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Indirect Growth Curves Remain the Best Choice for Lichenometry: Evidence from Directly Measured Growth Rates from Svalbard

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Abstract

Directly measured growth rates of two lichens (*Pseudephebe minuscula* and *Rhizocarpon* sections *Rhizocarpon* and *Superficiale*) from Svalbard made over a two-decade interval (1984–2007) are presented. Growth rates were determined by measuring the change in area of the lichen thalli from digital images and converting area to diameter. *Pseudephebe* diameter growth rates ranged from 0.2 to 1.5 mm yr^{-1} and *Rhizocarpon* grew 0.05 to 0.30 mm yr^{-1}. Growth rates of both are a function of thalli size—growth rates increase with increasing thallus size up to 70 mm diameter for *Pseudephebe* and 30 mm diameter for *Rhizocarpon*. While these directly measured growth rate results are consistent with other recent directly measured lichen growth studies, they are not consistent with indirectly determined age-size curves that show a negative correlation between size and growth rate (i.e., rapid ''great growth'' followed by slower ''linear growth''). We explore several reasons to explain the apparent discrepancy between directly measured and indirectly determined growth rates, including climate change, increased nutrient fluxes, and population sampling differences between the two methods. We argue that indirectly determined growth curves, which integrate the effects of changing growing conditions over time, remain the best basis for lichenometric dating.

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Introduction

Lichenometry, the use of lichen size to determine the age of geomorphic surfaces, is widely successful despite uncertainty and some controversy in its theoretical basis (see Innes, 1985a). The method, develop by Beschel in the 1950s (Beschel, 1950, 1961, 1973) remains in widespread use in arctic, antarctic, and alpine environments and is often the only method of determining limiting ages for young landforms. In its basic form, lichenometric dating is based on a locally derived calibration curve developed by measuring the size (usually largest diameter) of the largest, presumably oldest, lichen on surfaces of known age (e.g., tombstones, monuments, independently dated surfaces) (Locke et al., 1979). This ''indirectly determined'' method yields an age-size curve that can be used to determine ages of landforms based on the size of largest lichens found on them. In recent years, a second method of developing age-size curves—''directly measured'' lichen growth rates has been developed. In these studies, individual lichen thalli are repeatedly measured over a sufficient number of years to characterize their growth rates. Because the lichen species used for dating landforms grow slowly, careful measurements and long time spans (decades) are needed to generate accurate growth curves. Armstrong and Bradwell (2010) and Trenbirth and Matthews (2010) provided comprehensive reviews and data pertaining to directly measured lichen growth rates, including discussions of prior comparisons of direct and indirect methodologies.

Indirectly determined and directly measured growth studies, however, show very different lichen growth rates. Typical indirect growth curves show that small lichen grow quickly for several decades then grow more slowly or stabilize in size during subsequent centuries of growth. Beschel (1961) termed the rapid growth phase as the ''great growth period'' and the slower growth time as the ''linear phase''. Lichen growth rates measured directly, however, indicate that lichen growth rates start out slow, increase to a maximum for mid-size lichens, and then seem to decrease for the largest lichens.

Which growth rates should be used to develop lichenometric calibration curves for dating Holocene landforms? Beschel (1961) wrote (p. 1047), ''Direct measurement of the same plant at sufficiently long time intervals must remain the basis for any growth analysis.'' Trenbirth and Matthews (2010) also argued that direct measurements ''must be the final arbitrator'' for understanding lichen growth and providing a theoretical basis for lichenometric dating. However, we argue here that while directly measured growth curves are necessary for understanding the biology of lichen growth, they are not applicable to calibrating lichen size-age curves used by geologists for dating Holocene landforms.

In this paper, we present direct, photographic-based measurements of lichen thalli from Svalbard made over a two decade interval. Our growth measurements are based on calculating the total area of individual lichen thalli from digital images. We convert our area measurements to diameters for comparison with traditional studies that use linear measurements. Our resulting ''area-derived diameter'' (ADD) is more precise than single axis measurements because it measures growth around the entire perimeter of the thallus. We then compare our directly measured growth rates to indirectly determined growth curves for the same region created by Werner (1990). We argue that the lichen growth rates of the past few decades are different than growth rates during previous centuries due to climate change and other anthropogenic environmental changes. Indirectly determined growth curves, which are based on lichen that have lived through the changing conditions, remain the best basis for lichenometric dating.

