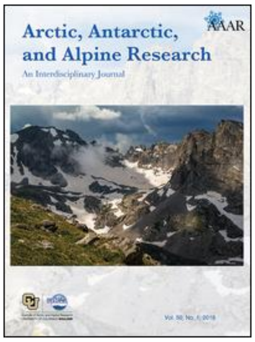

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DIRECT MEASUREMENT OF LICHEN GROWTH IN THE CENTRAL BROOKS RANGE, ALASKA, U.S.A., AND ITS APPLICATION TO LICHENOMETRIC DATING

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ABSTRACT

The growth of 92 *Rhizocarpon geographicum* s.l. and 57 *Alectoria minuscula* Nyl. lichens was measured over 4 to 6 yr in the Atigun Pass region of the central Brooks Range, Alaska. Absolute growth rates of *R. geographicum* s.l. were inversely related to thallus diameter and ranged from 0.35 to near 0 mm yr^{-1}. In contrast, *A. minuscula* growth rates were directly related to diameter and ranged from 0.14 to 2.01 mm yr^{-1}. A growth curve derived from mean rates of *R. geographicum* s.l. growth is similar to the indirectly controlled lichenometric dating curve for this region, but cannot yet be used to modify ages assigned to Holocene deposits. The derived growth curve for *A. minuscula* closely resembles those from the eastern Canadian Arctic.

INTRODUCTION

Circumpolar lichens of the slow-growing *Rhizocarpon* subgenus form the basis for lichenometric dating of Holocene glacial deposits in the central Brooks Range. For the youngest of these deposits, a faster-growing species, *Alectoria minuscula* Nyl., has also been used. In constructing a lichenometric dating curve for the central Brooks Range, Calkin and Ellis (1980) used absolute control points from historic, dendrochronologic, and radiocarbon ages. Our primary purpose in this paper is to focus on how growth of individual lichens changes with age and to derive lichen growth curves from measured growth rate data. We do this by measuring the growth of lichen thalli of many sizes over a period of years and from this deriving curves for growth over periods of decades to millennia. We hope to add to the development of an alternate method of constructing lichenometric dating curves, which in turn may someday be used to check the validity of the standard, indirectly controlled curves.

In 1977 a series of lichen measurement sites was established in the accessible Atigun Pass region where the Dalton Highway and trans-Alaska oil pipeline corridor transect the Brooks Range (Figure 1). These measurements, and additional sites added in 1979, became the baseline for remeasurements in 1983 when thalli were retraced and rephotographed (Table 1). The seven measurement sites are located north of the Continental Divide, as are all existing glaciers in this part of the range, and occur at altitudes ranging from 1020 to 1730 m.

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Mean annual precipitation in the region ranges from 300 to 700 mm and varies directly with altitude. About half of the precipitation is snow. Mean annual temperature is also dependent on altitude and ranges from -10 to -15°C over the measurement sites. The region is usually snow free from late June through August, including 500 to 1000 thaw degree-days (Haugen, 1982). Mean summer temperatures range from -1 to 3°C. All of the measured lichens are growing on resistant quartzose sandstone and conglomerate substrates. Sites at higher altitudes are located on stable areas of bouldery Holocene moraines fronting glaciers, whereas the lower sites are on bedrock or on boulders in stable colluvium of similar lithology. Measured lichens are growing 0.1 to 2.0 m above the surrounding land surface and have a full range of orientations.

TAXONOMIC OBSERVATIONS

Our lichenometric dating curve (Calkin and Ellis, 1980) was developed for *Rhizocarpon geographicum* (L.) DC but, because others of the Section *Rhizocarpon* (Thomson, 1979) may have been included, the lichens were referred to as *R. geographicum* sensu lato. This practice is continued in the present study because we believe the *R. geographicum* species predominates. However, we now suspect that some Section *Alpicola* lichens were included in the establishment of the lichenometric dating curve as well, particularly *R. eupetraeoides* (Nyl.) Blomb. and *R. inarense* (Vain.) Vain. (Calkin and Ellis, 1984). In addition, throughout the Brooks Range we have identified more thalli in certain size ranges as belonging to one section or the other, suggesting that some of the visible characteristics we use for identification (see Calkin and Ellis, 1980: 249) may be age rather than species dependent. The tests required to differentiate the two species of Section *Alpicola* are difficult to use in the field, so we refer to them together as *R. eupetraeoides/inarense.* Our records suggest that when thalli are less than 50 mm in diameter, *R. eupetraeoides/inarense* diameters are commonly 2 to 3 mm larger than *R. geographicum* maxima (Calkin and Ellis, 1980). Innes (1982) presents contradictory observations.

