Experiments on Lichen Growth, III. The Shape of the Age-Size Curve

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Abstract

A field experiment was conducted in the Front Range of the Colorado Rocky Mountains to test the hypothesis that lichen age-size curves differ in shape because an inherently sigmoidal growth pattern is interrupted at different stages in its development by a linear growth phase. Large, circular thalli of three morphologically dissimilar species were studied on smooth rock surfaces. Thallus interiors were removed with a knife and wire brush, creating curved wedges of lichen tissue. Distances from reference marks to the unmodified outer margins of the thalli were measured at various wedge widths. Measurements were repeated after 2–16 years, depending upon species. As predicted by the hypothesis, radial growth of *Xanthoparmelia coloradoensis* and *Lecanora novomexicana* accelerated with increasing wedge width, becoming linear at average rates of 2.01 and 0.12 mm yr^{-1}, respectively. Radial growth of *Rhizocarpon superficiale* accelerated to a maximum average rate of 0.016 mm yr^{-1}, then slowed, defining a more complete sigmoidal curve. This species showed no evidence of a linear growth phase, either because none exists or because the wedges were too narrow to detect it. The margins of *R. superficiale* thalli alternately advance and retreat due to changes in moisture availability and differences in photosynthate production within outer rings of areolate tissue. Hypothalli and areolae grow independently of each other over the short term, though their long-term growth rates must necessarily be similar. The data suggest that areolate crustose lichens are fundamentally different from foliose and placodioid lichens, and that inferences based on one group should not necessarily be extrapolated to another.

Introduction

If it were not for lichenometric dating, interest in lichen-growth patterns would be limited to a handful of mycologists. But glacial geologists, geomorphologists, and archaeologists have applied lichenometric techniques to problems of Holocene chronology on every continent. Lichenometric dating requires an understanding of growth processes and age-size relationships. This paper reports the results of a study designed to determine, by direct measurement, the growth characteristics of three lichen species with fundamentally different morphologies. Two of the species are important in lichenometry. The third has been useful in field experiments that have influenced our thinking about growth processes and lichen ecology.

Published age-size curves come in a variety of shapes (Mottershead, 1980). Two patterns, however, recur frequently in the literature. Growth of the *Xanthoparmelia* type (Fig. 1A) begins slowly, accelerates to a maximum rate, then becomes linear (Armstrong, 1976; Proctor, 1977; Benedict and Nash, 1990). Growth of the *Rhizocarpon* type (Fig. 1B) begins slowly, accelerates, but slows before it becomes linear (Beschel, 1950; Benedict, 1967; Miller and Andrews, 1972; Denton and Karlén, 1973; Calkin and Ellis, 1980; Gellatly, 1982; Rodbell, 1992; O'Neal and Schoenenberger, 2003; Larocque and Smith, 2004). One possible explanation for the difference in shape is that lichen growth is inherently sigmoidal—as it is for many plants, reptiles, birds, and mammals (Zullinger et al., 1984)—but that the basic S-shaped pattern is interrupted at different stages in its development by a linear growth phase (Benedict, 1985).

Why should lichen growth rates eventually become constant, and age-size curves linear? Laboratory studies of non-lichenized fungal colonies on solid media show that only the outermost parts of the colonies contribute to radial growth (Trinci, 1971). This is consistent with Beschel's (1958) suggestion that when lichenized fungi exceed a certain diameter their growth is controlled by processes operating in an outer ring of constant width. Trinci (1971) obtained experimental evidence that clogging of pores in the transverse crosswalls of fungal hyphae (the multicellular threads that make up the body of the thallus) limits the distances photosynthates can be transported to the growing margin of the colony. He referred to the ring in which transport occurs as the *peripheral growth zone*. No physiological, ultrastructural, or visible anatomical evidence of a peripheral growth zone has been reported in lichens (Hill, 1981). But foliose lichens whose centers have spalled, or have been artificially removed from their substrata, grow at rates similar to those of intact thalli (Vallot, 1896; Fink, 1917; Armstrong, 1974, 1979; Benedict and Nash, 1990; Armstrong and Smith, 1998), implying that the central portions of large lichens are irrelevant to the growth process.

According to the hypothesis outlined above, two factors determine the shape of a lichen's age-size curve: the radius at which sigmoidal growth begins to slow (*r*), and the width of the peripheral growth zone (*w*). Where $w \leq r$, a curve of the *Xanthoparmelia* type will develop (Fig. 1A). Where $w > r$, a curve of the *Rhizocarpon* type will develop (Fig. 1B). To test this hypothesis, I conducted a growth study at high altitude in the Front Range of north-central Colorado, U.S.A. When I began the study in 1985, I expected to complete it in five years. But slow growth of *Rhizocarpon superficiale* made it necessary to extend the observation period until 2002.
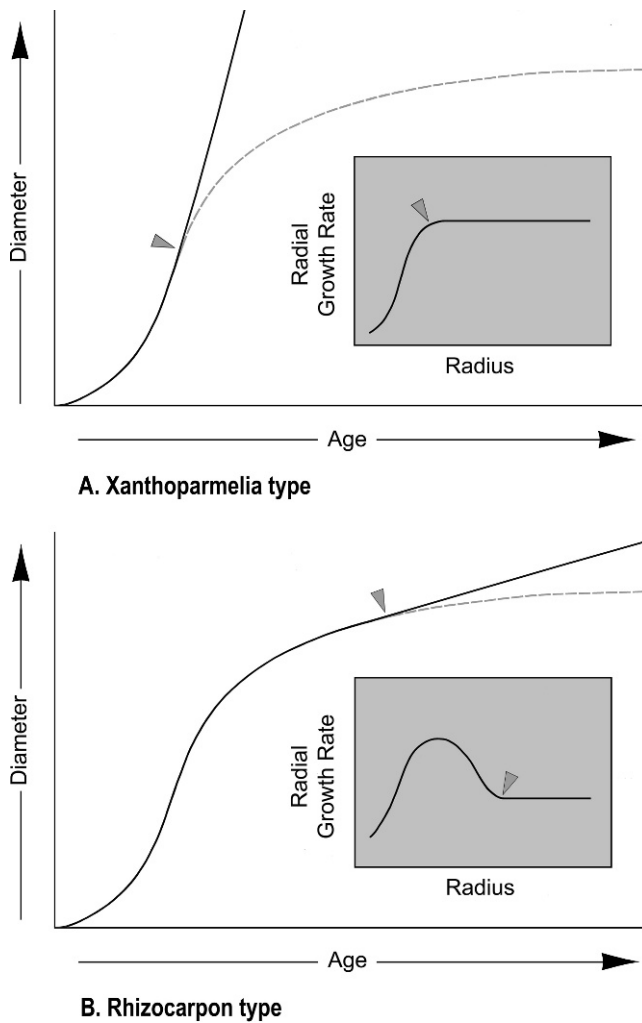
A. Xanthoparmelia type

B. Rhizocarpon type

FIGURE 1. Hypothetical age-size curves for fast-growing and slow-growing lichen genera, constructed at the beginning of the study (Benedict, 1985: Fig. 44). Shaded boxes show radial growth rates. Triangles mark the transitions from sigmoidal to linear growth, predicted to occur when the radius of the thallus first equals the width of the peripheral growth zone. In the absence of a linear phase, growth will continue to follow the sigmoidal course indicated by the dashed lines.