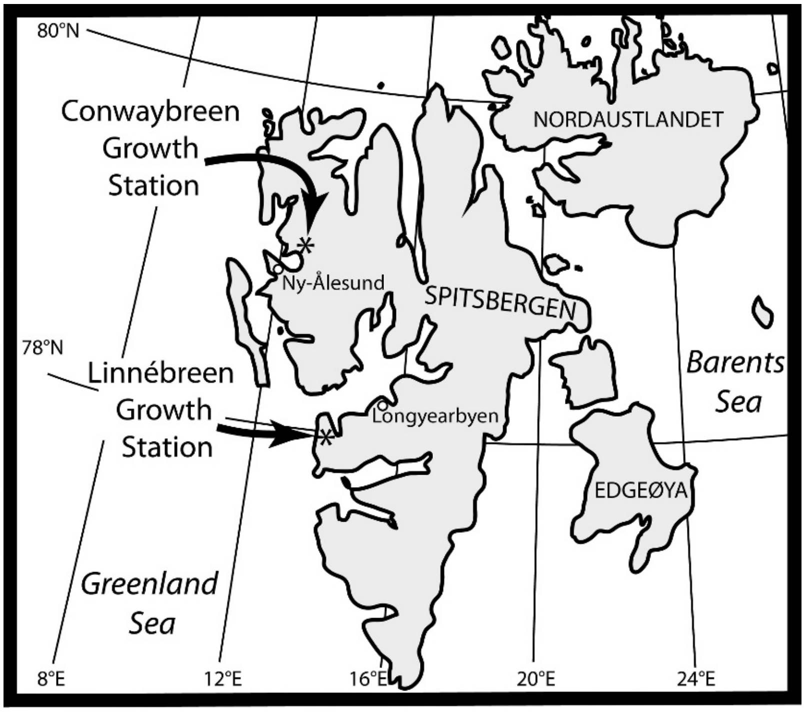

FIGURE 1. Svalbard lichen growth station locations.

Methods

LICHEN GROWTH STATIONS

Five lichen growth stations were established on Svalbard between 1984 and 1986 (Werner, 1990); two of these stations were revisited and are the focus of this paper. These two growth stations are located on stable areas of Little Ice Age moraines in the forefields of Conwaybreen near NyÅlesund (78°59′39″N, 12°22′6″E) and Linnébreen near Kapp Linné (77°58′22″N, 13°56′32″E) (Fig. 1). At each station, several boulders hosting a representative range of thallus diameters were selected. None of the boulders showed evidence of being used as bird perches and none was near water sources or harbored moss. Forty to fifty lichen thalli were measured at each station (typically 10–15 per boulder). The positions of individual thalli on the boulders were sketched and photographed. Individual lichen thalli were measured to the nearest millimeter with a ruler and photographed with a coin or machined square scale of known dimensions. When the growth stations were revisited, the host boulders were easily located and individual thalli were confidently identified on the rock surfaces using the photographs and sketches.

LICHEN IDENTIFICATION PROCEDURES

Lichen were originally identified by Werner during the 1980s and his identification procedures have been previously described (Werner, 1990, 1993). The fast growing *Pseudephebe minuscula* (previously named *Alectoria minuscula*) is a black, fibrous, subfruticose lichen (Miller and Andrews, 1972). The similar-appearing *Pseudephebe pubescens*, differentiated from *P. minuscula* by the length and texture of thallus fibers (Andrews and Webber, 1964; Calkin and Ellis, 1980), was excluded from the measurements. Differentiation of small thalli (<10–15 mm) is difficult, however, and it is likely that some *P. pubescens* thalli were measured. Where thalli of these two species of *Pseudephebe* have been confidently identified, they were of comparable size.