Thalli of *Rhizocarpon geographicum* s.l. of up to 370 mm diameter and of *R. eupetraeoides/inarense* up to 325 mm have been found in the central Brooks Range. These occur on surfaces which were covered during the latest Pleistocene glacier expansions (Hamilton, 1982). A maximum possible age of 10,000 to 11,500 yr has been assigned to them, although no closely associated dates are available. Andrews and Barnett (1979), working on Baffin Island, and Denton and Karlén (1973), working in Swedish Lappland, report *Rhizocarpon* lichens ~9000 yr old, with maximum diameters of 280 and 480 mm, respectively. The 280-mm lichen is particularly well dated and appears to have developed at a rate similar to that of the large thalli which we have found in the Brooks Range.

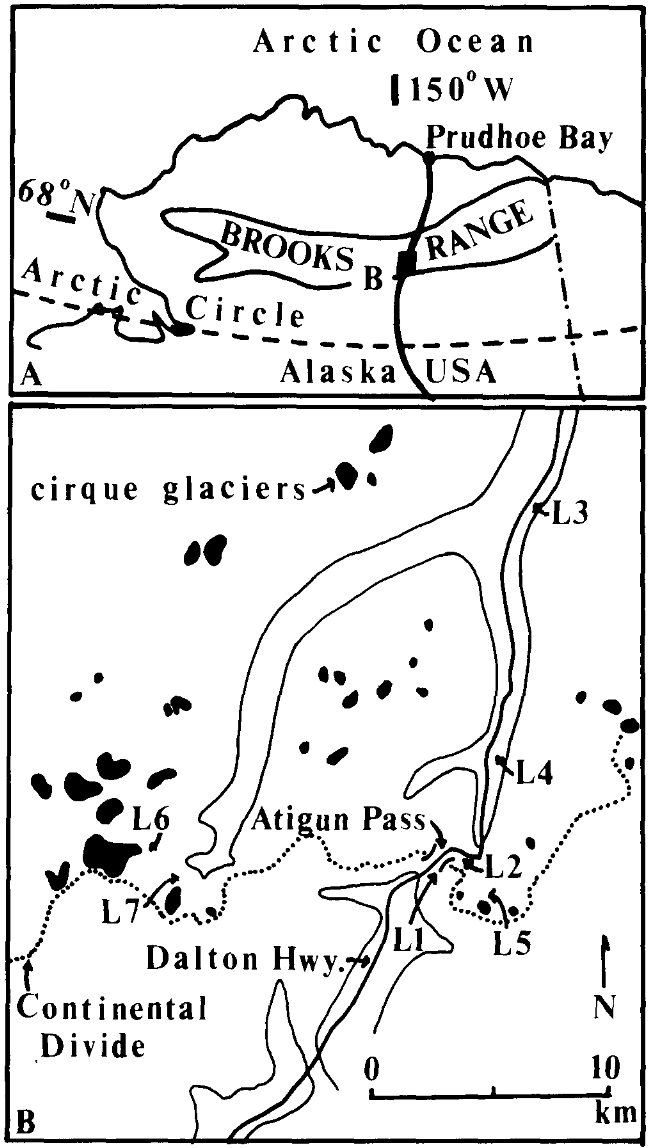

FIGURE 1. Location of lichen measurement sites, showing proximity to cirque glaciers and the Dalton Highway.

The shorter-lived *Alectoria minuscula* very rarely achieve diameters up to 140 mm in the Brooks Range, and thalli above 100 mm are uncommon. This is similar to maximum sizes found in several areas of Baffin Island (Andrews and Webber, 1969; Miller and Andrews, 1972). The maximum size may represent senescence or the destruction of these more delicate foliose thalli with time.