Methods

SELECTION OF SPECIES AND EXPERIMENTAL SITES

Large, circular thalli of three lichen species were selected at remote, high-altitude locations unlikely to be visited or disturbed by humans. All of the experimental sites are in the South St. Vrain Creek watershed, western Boulder County, Colorado (Fig. 2). Two are above tree limit in the Indian Peaks Wilderness Area. The third is on private ranchland in the lower fringes of the subalpine forest. All three localities provide smooth, stable rock substrata, ideal for growth measurements. Species identification was based upon thallus morphology, spore characteristics, and the chemistry of secondary metabolites, using keys in Runemark (1956a), Poelt (1988), Hale (1990), and Brodo et al. (2001).

Xanthoparmelia coloradoensis (Gyelnik) Hale is a fast-growing, light green, non-isidiate, foliose lichen capable of tolerating moderate quantities of winter snow. Because of its short life span and its susceptibility to spalling, the species is unsuitable for lichenometric dating. Its rapid growth rate, however, has made it a favorite subject of experimental studies (Benedict, 1990a, 1991;
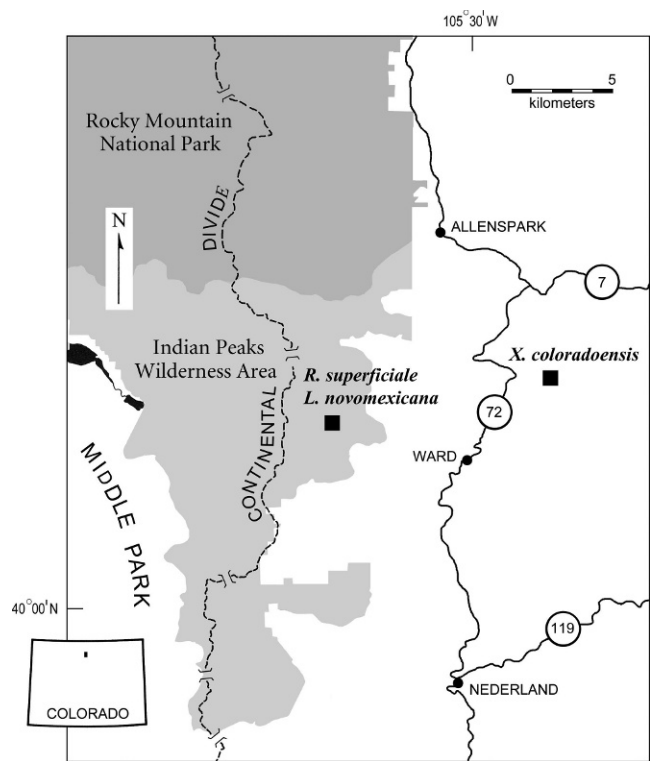

FIGURE 2. Map showing the locations of lichen-measurement sites. Route 72 is the Peak-to-Peak Scenic Byway.

Benedict and Nash, 1990). Formerly referred to in the Front Range as *Xanthoparmelia lineola* (Berry) Hale, it now is considered to be a separate species based on the ease with which it can be removed from rock substrata. Both species have similar chemical compositions and are said to intergrade in the western United States (Hale, 1990). The lobes of *X. coloradoensis*, like those of morphologically similar *Parmelia conspersa* (Armstrong, 1995), branch repeatedly to fill the spaces created by radial growth. Each lobe contains its own algal symbionts and grows independently, at different rates, though the thallus itself remains symmetrical (Hale, 1973; Armstrong, 1984, 2003). Five thalli were studied on unweathered outwash boulders of Precambrian granite and diorite on a catastrophic flood bar of South St. Vrain Creek, 2560 to 2570 m a.s.l. (Fig. 3). The site is shallowly snow-covered in winter and is partially shaded by trees. The experimental thalli grew on gently sloping rock surfaces with diverse orientations (Table 1). Thin-layer chromatography showed that usnic, salazinic, and consalazinic acids were present in all five thalli. Thallus 14 also contained a trace quantity of norstictic acid (Thomas H. Nash, III, personal communication, 1988).

Lecanora novomexicana H. Magnusson is a light green, placodioid lichen (crustose with a lobed, plicate margin) that contains usnic and psoromic acids. The species has been used in the Front Range to date rock surfaces with exposure ages as old as 1000 years (Reheis, 1975; Benedict, unpublished data). Within this time span, it provides excellent dating resolution. Previously referred to in the Front Range as *Lecanora thomsonii* (Benedict, 1968; Egan, 1970; Flock, 1978), it now is differentiated from that species based on its non-rugose thallus and distinct marginal lobation (Hale, 1982). Five thalli were studied in a glaciated, hanging valley on the southeast flank of Mount Audubon (Fig. 4, B). The lichens grew on boulders of Tertiary quartz monzonite (Gable and Madole, 1976), a rock type so siliceous that it requires a carbide-tipped chisel for sampling. Because of their extreme

FIGURE 3. Catastrophic flood deposit on the south bank of South St. Vrain Creek, Boulder County, Colorado. *Xanthoparmelia coloradoensis* thalli were studied on unweathered outwash boulders near the crest of the flood bar. Snow fills a backwater slough at the base of the cliff from which the photograph was taken. Photo: 2 May 1994.

hardness, the boulders show little or no evidence of granular disintegration. The *Lecanora* study site is in a depression behind the frontal ridge of a lobate rock glacier, at an altitude of 3550 m. Snow-covered in winter, it becomes snow-free by early July in most years. A sparse (10–30%) lichen cover is evidence that snow was more persistent at times during the Late Holocene (Benedict, 1999). Only snow-tolerant lichen species currently grow at this location. Like the moss polsters that occur alongside them, many of the *L. novomexicana* thalli have hollow centers. The experimental thalli grew on gently sloping rock surfaces with a variety of aspects (Table 1). All were unshaded.

Rhizocarpon superficiale (Schaerer) Vainio is an areolate, crustose lichen. Greenish-yellow areolae are crowded on a thin, black, fungal mat (the hypothallus or prothallus) that extends beyond the areolae to form the growing margin of the lichen. Each areole contains its own colony of the alga *Trebouxia*. The algae produce photosynthates, some of which are transported through fungal hyphae to the hypothallus margin, where they fuel growth (Armstrong and Smith, 1996). Black reproductive bodies (apothecia) develop among the areolae as the thallus matures. The apothecia produce sac-like structures (asci) containing eight spores, each divided into two cells by a central septum. *R. superficiale* is adapted to growth on siliceous rock types in alpine and polar environments (Runemark, 1956b; Thomson, 1967). Intolerance of late-lying snow (Benedict, 1990b) and of warm temperatures in the air-rock boundary layer (Coxson and Kershaw, 1983a, 1983b) explain its preferential occurrence in exposed, windy environments. With a lifespan of at least 5000 years, *R. superficiale* is one of the longest-lived species in the Front Range alpine region—hence is useful for dating relatively old substrata. Five thalli were chosen for study at altitudes of 3575 to 3585 m on blocky, stable talus a short distance east of the *Lecanora* locality (Fig. 4, A). The talus slopes northeastward at angles of 24–34°. A mature lichen cover (locally exceeding 95%) and large *R. superficiale* thalli (maximum diameter 162 mm) attest to its age, stability, and winter snow-free character. The talus consists entirely of light-colored quartz monzonite

boulders derived from an arête that has disintegrated so thoroughly that it no longer supplies fresh material (Fig. 4, upper left). The experimental thalli grew on steeply sloping to overhanging rock surfaces with southeasterly to northeasterly aspects (Table 1). Identification to the species level was based upon (a) two-celled spores, 10–18 μm long and 6–10 μm wide; (b) black epihymenia; (c) separation of hypothecia from rock substrata by white medullary tissue; and (d) coarsely verrucose areolae (Poelt, 1988; Benedict, 1988).