The slow-growing subgenus *Rhizocarpon* is a yellow-green crustose lichen used extensively in lichenometry. Although subdivision of the *Rhizocarpon* group to the section level is generally agreed upon, subdivision to species and subspecies is not well understood and generally not agreed upon (Innes, 1982). Earlier workers have avoided the problem of taxonomy by resorting to *Rhizocarpon geographicum sensu lato* (the yellow-green subgenus *Rhizocarpon*). More troubling is some work that suggests that not all specimens of the subgenus *Rhizocarpon* grow at the same rate (Luckman, 1977; Duford and Osborn, 1978) and that substantial growth rate variations exist between section *Alpicola* and section *Rhizocarpon* (Innes, 1982, 1983). Werner (1990) determined that section *Rhizocarpon* accounts for 47% of the lichens identified, section *Superficiale* 33%, and section *Alpicola* 20%. These data are in agreement with André (1986) who analyzed 50 thalli from Spitsbergen and determined that *Rhizocarpon* section *Rhizocarpon* was "the most abundant," *Rhizocarpon* section *Superficiale* was "rather common," and *Rhizocarpon* section *Alpicola* was "uncommon." This study supports the work of Innes (1985a), which suggests that subgenus *Rhizocarpon* section *Alpicola* (represented in the study area by *R. inarense*) can be field identified. Whenever confidently identified, Werner (1990) reported that section *Alpicola* lichens were consistently 10 to 15% larger than thalli from sections *Rhizocarpon* and *Superficiale*. The other five field groups, however, were not consistently applied; thalli that appeared identical and thalli that appeared distinctly different could in fact be from the same section (Werner, 1990). No taxonomic identification was included as part of this study, and we adopted Werner's previous work that suggests that "*Rhizocarpon*" refers to *Rhizocarpon* sections *Rhizocarpon* and *Superficiale* and excludes section *Alpicola*.

LICHEN MEASUREMENTS

We used a photogrammetric method similar to that of Miller (1973), updated to use digital images and image processing software, to measure the size of the lichen thalli in this study.

Lichen thalli were originally photographed in August 1984 (Conwaybreen area) and August 1985 (Linnébreen area) using a 35 mm Minolta SLR camera with a 55 mm macro lens. Contact