TABLE 1
Measurement site data

Site	Altitude (m)	Type of substrate	Measurement dates	No. of thalli	Size range (mm)	Added to study July 1984
L1	1440	Stable colluvium	25 Jul. 1977 15 Jul. 1983	1 *R. geog.*	35	
L2	1390	Stable colluvium	31 Jul. 1977 15 Jul. 1983	9 *R. geog.*	29–308	
L3	1020	Stable colluvium and bedrock	1 Aug. 1977 27 Jul. 1983	11 *R. geog.*	37–135	22 *R. geog.* (4–34 mm)
L4	1040	Stable colluvium	1 Aug. 1977 17 Jul. 1983	10 *R. geog.*	18–61	
L5	1730	Neoglacial moraine	2 Aug. 1977 9 Aug. 1979 31 Jul. 1983	18 *R. geog.* 13 *A. min.*	3–19 5–67	
L6	1540	Neoglacial moraine	1 Jul. 1979 19 Jul. 1983	22 *R. geog.* 35 *A. min.*	6–15 6–107	
L7	1510	Neoglacial moraine	2 Jul. 1979 21 Jul. 1983	8 *R. geog.* 9 *A. min.*	3–7 3–31	
L8 (near L5)	1530	Stable colluvium and bedrock				22 *R. geog.* (43–144 mm)

LICHEN MEASUREMENT

Near-circular thalli of 92 *Rhizocarpon geographicum* s.l. and 57 *Alectoria minuscula* Nyl. were measured by tracing and photographic techniques, after the methods described by Miller (1973). The accuracy of tracing methods is often restricted to the width of the tracing pen plus human and instrument errors. However, *Rhizocarpon* lichens do not grow equally in all directions, rather, yearly growth is usually concentrated in one or more lobes of the thallus. As long as growth in these select areas exceeds total measurement errors, growth rates can still be determined even when *average* radial expansion is extremely small. Accuracy is thus somewhat greater for large thalli and somewhat less for small ones because lobate growth is averaged over a greater or lesser perimeter. Because of this averaging and the 4- to 6-yr span between our measurements, detection of radial growth as small as 0.03 mm yr^{-1} is possible. The work of others with the photogrammetric method suggests that improvement in our procedures is possible. In the future we will use a thinner scale and shorter camera-to-lichen distance.

Tracing and photographic measurements of *A. minuscula* individuals resulted in growth rates which differ by only 10%, therefore thalli measured by both methods are included. For *R. geographicum* s.l., only tracing data are used.

GROWTH RATES

Growth rates are expressed as mean annual change in diameter. This was calculated by converting the area of each measured thallus into the equivalent circular area so that lobate growth was redistributed. Measurement data are plotted as absolute annual growth for *R. geographicum* s.l. in Figure 2 and for *A. minuscula* in Figure 3. Growth of both *R. geographicum* s.l. and *A. minuscula* thalli was extremely variable, even between thalli of the same size and between measurement periods for the same individuals.

Thallus diameter increase in *R. geographicum* s.l. ranged from 0.35 mm yr^{-1} to near 0 mm yr^{-1}, and has an inverse, though poorly defined, relationship to thallus size (Figure 2). After 6 yr there was no measurable change in 30% of those lichens measured; even many of the small thalli, which tend to grow fastest, showed no change (see Proctor, 1983, for other observations of slow-growing small thalli).

Alectoria minuscula absolute growth in diameter ranged from 2.01 to 0.14 mm yr^{-1}. Growth of this species generally increased (in contrast to that of *R. geographicum* s.l.) with increasing diameter (Figure 3). However, as with *R. geographicum* s.l., the relationship is poorly defined.