PREPARATION OF THALLI FOR MEASUREMENT

The technique used in this study was inspired by Trinci's (1971) experimental research on non-lichenized fungi. Trinci inoculated plate cultures with fungal spores, applying them in straight lines so that the resultant fungal colonies grew to be approximately rectangular. After growth rates had become constant, he cut the colonies diagonally using a sterile razor blade, forming wedges of severed tissue. He monitored each wedge photographically at 15-minute intervals under a microscope. Growth was slowest at the tip of the wedge. It accelerated as the wedge widened, then became constant. The width of the wedge at the inception of linear growth was interpreted to be the width of the peripheral growth zone. This varied from 0.4 to 8.7 mm, depending upon fungal species and strain. In the present study I modified Trinci's technique for use under field conditions on lichenized fungi whose growth rates are three to seven orders of magnitude slower than those of the fungal colonies studied in the laboratory.

Large lichen thalli with approximately circular outlines were selected for measurement. Interior tissue was removed with a knife and wire brush, leaving curved wedges with widths that tapered from a maximum of 38 mm to as little as 0.8 mm. The growing margins of the wedges were left unmodified. To eliminate the influence of competition, areas surrounding the wedges were cleared of all lichens. Rings of white enamel paint provided backgrounds for India ink benchmarks and aiming lines ruled and

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TABLE 1

Thallus characteristics, microenvironments, and growth rates.

Thallus number	Maximum diameter (mm)	Exposure of boulder surface	Slope of boulder surface	Original lichen cover (%)	Mean growth rate (mm yr^{-1})	
Xanthoparmelia coloradoensis (Gyelnik) Hale						
Precambrian granite and diorite, 2560–2570 m a.s.l., 1985–1987						
11	212	SE	13°	40	1.130	
12	202	WNW	18°	60	1.914	
13	144	WNW	32°	35	1.736	
14	293	ENE	23°	60	2.032	
15	123	ESE	33°	40	2.455	
Lecanora novomexicana H. Magnusson						
Tertiary quartz monzonite, 3540–3580 m a.s.l., 1985–1990						
6	124	NE	21°	30	0.136	
7	114	SE	15°	20	0.169	
8	143	NE	20°	15	0.125	
9	158	NNW	19°	20	0.096	
10	236	SE	20°	10	0.107	
Rhizocarpon superficiale (Schaerer) Vainio					Hypothallus Margins	Marginal Areolae
Tertiary quartz monzonite, 3575–3585 m a.s.l., 1986–2002						
1	101	ESE	Overhanging (24° from vertical)	50	−0.006	0.006
2	93	ENE	65°	50	0.026	0.024
3	115	ENE	70°	50	0.012	0.017
4	105	SE	Overhanging (16° from vertical)	70	−0.004	0.003
5	81	NE	Overhanging (9° from vertical)	50	−0.005	0.007

Note: Thallus 12 grew on diorite, all other *X. coloradoensis* thalli on granite. Thalli of other species grew on quartz monzonite. Growth-rate data for Thalli 4, 5, 6, and 7 are based on undersized samples due to unsatisfactory photography or spalling of tissue. Partial data for these thalli are included in the table to provide an approximate indication of growth response.

numbered with a 00 Rapidograph pen (Fig. 5). Each pair of markers was oriented so that the imaginary line between them bisected a lobe or bulge in the thallus margin. Gloss varnish, used to protect the ink lines, was refurbished at two-year intervals.

To evaluate the possibility, suggested by Jonasson et al. (1991), that water seeping across painted markers is toxic to lichens, ten intact thalli of *X. coloradoensis* growing on the sloping surfaces of Pleistocene outwash boulders a short distance west of the *Xanthoparmelia* study site were selected. Using the same paint and varnish employed in the experimental study, a broad stripe was painted up-dip from half of each thallus, leaving the other half in its natural state. Five boulders received stripes of white gloss enamel and five received stripes of varnish. Each thallus was photographed annually from 1993 until 2000, by which time the lichens had completely overgrown the stripes. There was no indication that moisture drainage across paint or varnish had damaged thallus tissue or caused differences in growth rate. Some brands and types of paint may be toxic to lichens, but the materials used in this study (Coast to Coast Anti-Rust Gloss Oil Enamel and Coast to Coast Interior/Exterior Gloss Varnish) are unlikely to have influenced marginal growth.

MEASUREMENT TECHNIQUES

Measurements were made after at least 24 hours without precipitation. *X. coloradoensis* and *L. novomexicana* were measured using dividers. One tip of the dividers was placed at the center of the India-ink "+", and the other at the leading margin of the lobe indicated by the aiming line (Fig. 5). The spacing of divider tips was recorded by pricking holes in an index card. Distances between the centers of the holes were measured in the

laboratory using a 7× comparator. Annual growth was calculated by subtracting final measurements from initial measurements, then dividing by the number of years in the measurement period. The widths of thalline wedges at each measurement location were determined at the beginning and end of the study; average width values were used in the data summaries. The technique worked well for both species, which grew relatively rapidly and were on gently sloping rock surfaces, well illuminated and easily accessed. Measurements of *X. coloradoensis* were begun in 1985 and repeated in 1987, by which time the margins of the thalli had begun to encroach upon the outer painted rings (Fig. 5). Measurements of *L. novomexicana* were made in 1985 and 1990. Spalling of tissue, benchmarks, and aiming lines made it necessary to exclude Thalli 6 and 7 from the growth-rate summary for this species (Fig. 7). Spalling appeared to have been purely a physical process, caused by the severity of the local environment, the smoothness of the quartz-monzonite joint surfaces, and the fragility of knife-cut wedge margins. Partial data for Thalli 6 and 7 are included in Table 1.