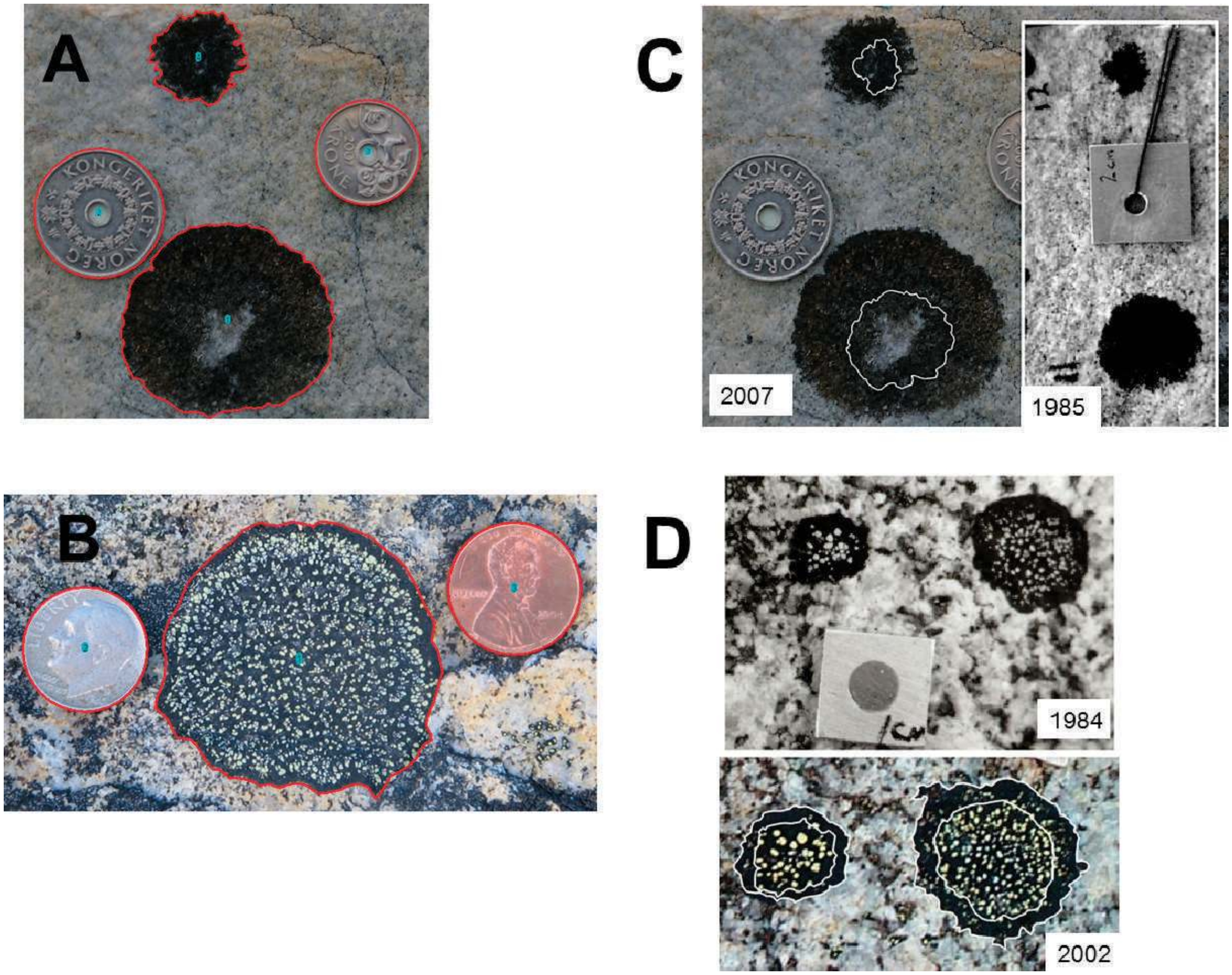

FIGURE 2. **(A, B) Examples of digital images of lichen thalli, which were traced with image processing software in order to measure their area in mm^2 (see Methods). (A) *Pseudephebe*, (B) *Rhizocarpon*. (C, D) Lichen images following georeferencing to determine percent growth. Each pair of images was scaled to be the same size by georeferencing using ArcGIS software using matching mineral grains and cracks in the underlying rock. The older images have been slid aside in this figure to allow before/after comparison of each thallus. The white trace shows the 1980s' thallus outlines superimposed on the newer images. (C) *Pseudephebe* from the Linnébreen growth station. (D) *Rhizocarpon* from the Conwaybreen growth station.**

prints of the 1984 and 1985 photographs were scanned at 300 DPI or higher, depending on the image size. The Conwaybreen lichens were re-photographed in 2002 using a Kodak DC3400 digital camera at 896 × 592 DPI image resolution. The majority of the Linnébreen lichens were re-photographed May 2007 using a Canon Powershot A400 at 1600 × 1200 DPI; those that were snow covered in May were photographed in August 2007 using a Pentax K100D digital SLR at 3008 × 2000 DPI. In all cases, a square or circular scale of accurately known area was placed next to each thallus. Cameras were always set to the longest possible focal length to minimize fish-eye distortion of the image. Digital images were saved as jpeg files and analyzed with no post-exposure processing. Test photographs with each of the digital cameras confirmed that spatial distortion from the center to the edges of the images was less than 10%; unfortunately, the Minolta camera and lens used in 1984 and 1985 is not available for testing. The majority of the digital images have a resolution better than 0.1 mm per pixel, and all but two were better than 0.2 mm per pixel (the two lowest resolution images were 0.23 and 0.24 mm per pixel).

The areas of the digital lichen images from all years were measured either using ArcGIS (http://www.esri.com/) or ImageJ (http://rsbweb.nih.gov/ij/) software, both of which can calculate the area of polygons. In all cases, polygons outlining the thalli and adjacent scale(s) were manually traced by the same person (Fig. 2, a and b). A scale ratio (mm^2 pixel^{-1}) was calculated for each image by dividing the pixel area of the scale(s) by their known area and was used to convert thalli areas in pixels to mm^2. Repeated outlining of thalli (on different days) indicated that the calculated area was reproducible to better than 3%. In most published studies, thalli sizes are described in terms of diameter. In order to facilitate comparison with these studies, we used the method of Miller (1973) to convert thallus area to an ''area-derived diameter'' (ADD), by the formula: diameter = $2*(\text{Area}/\pi)^{0.5}$ (a simple rearrangement of Area = $\pi * r^2$).