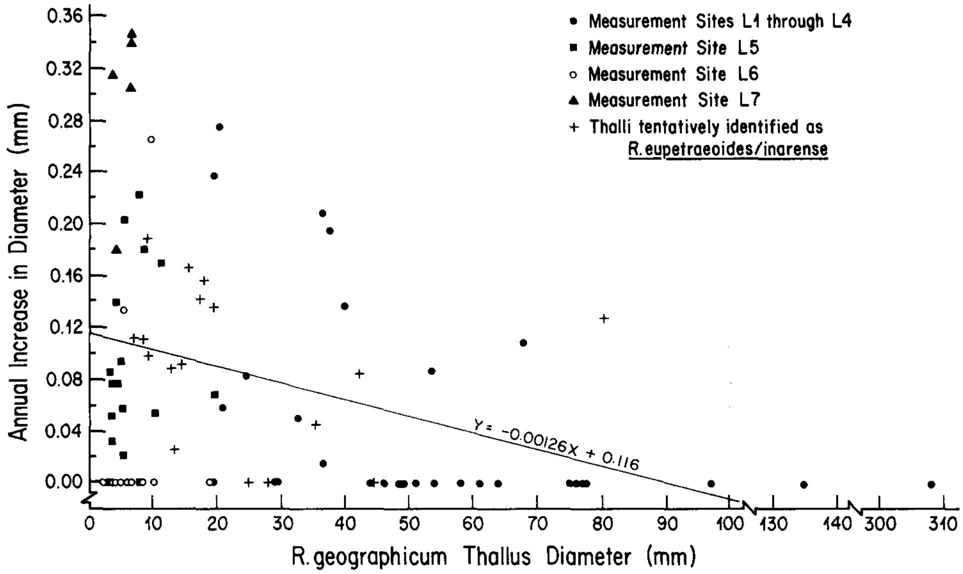

FIGURE 2. Absolute radial growth per year of *Rhizocarpon geographicum* s.l., identified by measurement site. Regression line represents the mean change in growth rate as diameter increases.

ENVIRONMENTAL CONTROL OF GROWTH RATES

This study attempts to define how growth of individual lichens changes with age. However, age is only one of many factors which must contribute to intraspecific variation in lichen growth, including the nature of the substrate, biological interactions, and macro- and microclimate (e.g., Pentecost, 1979; Hooker, 1980). By choosing appropriate sampling sites and thalli, we have attempted to eliminate the influence of the first two of these other factors. Two easily measured parameters related to climate are site altitude and substrate orientation; these are considered below.

Comparison of similar-size lichens growing at different altitudes was possible between the highest site and the next two lower of our measurement sites. The total altitudinal difference between these sites is 220 m. Large thalli were excluded from this comparison because there were not enough measured thalli from each site. Results are displayed in Table 2. Growth rates of *R. geographicum* s.l. are more variable within each site than between sites. Small *R. geographicum* s.l. at the highest site on average grew at 0.09 mm yr^{-1} and growth at the lower sites averaged 0.12 mm yr^{-1}. However, standard deviations of these growth rates are too high to distinguish between them. Growth rates of small to mid-sized *A. minuscula* appear to have increased with altitude. At the highest site, growth averaged 0.89 mm yr^{-1}, whereas at the next two lower sites, growth averaged 0.63 mm yr^{-1}. If this difference is in fact related to altitude, it may indicate that the two species react differently to climatic factors.

The effect of substrate orientation as it bears on insolation was examined in a preliminary way by comparing the growth rates of lichens with orientations which have a potential for high, moderate, and low amounts of insolation (Figure 4). In doing this, we assume that south-facing surfaces nearest perpendicular to the midsummer solar inclination will, on average, receive most sunshine. Results are summarized in Table 3. We recognize that substrate orientation affects growth factors other than sunshine, most notably water retention by the boulder surface; groupings of orientations different from that in Figure 4 would test this better. Growth of *R. geographicum* s.l. thalli on boulder faces with high and moderate insolation potential could not be distinguished from each other. However, each of these groups grew more than twice as fast as thalli in positions which receive little sunshine. The fastest growing *A. minuscula* thalli were those on sur-

TABLE 2
Lichen growth versus altitude

Species	Diameter range (mm)	No. of thalli	Site altitude (m)	Mean growth rate (mm yr^{-1})	Standard deviation (mm yr^{-1})
R. geographicum	0–20	20	1730	0.09	0.06
R. geographicum	0–20	26	1510–1540	0.12	0.12
A. minuscula	0–35	8	1730	0.89	0.38
A. minuscula	0–35	28	1510–1540	0.63	0.28