Attempts to measure growth of *R. superficiale* using dividers proved unsatisfactory. This was due partly to the species' extraordinarily slow growth rate, and partly to the fact that the experimental thalli grew on steep-to-overhanging, poorly illuminated rock surfaces that required lying for hours in awkward positions on coarse, angular talus. Replicate measurements made to the hypothallus margin at 40 locations around the periphery of Thallus 1 in 1995 showed a mean difference and standard deviation of 0.21 ± 0.16 mm. During a 16-year period (the eventual duration of the study), this would introduce an average error of 0.013 mm yr^{-1}, unacceptably large for such a slow-growing species. A midcourse change in methodology was required.
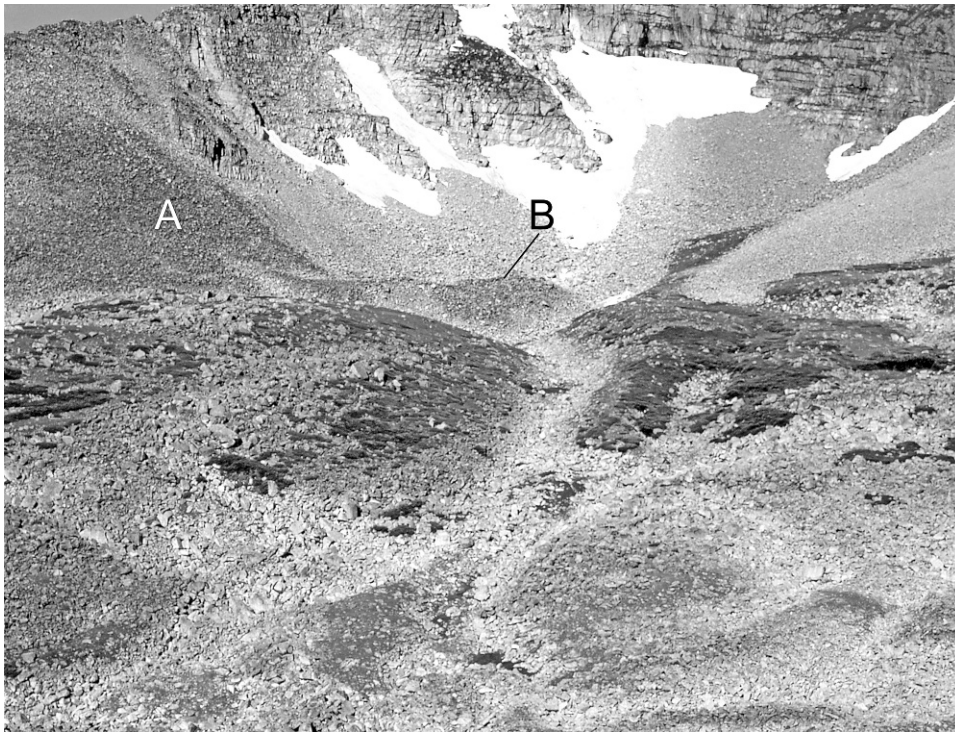
FIGURE 4. Floor of the hanging valley on the southeast flank of Mount Audubon. Thalli of *Rhizocarpon superficiale* were measured on stable talus (A). Thalli of *Lecanora novomexicana* were measured in a depression behind the front of a lobate rock glacier (B). Areas of dark-colored debris are blown free of snow in winter and have mature lichen covers. Areas of light-colored debris experienced lichen snow-kill during the Late Holocene (Benedict, 1999). Photo: 27 August 1990.
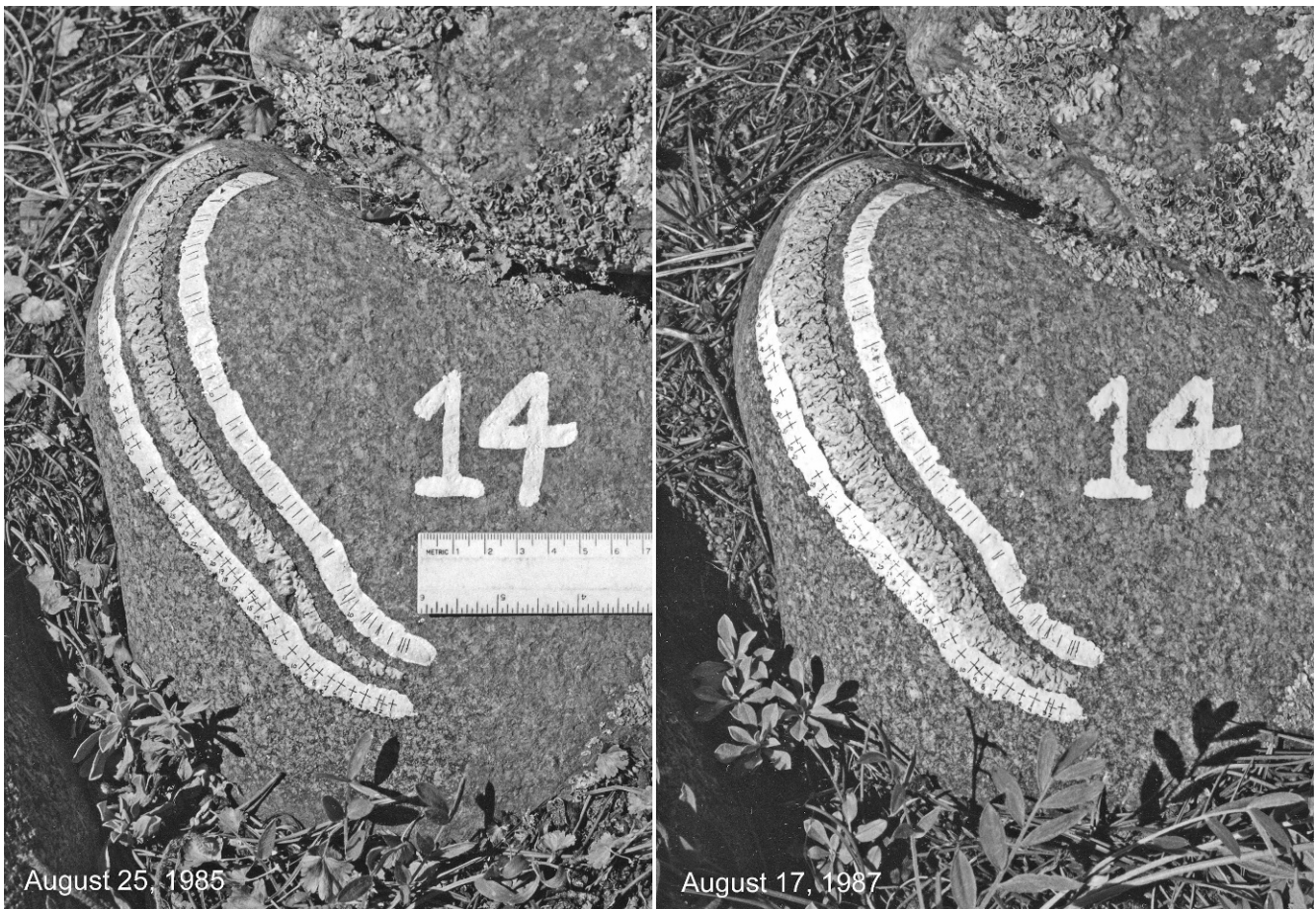