The growth of each lichen thallus was also measured using a second method. In this approach, the 1984 or 1985 image was scaled and aligned to the corresponding 2005 or 2007 image using the georeferencing tool in ArcGIS in a fashion similar to that described by Brabyn et al. (2005). Mineral grains and rock cracks around the perimeter of each thallus that were visible in both images provided the necessary control points to align and scale the images. Between 8 and 16 control points, distributed roughly evenly around the borders of each thallus, were used for each image set, resulting in

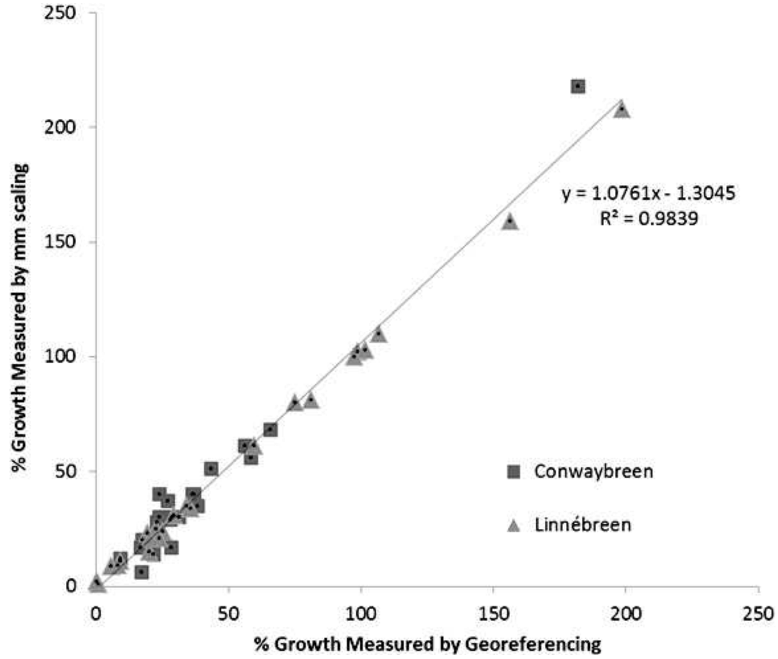

FIGURE 3. Comparison of percent growth of the various lichen thalli determined by the georeferencing approach and the millimeter scaling approach. A best fit line shows very nearly a 1:1 correspondence between the two measurement approaches.

alignment better than 0.2 mm root mean square error (RMS) using second-order polynomial transformations. The lichen thallus on the georeferenced image was subsequently re-traced and its area (in pixels) was compared to the thallus area (also in pixels) traced from the 2005 or 2007 image to determine the percent growth of the thallus over the study period (Fig 2, c and d). In this process, distortion in the images is not removed, but is equalized in each image set so that relative areal measurements can be determined. This method does not use the square or circular scales of known area, so it cannot be used to determine growth rates in mm yr^{-1}. But this approach eliminates several possible measurement errors that could arise if (1) the scales were not perfectly parallel to the lichen thallus, (2) the scales were not perfectly parallel to the camera's imaging plane, and/or (3) the scales were closer to (or farther from) the image edges than the lichen thallus (''fisheye'' or ''barrel'' distortion changes the apparent size of objects near the center of the image relative to those closer to the edges). When the percent growth calculated by the georeferencing approach was compared with percent growth calculated from millimeter-scaled measurements, the two measuring techniques gave essentially identical results (Fig. 3), demonstrating that image distortion is minimal and the digital measuring technique is both precise and accurate.

Our ADD measurement differs from most recent direct measure studies. For example, Trenbirth and Matthews (2010) marked the longest diameter of each thallus at the beginning of their study and always measured along this same axis. It is possible that the fastest growth in any time interval occurred along some other axis. In fact, since lichen thalli tend to remain roughly circular as they grow, one should expect that the fastest growth will not always occur along the same axis; otherwise, the lichen would become increasingly oblong over time. Our method of measuring diameter based on the total area of the thalli accounts for growth that is spatially and temporally variable. This approach is now far easier than the photogrammetric method described by Miller (1973). Suitable digital cameras are inexpensive and free image processing software is readily available (i.e., ImageJ, available from http://rsbweb.nih.gov/ij/). While this process is a bit more time consuming than single axis measurements, ADD provides a much better characterization of lichen growth.