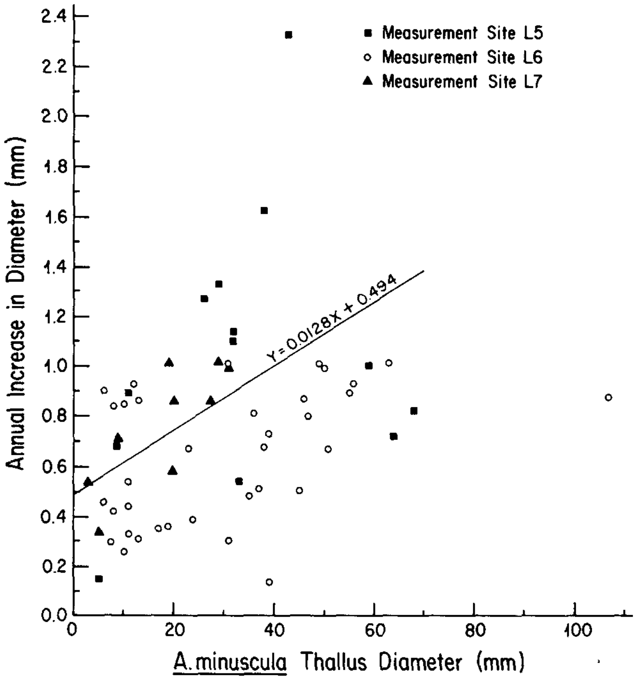

FIGURE 3. Absolute radial growth per year of *Alectoria minuscula,* identified by measurement site. Regression line represents the mean change in growth rate as diameter increases.

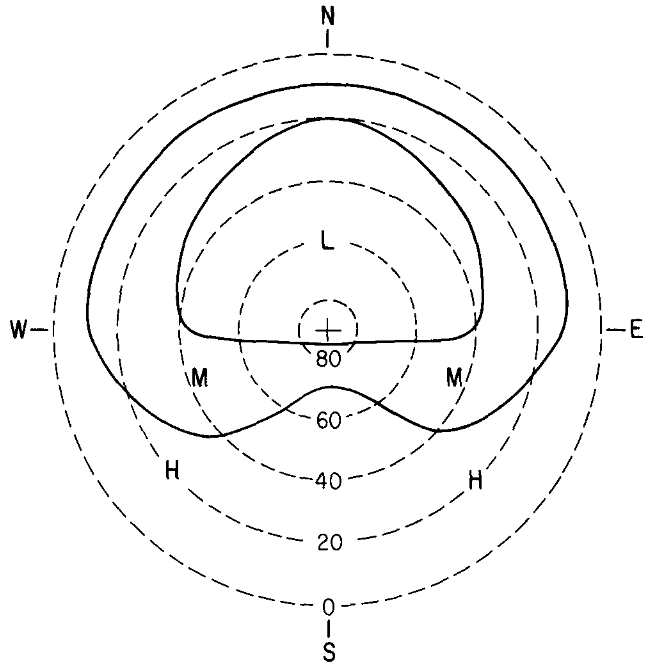

FIGURE 4. Potential insolation classes, plotted by orientation and dip of substrate, where L = low, M = moderate, and H = high insolation potential.

faces with a moderate insolation potential. As is the case with *R. geographicum* s.l., low insolation is correlated with slower growth in *A. minuscula*. The observed growth of both species may be consistent with studies of Hooker (1980), who found moderate insolation most conducive to growth of Antarctic crustose lichen.

DERIVATION OF LICHEN GROWTH CURVES FROM DIRECT MEASUREMENT

Traditional lichenometric curves used to date Holocene surfaces are based on maximum diameters of lichens found on deposits dated by other absolute methods. However, lichen growth curves can also be developed from direct measurement data. These curves show projected changes in the diameter of a hypothetical lichen thallus throughout its life and make it possible to equate lichen thallus diameters with age. The curves presented here are derived from the growth rates presented in Figures 2 and 3.