August 25, 1985

August 17, 1987

FIGURE 5. Photographs of an experimentally modified *Xanthoparmelia coloradoensis* thallus, showing reference crosses and aiming lines used to measure radial growth. By the conclusion of the two-year study, new lobes had begun to form along the knife-cut inner margin of the wedge. The lobes were widely spaced, however, and were too small to be clearly visible in the photograph.
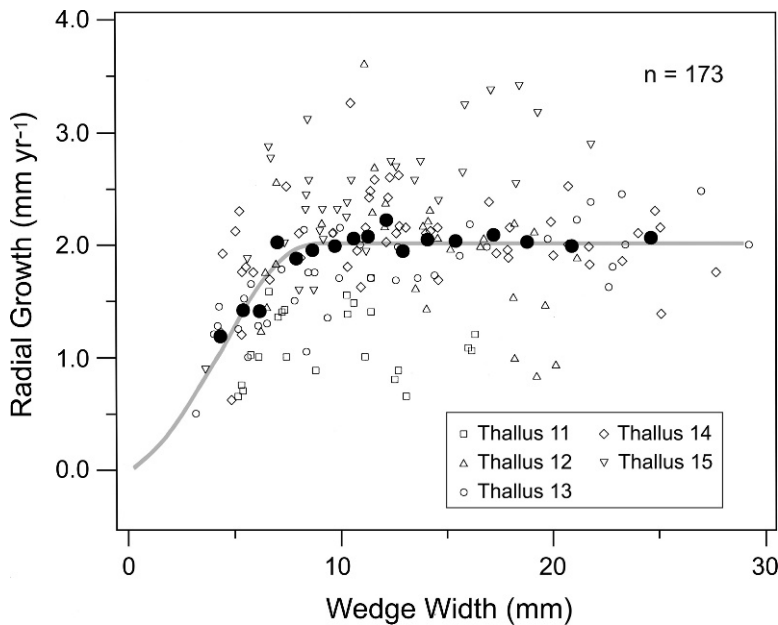
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FIGURE 6. Radial growth of experimentally modified *Xanthoparmelia coloradoensis* thalli (1985–1987), measured to the tips of well-defined lobes. Black dots are 10-measurement averages except for the final dot, which is based on 13 measurements. The curves in Figures 6–8 are fit by eye to the average values.

The incised *R. superficiale* thalli, first photographed on 15 July 1986, were rephotographed on 25 July 2002. The camera was a handheld Hasselblad 500C single-lens reflex with an 80-mm lens and 0.5-m Proxar close-up lens, focused at infinity. Medium-format (6 × 6 cm) black-and-white negatives were enlarged in the chemical darkroom and scanned at 600 ppi for use in Adobe Photoshop 6.0. Images were adjusted so that the plastic millimeter scale included in each photograph was reproduced at natural size, precisely 23.62 pixels per millimeter. Original and repeat photographs were viewed side by side, on screen, to ensure that measurements were made to the same locations, and to note morphological changes during the 16-year period. Distances from the center of each benchmark to the outer margins of hypothalli and areolae were measured in pixels, as were the widths of thalline wedges at these locations. Measured distances between benchmark centers and the tips of aiming lines were used to correct for parallax caused by slight differences in 1986 and 2002 camera positions. Repeat measurements made in this manner at 25 locations around the periphery of Thallus 1 showed a mean difference and standard deviation of 0.079 ± 0.079 mm for the marginal hypothallus and 0.072 ± 0.052 mm for areolae. This

introduces average potential errors of 0.005 and 0.004 mm yr^{-1} into the annual growth-rate values for the species. Measurement errors are caused primarily by (a) the difficulty of locating the precise centers of benchmarks, particularly after they have begun to deteriorate with age; (b) the sometimes-indistinct outer margins of *Rhizocarpon* hypothalli and areolae; and (c) imperfect correction for parallax. Because these errors are nonsystematic, the 10-point average values in Figure 8 are believed to be reliable. The strongly negative average values for wedge widths of 27–30 mm are exceptions. All but one of the measured lobes in this width range were from Thallus 1, which consistently showed below-average growth (Fig. 8). If Thallus 2 had provided a comparable number of measurements, the curves would almost certainly have declined more gently. Thallus 4 was excluded from the summary graph due to shading and lack of detail in critical parts of the 1986 photograph, and to the need for unacceptably large parallax corrections. Thallus 5 was excluded due to severe spalling of lichen tissue and painted markers during the first years of the study. The limited data available for these thalli are included in Table 1 for comparative purposes.
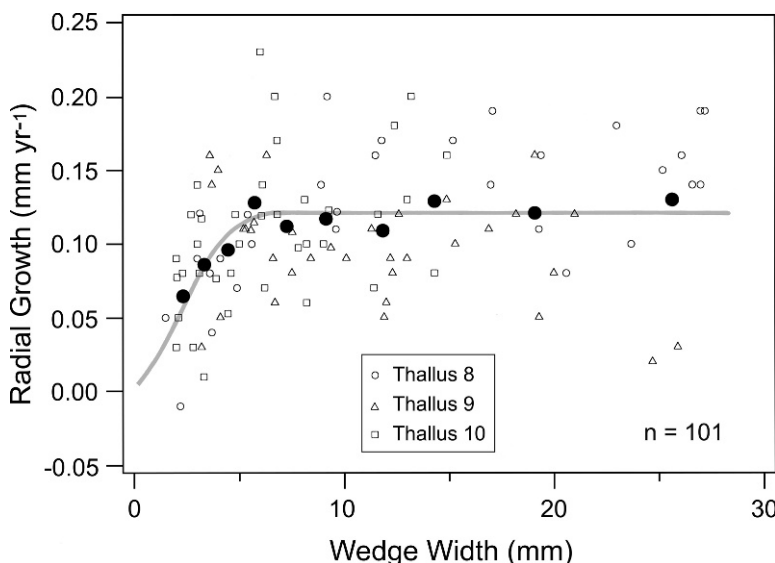