Results

OBSERVED GROWTH RATES

This study monitored 28 *Pseudephebe miniscula* thalli ranging from 3 to 80 mm ADD at the beginning of the study. Growth rates and sizes were very similar at the Conwaybreen and Linnébreen sites. This study also monitored 21 *Rhizocarpon* thalli ranging from 19.4 to 60 mm initial ADD. *Rhizocarpon geographicum* thalli from the Conwaybreen site were smaller that those at the Linnébreen site, reflecting the selection of lichen thalli for the long-term study and not the complete range of sizes on the Conwaybreen moraine (Werner, unpublished data). *Pseudephebe* and *Rhizocarpon* growth rates as function of ADD from both study sites are shown in Figure 4 and listed in Table 1.

Pseudephebe is a fast-growing lichen—most *Pseudephebe* thalli doubled or tripled in area over the two decade study period. *Pseudephebe* ADD growth rates range from 0.2 to 1.5 mm yr^{-1}. Our *Pseudephebe* growth rates are consistent with Hansen (2010), who reported *Pseudephebe* growth rates of 1 mm yr^{-1} from Greenland, and Miller (1973), who reported growth rates of 0.6 to 1.0 mm yr^{-1} from eastern Baffin Island.

The monitored *Rhizocarpon* thalli increased in area by 25 to 80% over the study period and annual growth rates ranged from 0.05 to 0.30 mm yr^{-1} in ADD. A few *Rhizocarpon* thalli appeared to decrease in size during the study period; these individuals showed either evidence of a dying core or extreme competition by surrounding lichen. Any lichen thalli with negative growth were eliminated from analyses presented here.

Growth rates increase with increasing thallus size up to 70 mm ADD for *Pseudephebe* and ca. 30 mm ADD for *Rhizocarpon*. There is weak evidence (just a few specimens) of decreasing growth rates for the largest thalli (>70 mm ADD for *Pseudephebe* and >30 mm ADD for *Rhizocarpon*).

The ADD growth rates of both the *Pseudephebe* and *Rhizocarpon* thalli can be modeled with several best-fit curves (Fig. 4 and Table 2). Using a 95% confidence cutoff ($p < 0.05$), logarithmic and second-order polynomial (parabolic) curves both successfully describe the relation between growth rates and ADD for *Pseudephebe*. For *Rhizocarpon*, only the second-order polynomial fit successfully describes all the measured thalli. If the single largest