The first step in curve construction was to fit regression lines to these data (Figures 2 and 3); these lines are intended to represent mean growth at various ages of each species. Because measured growth rates varied so widely among same-sized thalli, the correlation coefficients of both regression lines are low, i.e., 0.3 and -0.3 for *R. geographicum* s.l. and *A. minuscula,* respectively. However, the probability of these correlations occurring in populations with random relationships between thallus size and thallus age is less than or equal to 0.01. It is interesting that growth of the faster-growing (and therefore presumably more accurately measured) *A. minuscula* was no more uniform than that of the slower-growing and difficult to measure *R. geographicum* s.l. This leads us to believe that the extreme variability of lichen growth which we measured is real. Next, an equation was derived from the regression lines to present thallus diameter as a function of age. In the general case, this line can be represented by $x' = ax + b$, where x' is change in thallus

TABLE 3
Growth rate versus insolation

Species	Relative potential[a] High	Moderate	Low
R. geographicum	$n=40$ $\bar{x}=0.10$[b] $\sigma=0.11$	$n=13$ $\bar{x}=0.10$ $\sigma=0.13$	$n=28$ $\bar{x}=0.04$ $\sigma=0.06$
A. minuscula	$n=23$ $\bar{x}=0.77$ $\sigma=0.28$	$n=12$ $\bar{x}=0.93$ $\sigma=0.21$	$n=11$ $\bar{x}=0.66$ $\sigma=0.21$

[a]See text and Figure 4 for explanation.
[b]Growth rates and standard deviations given in mm yr^{-1}.

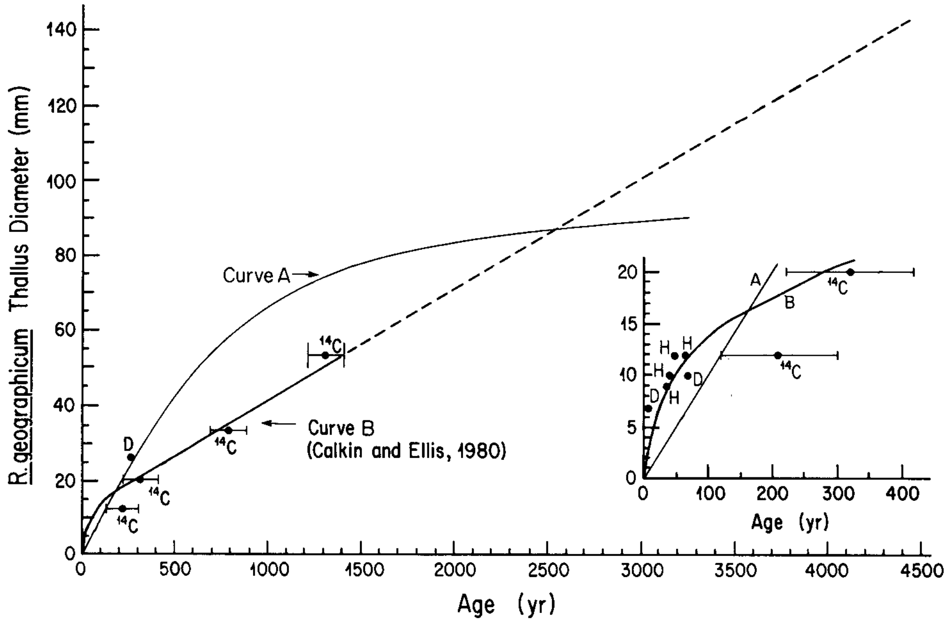

FIGURE 5. Growth curves for *Rhizocarpon geographicum* s.l. which predict thallus age given maximum diameter. Curve A is derived from the measured growth data of this study. Curve B is the lichenometric dating curve established from indirect evidence as documented in Calkin and Ellis (1980). Thallus age for curve A is in calendar years, but for curve B is radiocarbon years BP. Data points used to draw curve B are shown, where D represents dendrochronologic data, H represents historic data and ^{14}C represents radiocarbon ages. The inset expands the early portion of both curves.

diameter and a and b are constants. From this relationship and the condition that a thallus has an initial diameter of zero, or $x(0) = 0$, the following relationship is derived (Herrmann, pers. comm., 1986): $x(t) = b/a(e^{at}-1)$, where *x(t)* represents the diameter of a thallus at age *t*. Growth curves resulting from this derivation are shown in Figure 5 for *R. geographicum* s.l. and in Figure 6 for *A. minuscula.*

ANALYSIS OF DIRECT MEASUREMENT CURVES

The growth curve developed for *Rhizocarpon geographicum* s.l. shows continuously slowing increases in diameter throughout the life of the thallus. This continuous curve contrasts with the long-term linear shape of the lichenometric dating curve of Calkin and Ellis (1980) and is determined by the linear regression used to resolve the measurement data of Figure 2. Our derived curve is similar enough to the dating curve to encourage the continued monitoring of *R. geographicum* lichen growth. However, it is clear that a curvilinear best-fit line through the growth rate data is needed before a derived growth curve can be consistent with previous knowledge of lichen growth in this area (e.g., that *R. geographicum* of 370 mm diameter exist and are at most 10,000 to 11,500 yr old). Unfortunately, our data do not justify a curvilinear best-fit at this time.

