.006 mm^{-1} (SD = 0.020) on Mount Audubon, Colorado, United States (J.B. Benedict, 2003, personal communication). The data also imply considerably lower growth rates for the Cascades than suggested by lichenometric studies by Porter (1981) at Mount Rainier. Extrapolating from the growth curves of Porter (1981) suggests a RGR for thalli as much as 10 mm in diameter of 0.57 mm yr^{-1}, whereas direct measurement of thalli 3–10 mm in diameter suggests a rate of 0.06 mm yr^{-1}. This discrepancy implies that there are factors other than growth rate of the hypothallus that may determine the size of small *Rhizocarpon* thalli such as the process of lichenization and whether individual thalli can fuse together to form larger colonies.

Lichens are poikilohydric organisms, and their growth is essentially determined by how long thalli are kept moist and, therefore, on total rainfall, number of rain days, and relative humidity (Armstrong, 1988, 1993). At higher altitudes, the length of the growing season is likely to be a critical factor (Beschel, 1950; Benedict, 1967, 1990, 1991; Webber and Andrews, 1973). Most of the annual rainfall at Snoqualmie Pass falls as snow (McKee, 1972); the site being snow covered from late November until early June. Photosynthetic activity, and hence growth, is likely to be reduced considerably during this period (Crittenden and Kershaw, 1979; MacFarlane and Kershaw, 1980; Porter, 1981). In the present study, 18% of the thalli sampled showed evidence of disintegration or hypothallus shrinkage—a much higher frequency compared with rock surfaces at low altitudes in Wales, U.K. (Armstrong and Smith, 1997)—and indicates the severity of the environment for lichen growth. During the summer months, snow melt may provide moisture early in the summer, but later, under conditions of high irradiance, the temperature of the rock surface may be considerably higher than the air temperature and water condensation may not be possible (Kappen

TABLE 2

Analysis of variance (ANOVA) of the within- and between-thallus growth variability and variation between growth periods of *Rhizocarpon* section *Rhizocarpon* thalli at Snoqualmie Pass. F = variance ratio. s^2_Y = component of variance between growth periods. s^2_{BT} = component of variance between thalli. s^2_{WT} = component of variance associated with difference locations within a thallus.

	ANOVA		Components of variance		
Period	F(yr)	F(thalli)	s^2_Y	s^2_{BT}	s^2_{WT}
1988–1990	0.23	1.81**	0	4.79×10^{-3}	1.77×10^{-2}
1991–1994	0.97	2.43**	0.12	5.83×10^{-2}	2.47×10^{-1}

** $P < 0.01$.

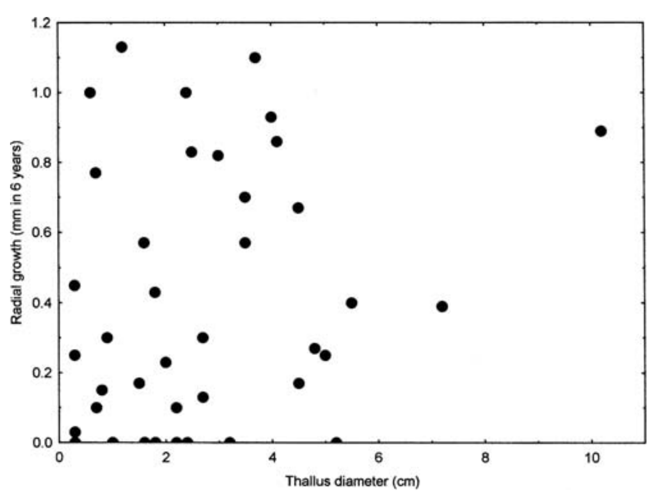

FIGURE 2. Relationship between the radial growth (millimeters in 6 yr) of thalli of *Rhizocarpon* section *Rhizocarpon* and thallus diameter at Snoqualmie Pass, Washington State (correlation, excluding thalli exhibiting zero growth: $r = 0.21$, $P > 0.05$).

et al., 1998). Hence, there may be a relatively short period when lichen thalli are exposed at Snoqualmie (Kappen et al., 1998), and within this period, relatively few days when photosynthesis and a positive net assimilation of carbon may be possible.