FIGURE 7. Radial growth of experimentally modified *Lecanora novomexicana* thalli (1985–1990), measured to the tips of marginal lobes. Black dots are 10-measurement averages except for the final dot, which is based on 11 measurements.
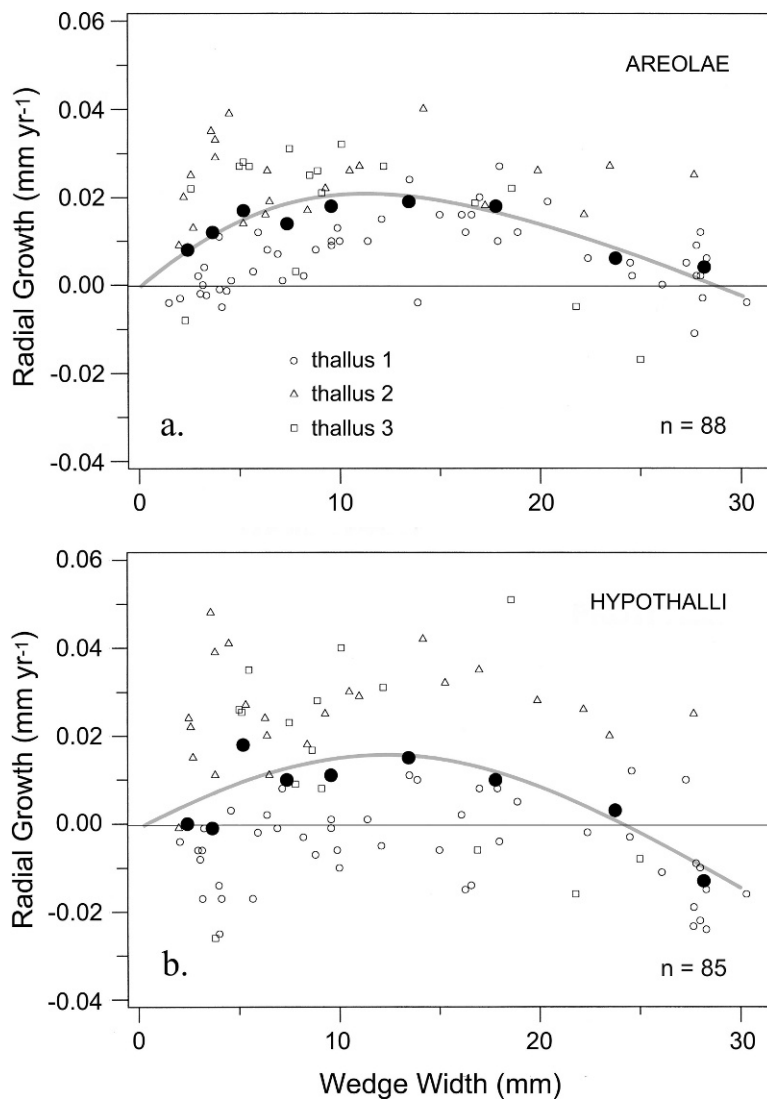
FIGURE 8. Radial growth of experimentally modified *Rhizocarpon superficiale* thalli (1986–2002), measured to the leading edges of marginal areolae and hypothalli. Black dots are 10-measurement averages except for the initial dot in each graph, which is the average of 8 or 5 measurements, depending upon sample size.

DETERMINATION OF PHOTOSYNTHETIC AREA AND AREOLE SIZE

Adobe Photoshop 7.0 was used to determine the photosynthetic areas of *R. superficiale* Thalli 1 and 2, representing opposite extremes of radial growth (Table 1). Scanned black-and-white photographs taken in 1985, before removing interior tissue and competing lichens (Fig. 9), were viewed on-screen at actual size and a resolution of 600 ppi. Representative areas of thallus tissue in central and marginal parts of the thalli were selected using the rectangular marquee or lasso tools. Areolae were easily distinguished from black apothecia and hypothalli by their light gray photo colors, making it possible to select them *en masse* based on color range (Select → Color Range → Fuzziness = 200). Total coverage by areolae was measured in pixels (Image → Histograms). This value was converted to a percentage basis by comparing it to the number of pixels in the original selection.

To determine the average sizes of individual areolae, representative areas of thallus tissue were chosen using the lasso tool, taking care not to truncate areolae in the process. Total coverage by areolae, determined in pixels as described above, was divided by the number of areolae in the selection to obtain mean individual area. This value was divided by 558 (the number of pixels in a 1 mm^2 area viewed at a resolution of 600 ppi) to obtain its metric equivalent.

Results

XANTHOPARMELIA COLORADOENSIS

All of the 173 measured lobes of *X. coloradoensis* registered positive growth during the two-year period of observation (Fig. 6). Individual lobes grew at radial growth rates of 0.50 to 3.60 mm yr^{-1} (Table 2). Thallus 15, which received partial shade and was the last of the thalli to become snow-free in spring, grew fastest (Table 1). Thallus 11, which was unshaded and became snow-free two to three weeks earlier than Thallus 15, grew less than half as rapidly. New growth along the incised margins of the wedges was limited to the formation of widely spaced, thin-necked lobes (Fig. 5).

LECANORA NOVOMEXICANA

The growth-rate curve for *L. novomexicana* (Fig. 7) is based upon Thalli 8, 9, and 10, which were unaffected by spalling. All but one of the 101 measured lobes of these thalli registered positive growth during the five-year period of observation (Fig. 7). Individual lobes grew at rates of –0.01 to 0.23 mm yr^{-1} (Table 2). As was the case with *X. coloradoensis*, the data show considerable scatter. Thallus 8, which occupied a northeast-facing rock surface, grew more rapidly than Thalli 9 and 10, which were on surfaces less favorable for moisture retention (Table 1). Development of
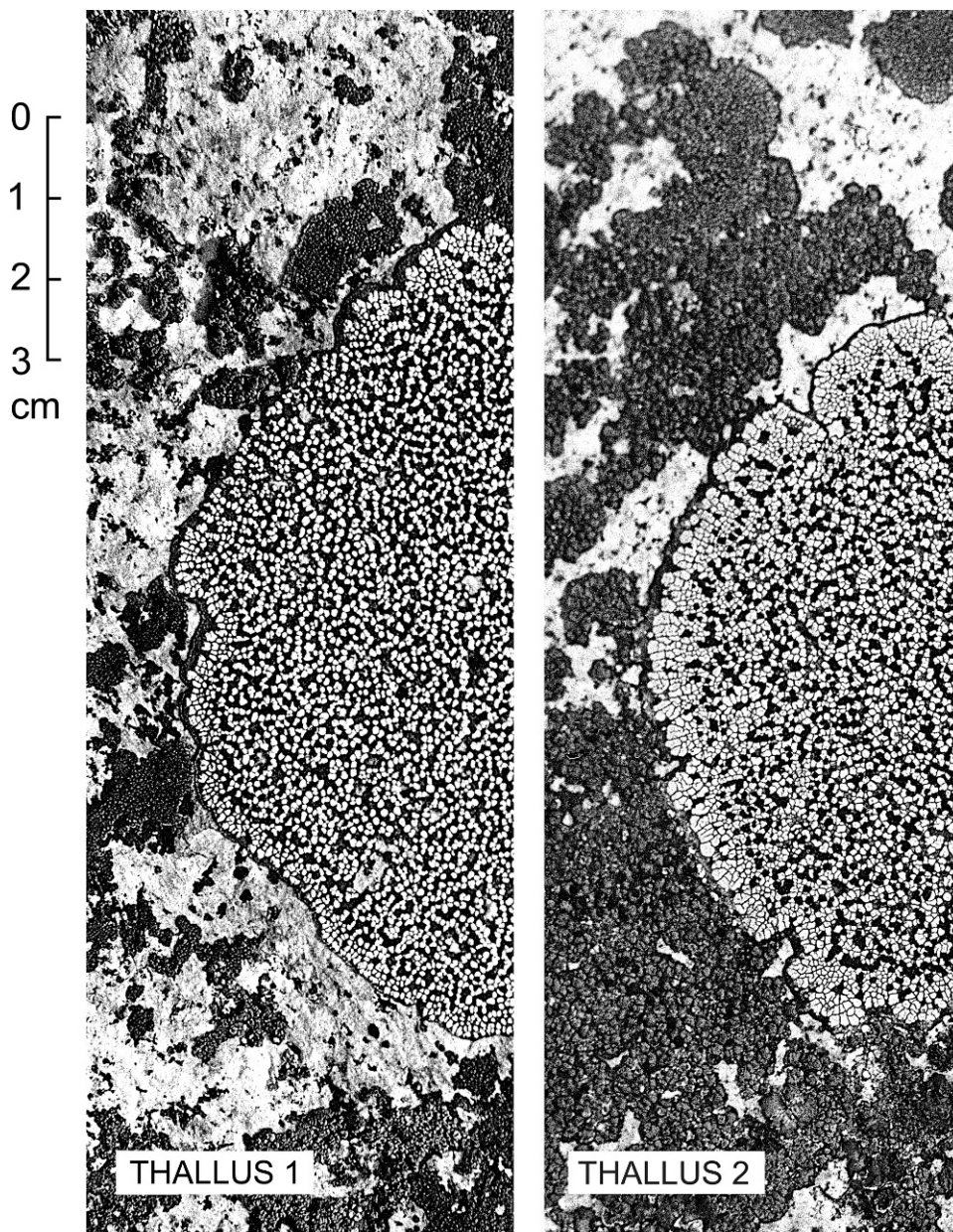
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FIGURE 9. Thalli of *Rhizocarpon superficiale* photographed on 1 July 1985, before removing their interior portions. The central areas of both thalli were morphologically similar. But outer rings of areolate tissue that had not yet developed mature apothecia were strikingly different. Within these rings the areolae of fast-growing Thallus 2 were 2.6 times larger, and provided 26.3% more total photosynthetic area, than those of slow-growing Thallus 1 (Table 3). This allowed Thallus 2 to supply larger quantities of photosynthates to the growing hypothallus margin.