At least two other measurement studies have considered the growth of *R. geographicum* in detail. In contrast to our study, Proctor (1983), studying *R. geographicum* less than 200 yr old, found that absolute growth rates increased as thallus size increased. Our data shows no trend for this age (corresponding to lichen of diameters 18 mm and smaller in our study) because growth rates are so variable. However, Armstrong (1983) collected data which were resolved into growth curves of the same general form of decreasing growth rate with age as that of our study.

The mean growth curve for the faster-growing *Alectoria minuscula* (Figure 6) shows that growth rates for this species gradually increase throughout the life of each individual, from an initial 0.5 to 1.3 mm yr^{-1} as it reaches 60 mm in diameter. According to the growth curve de-

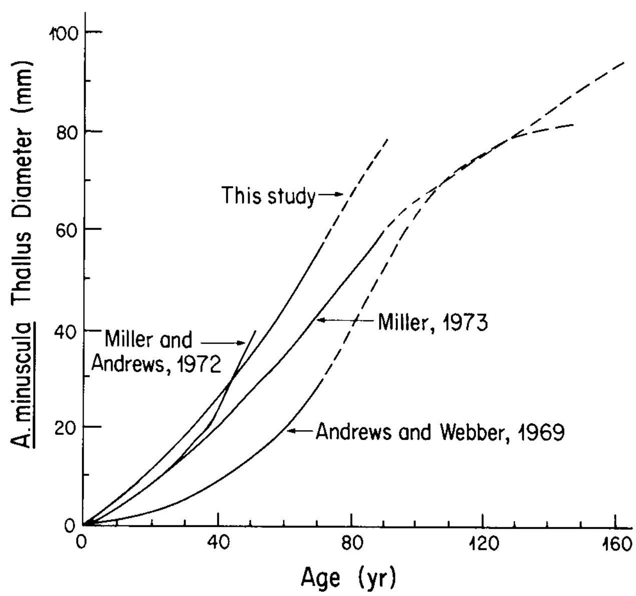

FIGURE 6. Growth curves for *Alectoria minuscula* predicting age, given diameter. Curves generated by this study as well as others which measured thallus growth directly are shown.

TABLE 4
Interspecific ratios

Lichen age (yr)	*A. minuscula* diameter (mm)	*R. geographicum* diameter (mm)	Ratio with synchronous colonization	Ratio with 10-yr lag of *R. geographicum* after *A. minuscula*[a]
10	5.3	1.1	4.8	
20	11.2	2.3	4.9	10.2
30	18.0	3.4	5.3	7.8
40	25.8	4.5	5.7	7.6
50	34.5	5.6	6.2	7.7
60	44.5	6.7	6.6	7.9

[a]Lichen age given is age of *A. minuscula.*

rived from these data, the few lichens of this species in the study area that reach 110 mm diameter might be expected to be 60 yr old. *Alectoria minuscula* growth curves derived from direct measurement of lichen growth in the eastern Canadian Arctic are remarkably similar to our curve from the Brooks Range (Figure 6).

Interspecific ratios between maximum thallus sizes of fast-growing species and of *Rhizocarpon geographicum* are sometimes used to augment lichenometric dating where *R. geographicum* are sparse or missing (e.g., Calkin and Ellis, 1984). These ratios are usually the result of field observations; here we derive size ratios of *A. minuscula* to *R. geographicum* s.l. from the theoretical growth curves of Figures 5 and 6. These ratios are presented in Table 4. Assuming synchronous colonization of the two species 30 yr after stabilization of the substrate (Calkin and Ellis, 1984), ratios of *A. minuscula* to *R. geographicum* s.l. diameter initially increase rapidly and then more slowly as the lichen colony ages. Diameter ratios of oldest individuals range from 4.8 to 6.6. Higher average ratios of 6.5 to 7.0 were observed in the field from measurements of maximum diameters of the two species coexisting on boulders (Calkin and Ellis, 1980). The observed ratios might be the result of a lag in *R. geographicum* colonization behind *A. minuscula* of about 10 yr (Table 4). We have not recorded a consistent difference in colonization time between the two species; however, workers who may have measured interspecific ratios in more detail (e.g., Miller and Andrews, 1972) report that colonization of *R. geographicum* follows that of *A. minuscula.*