VARIATION IN RADIAL GROWTH RATE

There was little variation in RGR in successive growth periods, suggesting a relatively uniform pattern of growth from year to year at Snoqualmie. By contrast, significant within- and between-thallus variation was observed similar to that seen in lobed foliose lichens (Armstrong and Smith, 1992). The within-thallus variability was greater than that between thalli, leading to considerable differences in hypothallus width around the perimeter of the thallus. Previous studies have suggested that variations in the width of the hypothallus in *Rhizocarpon* are related to RGR (Proctor, 1983; Armstrong and Bradwell, 2001), faster-growing thalli and faster-growing regions of individual thalli being identified by their wider hypothalli. If the results from a small sample of thalli were consistent across size classes and ecotypes of *Rhizocarpon*, then (1) measuring only thalli with similar hypothallus widths and (2) averaging the growth at several locations around the thallus perimeter might reduce the variability in measurements of growth.

INFLUENCE OF ASPECT AND SLOPE

Lichen growth at Snoqualmie is likely to be controlled by many factors including microscale differences in the snow-free period, surface permeability and roughness, differential flow of nutrients associated with slope as well as differences in genotype and ecotype. Although slope of facet did not appear to influence growth rates, growth was dependent on aspect such that greatest growth was measured on facets facing east-southeast and south-southeast. McCarthy (1997) found that the largest thalli of *Xanthoria elegans* (Link)Th. Fr. were to be found on steep or overhanging facets of limestone clasts embedded in moraines and especially on surfaces of east-facing aspect. In addition, Haworth et al. (1986) found variations in the growth of *Rhizocarpon* thalli both between and within sites in the central Brooks Range, Alaska. Thalli at sites subjected to high to moderate light intensities grew approximately twice as fast as those at shaded sites (Haworth et al., 1986). In Iceland, Bradwell (2001) found the largest thalli of *Rhizocarpon* on south-facing surfaces of boulders. This particular preference for sunnier aspects could be attributable to the longer thermal operating period and the higher light intensities throughout the year (Bradwell, 2001).

RELATIONSHIP BETWEEN RADIAL GROWTH RATE AND THALLUS SIZE

The present study failed to provide conclusive data on the growth curve of *Rhizocarpon* section *Rhizocarpon* at the Snoqualmie Pass site and especially on whether there is a declining phase of growth in larger thalli. However, only 2 out of 39 of the thalli measured were >55 mm in diameter, the size associated with a slowing of RGR in *Rhizocarpon* in Wales (Armstrong, 1983). The majority of the previous studies carried out in arctic and alpine environments have also been inconclusive because of the high degree of variation in growth rates between thalli and lack of larger-diameter thalli included in the studies (Proctor, 1983; Matthews, 1994). The present study suggests that there are several sources of this variation. First, the inclusion of individuals of different species within the section *Rhizocarpon* may be a factor (Innes, 1985). There may be at least 16 species in the section *Rhizocarpon*, several of which may occur in the Cascades, and there may be significant differences in growth rate between species. Second, growth varies considerably at different points around an individual thallus, and data relying on a single or small number of measurement points will be highly variable. Third, microclimatic differences between sites are likely to be a significant source of variation. The present study indicates that although slope angle did not appear to be important, aspect did influence growth (Armstrong, 1975; McCarthy, 1997; Haworth et al., 1986; Bradwell, 2001). Hence, to attempt a determination of the growth curve of a yellow-green *Rhizocarpon* in an alpine environment by direct measurement will require large samples of thalli to allow for a high rate of mortality, and standardization of the species studied, aspect of the substratum, and the hypothallus width of the thalli.

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