new lobes along the incised inner margins of the wedges suggests that photosynthesis fueled growth in two directions.

RHIZOCARPON SUPERFICIALE

Figure 8 summarizes the combined growth data for Thalli 1–3, treating areolae and hypothalli separately. Thallus 1 showed predominantly negative hypothallus growth (shrinkage) and resorption of some incipient marginal areolae. Thallus 2 registered only positive growth, marked by expansion of the hypothallus, elongation and segmentation of marginal areolae, and emergence of new areolae. Thallus 3 showed intermediate characteristics, with net positive growth. Thalli 4 and 5, which were omitted from Figure 8 due to the limited number of reliable measurements, experienced

TABLE 2

Growth data for thalli used to construct Figures 6B8.

Species	Number of lobes measured	Radial growth (mm yr^{-1})		
		Range	Mean and standard deviation	Median
X. coloradoensis	173	0.50 to 3.60	1.90 ± 0.60	1.98
L. novomexicana	101	–0.01 to 0.23	0.11 ± 0.05	0.11
R. superficiale:				
Outermost areolae	88	–0.017 to 0.040	0.013 ± 0.012	0.012
Marginal hypothalli	85	–0.041 to 0.051	0.006 ± 0.020	0.002

Note: Growth values are based on all measured lobes. Mean growth rates for *X. coloradoensis* and *L. novomexicana* during their linear phases are 2.01 ± 0.56 and 0.12 ± 0.04 mm yr^{-1}.

TABLE 3
Comparison of areolae in slow-growing and fast-growing thalli.

Thallus no.	Mean growth rate (mm yr^{-1})	Photosynthetic area (percentage of total area occupied by areolae)		Average size of individual areolae (mm^2)	
		Marginal ring	Thallus interior	Marginal ring	Thallus interior
1	–0.006	49.4	40.9	0.28	0.42
2	0.026	62.4	42.9	0.74	0.40

negative average hypothallus growth (Table 1). All three negatively growing thalli occupied overhanging rock surfaces that rarely receive direct precipitation. Both positively growing thalli occupied surfaces that are moistened more frequently and that dry slowly due to their shaded, sheltered, east-northeast–facing orientations (Table 1). In retrospect, the sizes and photosynthetic areas of areolae in narrow (4–7 mm) outer rings of areolate tissue at the beginning of the study (Table 3) were leading indicators of the growth-rate differences that would later emerge. The larger the areolae and more extensive their coverage (Fig. 9), the more likely the hypothallus would show positive growth. Except for Thallus 2, areolae grew faster than hypothalli (Table 1). The incised margins of positively growing wedges developed new hypothalli along their entire lengths, suggesting that photosynthates were transported radially in both directions from wedge interiors.

Evaluation of the Hypothesis

Xanthoparmelia coloradoensis and *Lecanora novomexicana* both followed the *Xanthoparmelia*-type growth pattern illustrated in Figure 1A. Growth began slowly, accelerated to a maximum rate, then became constant. For *X. coloradoensis*, the transition to linear growth occurred at a wedge width of 8 mm and an average growth rate of 2.01 ± 0.56 mm yr^{-1}. For *L. novomexicana*, it occurred at a wedge width of 6 mm and an average growth rate of 0.12 ± 0.04 mm yr^{-1}. In both cases, the transition to linear growth was abrupt. New growth along incised margins suggests that by the end of the study, wedge widths had become equivalent to thallus diameters rather than thallus radii. The change from radius to diameter may have occurred gradually, or soon after incision. Because of this uncertainty, the width of the peripheral growth zone of *X. coloradoensis* is best treated as 4–8 mm, and the width of the peripheral growth zone of *L. novomexicana* as 3–6 mm. Regardless of the exact values, they fall in the ranges determined by Trinci (1971) for nine species of non-lichenized fungi (0.4–8.7 mm), and estimated by J. F. Farrar (unpublished, cited by Hill, 1981) for 10 species of lichenized fungi (2–11 mm).

The growth pattern of *R. superficiale* was radically different. Growth of the hypothallus margin accelerated to a maximum average rate of 0.016 mm yr^{-1}, reaching that rate at a wedge width of 10–15 mm. Growth then slowed significantly (Fig. 8), tracing the sigmoidal course predicted by Figure 1B. There was no evidence, however, of the anticipated linear growth phase. Whether or not the species ultimately grows at a constant rate (Fig. 1B) remains open to question. Based on the measurements reported in this paper, and on direct measurements by Armstrong (1983, 2005b) and Matthews (1994), there is little reason to be confident that it does so. The studies suggest that sigmoidal growth continues uninterrupted throughout the lifespan of the rhizocarpon thallus, following the dashed line in Figure 1B, and becoming asymptotic to a low average growth rate that remains positive over the long term (though it was negative in this short-term study due to unfavorable moisture conditions).

It also is possible that a linear growth phase exists, but went undetected due to an error in experimental design. Like Trinci (1971), I assumed that wedge widths would be equivalent to thallus radii. Based on an age-size curve constructed by measuring the diameters of the largest yellow rhizocarpon thalli on dated substrata in the Colorado Front Range (Benedict 1985: Fig. 43), I expected the linear growth phase to begin at a radius of 10.0–12.5 mm. Thus wedges with maximum widths of 25–30 mm would be amply large to record the onset of linear growth. But growth proceeded in two directions. If only the outer half of the wedge contributed photosynthates to the hypothallus margin, the wedges may have been too narrow to show clear evidence of linear growth. The disproportionate influence of negatively growing Thallus 1 in the largest width class (Fig. 8) may also have clouded the issue.