APPLICATIONS TO LICHENOMETRIC DATING

The *Rhizocarpon geographicum* s.l. dating curve which has been applied to Holocene deposits in the Brooks Range is controlled by historic and dendrochronologic ages to 300 yr BP and to 1300 yr BP by the radiocarbon method (Calkin and Ellis, 1980, 1984). The curve was extended beyond 1300 yr by correlation with curves from areas of similar climate where some extended control was available. In Figure 5, this indirect lichenometric dating curve (B) is superimposed on the growth curve from direct measurement of *R. geographicum* s.l. (curve A).

Should there be any similarity between the two curves, when one represents maximum growth of a lichen population through a period of several millennia and the other represents growth of individual lichens over a period of 6 yr? Data gathered at Atigun Pass suggest that there may have been comparable climatic variation during the two periods. For example, in 1980 and 1981, unusually low summer temperatures produced conditions which, if sustained, could cause glacier advances similar to those marked by late Holocene moraines (Calkin et al., 1985). During these two cold years only 400 to 680 thaw degree-days were recorded, in contrast to the four warm years, 1977, 1978, 1979, and 1983, when longer and warmer summers resulted in 630 to 900 thaw degree-days. Thaw season precipitation during the period of this study varied from 200 to 300 mm yr^{-1}(Haugen, 1982, and pers. comm., 1980).

Growth curve A, based on mean measured growth, and curve B, the indirectly controlled lichenometric dating curve, have some similarities, although curve A lies for the most part above curve B (Figure 5). This suggests that the largest thalli measured on substrates, and used to form the lichenometric dating curve, are ones whose growth generally approximates mean rates or which at most grow at somewhat less than optimum rates throughout their lives (see also Proctor, 1983). Apparently, if *R. geographicum* s.l. lichens sustain growth at optimum rates, it is for relatively short periods of time.

The measured growth curve A shows faster growth than the lichenometric dating curve between about 150 and 1000 yr of age; if this curve were used to date deposits which are older than 150 yr, it would predict younger ages. However, the form of the measured curve is confined by its derivation from a linear regression (Figure 2). When the relationship between growth rate and lichen diameter is more accurately defined for *Rhizocarpon geographicum,* a growth curve may be derived which more closely approximates the long-term linear form of the lichenometric dating curve and can be more fruitfully compared with it.

The practice of using an average diameter of the five largest lichens to represent the maximum lichen diameter found on a deposit (Locke et al., 1979) is especially important in view of the great variability of growth rates shown by our measurements. This is particularly crucial for young deposits where growth is most variable and where there is the greatest chance for survival of lichens which sustain optimum rates. If our lichenometric curve (Figure 5, curve B) predicts reasonably accurate ages, measurement of single largest lichens exclusively may yield lichenometric ages which are too old.

We suggest that for those who use lichenometry as a dating tool, growth curves derived from direct measurement of *Alectoria minuscula* lichens can be used for dating purposes, although the variability of growth rates necessitates that large numbers of thalli be measured. The resemblance of growth curves from climatically similar eastern and western North American arctic regions is striking and adds credence to the individual curves. However, measurement of slower-growing *R. geographicum* s.l. lichens has not continued long enough to use measured growth curves as substitutes for lichenometric dating curves derived from indirect data. More studies such as ours may show that direct measurement curves of slow-growing species might be used to give preliminary estimates of substrate age where lichenometric curves cannot be established by traditional methods. We have made no changes in lichenometric ages assigned to Holocene moraines and other landforms in the Brooks Range based on the results of this study. The plurality of factors affecting growth rates, in combination with the relatively short interval between measurements of *R. geographicum* s.l., caution us to limit our dependence on the direct measurement curve. However, continued monitoring of lichen growth in the Brooks Range may lead in the future to modifications of the lichenometric dating curve.

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