The initial, accelerating growth phases of all three lichen species (Figs. 6–8) are attributed to the exponential increase in photosynthetic area that occurs as the thallus becomes larger. As a result of this increase, progressively larger quantities of carbohydrate become available to fuel marginal expansion. The linear growth phases of *X. coloradoensis* and *L. novomexicana* reflect the limited distances that photosynthates can be transported by fungal hyphae. As suggested by Trinci (1971), transport distances are probably determined by clogging of pores in hyphal septa. The decelerating growth phase of *R. superficiale* is best explained by the diversion of photosynthates from radial growth to the formation of spore-bearing apothecia, and the concomitant decrease in photosynthetic surface area (Table 3). As measured along aiming lines in the 1986 photographs of Thalli 1–3, mature apothecia first appear at average distances of 4.8–7.3 mm from thallus margins, similar to the wedge radii at which growth rates begin to decline (5.0–7.5 mm). If *R. superficiale* experiences a linear growth phase, which remains unproven, clogging of pores in hyphal septa may be responsible.

Additional Thoughts on the Growth of *R. superficiale*

Mean radial growth of *R. superficiale* on the Mount Audubon talus, measured to hypothallus margins and calculated for the entire sample, was 0.006 mm yr^{-1} (Table 2). This value is 1–2 orders of magnitude slower than rates determined by direct measurement of yellow rhizocarpon species in the Swiss Alps (Proctor, 1983), the Columbia Mountains of western Canada (McCarthy, 2003), and the Cascade Range of Washington State (Armstrong, 2005a). It is 2–3 orders of magnitude slower than rates measured in Wales (Armstrong, 1983, 2005b) and southern Norway (Matthews, 1994). Why was growth so remarkably slow at the Colorado locality? One possible explanation is that *R. superficiale* is inherently slower-growing than other members of the subgenus. But in New Zealand, Bull and Brandon (1998) found that *R. superficiale* grew at approximately the same rate as *R. geographicum*—a conclusion supported by similar maximum dimensions where the species occur together in the Front Range. Another possibility is that trauma resulting from wedge preparation caused thalli to divert energy from marginal growth to the repair of damaged tissue. There is no evidence, however, that trauma affected the growth rates of experimentally modified thalli of *X. coloradoensis* or *L. novomexicana*.

The high frequency of hypothallus retreat on overhanging rock surfaces that seldom receive moisture (Table 1) suggests that slow growth is a result of the dry talus microenvironment. Mean annual precipitation at the University of Colorado's nearby D–1 weather station was 1175 mm during the measurement period (INSTAAR, 2005). Almost three-quarters of the annual total fell as snow during the months of November to May. Much of the winter snow was blown eastward by westerly winds, making it unavailable to lichens on the Mount Audubon talus. Summer rain fell mainly during fast-moving convectional thunderstorms, which can be deleterious to lichen growth. Laboratory studies have shown that when dry thalli are rehydrated, photosynthesis recovers more slowly than respiration. Several hours can elapse before the thallus shows a net gain in carbon assimilation (Smith and Molesworth, 1973; Farrar and Smith, 1976; Brown et al., 1983). By then the storm has usually passed, the sun is shining, and Front Range lichens have dried or are drying. Bimonthly growth measurements of *X. coloradoensis* confirm that long periods of mist and gentle rainfall are more favorable for growth than periods of clear weather punctuated by thunderstorms, though the latter provide much greater total precipitation (Benedict, 1990a). In a continental environment such as the Front Range, growth of yellow rhizocarpon thalli is probably episodic. Negative growth may be the rule, with positive growth restricted to rare years or decades in which cloud and drizzle maintain thallus saturation for weeks at a time. If the measurement period had included long intervals of sustained moisture, the growth-rate curves would probably have been shaped similarly to those in Figure 8, but would have remained in positive territory throughout their courses. For a species as slow-growing and long-lived as *R. superficiale*, a 16-year study provides only a small (potentially unrepresentative) sample of the conditions a thallus will experience during its lifespan. Assuming significant long-term changes in moisture availability during the Holocene, a stepped age-size curve of the sort suggested by Curry (1969) may be most appropriate for lichenometric dating. To develop such a curve, however, will require more numerous and better-dated control points than are available in the best of existing age-size curves.

Areolae and hypothalli of *R. superficiale* grew independently of each other between 1986 and 2002 (Table 1). During this period, marginal areolae grew 2.2 times faster, on average, than the outer margins of hypothalli ($t = 2.62$, $p = <0.01$). Differences were largest on Rocks 1, 4, and 5, representing the three most xeric microenvironments (Table 1). In Wales, Armstrong and Smith (1987) found the opposite to be true. There, areolae of *R. geographicum* grew slower than hypothalli during a 15-month study period. Large seasonal differences also were noted. (Armstrong and Smith, 1987; Armstrong and Bradwell, 2001). Such imbalances, however, can only be temporary. Under favorable moisture conditions, the marginal hypothallus will colonize new terrain. But if the hypothallus advances more rapidly than areolae can keep pace, it will outrun its supply of carbohydrates and be forced to slow or retreat. The Mount Audubon study may have begun at the end of a period of hypothallus expansion, leaving areolae in a catch-up mode, and causing the observed differences in hypothallus and areole growth rates (Table 1).

Morphological differences between slow-growing Thallus 1 and fast-growing Thallus 2 (Fig. 9) suggest that radial growth rates of *R. superficiale* depend in large part on the production of photosynthates in an outer ring of areolate tissue that supplies nourishment to the hypothallus margin. If areolae within this ring are large and densely packed, the lichen will grow vigorously. If areolae are small and widely spaced, the lichen will grow poorly. Measured ring widths vary from about 4 to 7 mm, similar to the widths of the peripheral growth zones of *X. coloradoensis* and *L. novomexicana*. The origins of the rings, however, may differ.

For the user of lichenometry, the most important conclusion of this study is that areolate crustose lichens grow differently than foliose and placodioid lichens. Inferences based on the direct measurement of fast-growing foliose species are not necessarily applicable to slow-growing areolate species such as *R. superficiale*.

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Appendix A

SUGGESTIONS FOR IMPROVING MEASUREMENT TECHNIQUES

The techniques used in this study could be improved in several ways. An incision that severed hyphal connections without removing interior parts of the thallus might discourage new growth along the incised margin, simplifying the interpretation of peripheral growth-zone width. It might also reduce spalling of thallus tissue, which in this study commonly (though not invariably) began at incised edges. The need to correct for parallax when using the photographic technique could be eliminated by mounting the camera on permanent supports cemented or bolted to stable boulders. Use of paired electronic flash units (Brodo et al., 2001) would provide uniform lighting and improve image sharpness. Adobe Photoshop is a useful tool for lichen growth measurement, greatly increasing its precision. Other applications of Photoshop technology to lichenometry should be explored, as McCarthy and Zaniewski (2001) have done in the measurement of percentage cover, and I have done in the determination of photosynthetic area (Fig. 9). Studies of subgenus *Rhizocarpon* are best conducted in regions where growth rates are faster than in the Front Range, making it possible to obtain results in a reasonable period of time, and reducing the influence of measurement error. The importance of large sample sizes cannot be overemphasized.