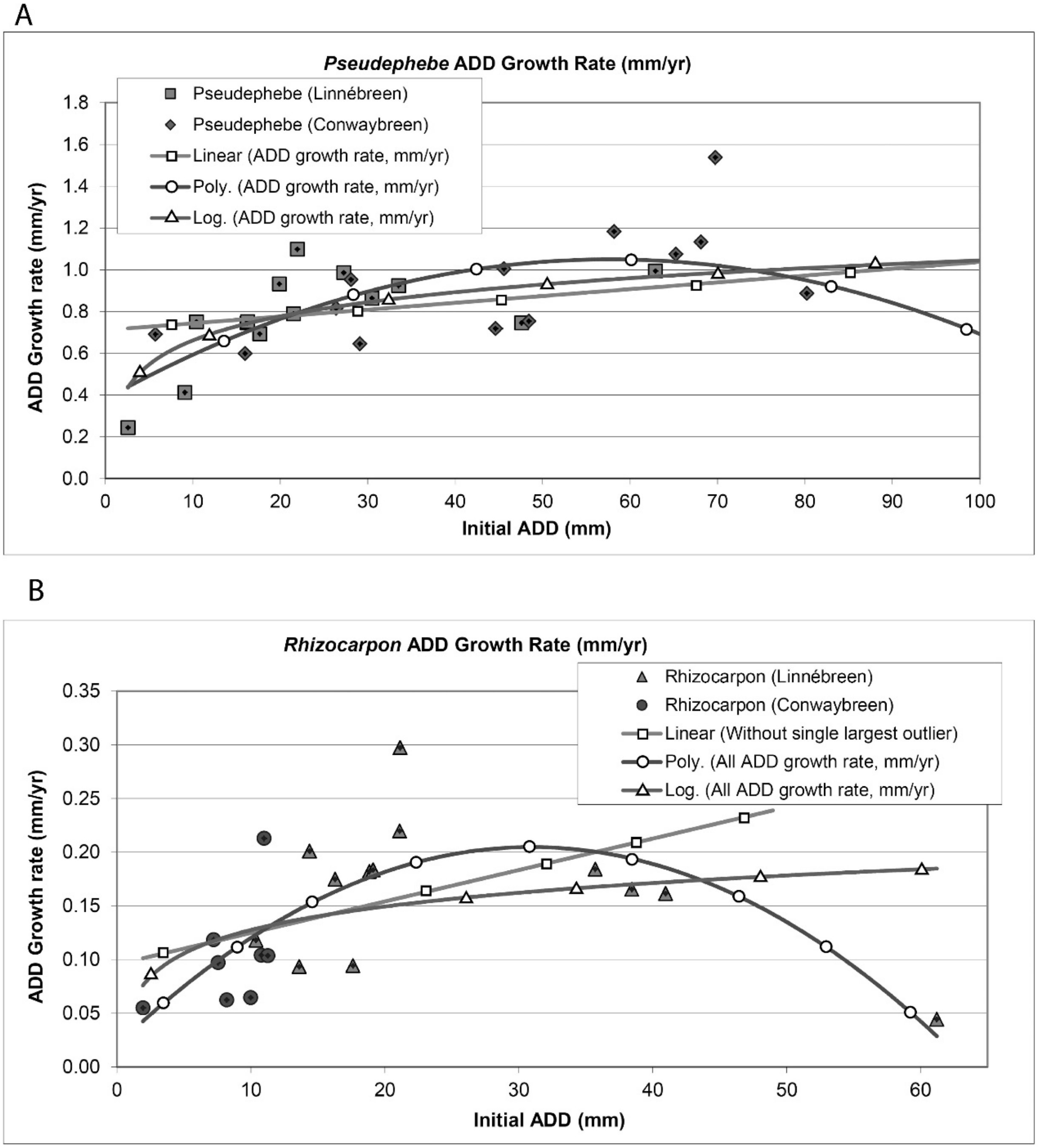

FIGURE 4. Lichen growth "Area-Derived Diameter" (ADD) rates versus starting size. Growth rates were calculated by dividing the change in ADD by the time of the study period (18 yrs for Conwaybreen, 22 for Linnébreen).

lichen thalli is excluded as an anomalous outlier, then logarithmic and linear curve fits pass the statistical significance test (Table 2).

Discussion

COMPARISON OF DIRECT MEASURED GROWTH RATES

Our *Rhizocarpon* results are consistent with other directly measured growth studies showing changing growth rates as lichens get larger (e.g., Armstrong, 1983, 2005; Armstrong and Bradwell, 2010; Benedict, 2008; Bradwell and Armstrong, 2007; Bradwell, 2010; Trenbirth and Matthews, 2010) (Fig. 5). These studies show increasing growth rates up to ca. 30 mm diameter and decreased growth rates for the largest thalli. In all published growth curves, the growth rates of the largest lichen are poorly constrained due to the rarity of very large *Rhizocarpon* thalli. While the growth rates of the very largest lichen remain uncertain, all these direct measurement studies show that lichen growth is either positively correlated to thallus size (although the size at which growth rates begins to level out is dependent on location and growing conditions) or is largely independent of lichen size (Trenbirth and Matthews, 2010).

COMPARISON OF INDIRECT AND DIRECT GROWTH MODELS

The relation between lichen size and lichen age predicted by direct measurement studies do not match well the age-size models developed by lichenometrists using the *indirect* approach of measuring

TABLE 1

Size and growth rate data for measured lichen thalli. For all specimens at the Linnébreen growth station, the initial and final measurement years were 1985 and 2007. For the Conwaybreen growth station, the initial and final measurement years were 1984 and 2002. Percent growth and area-derived diameter (ADD) growth rate are calculated over the entire time period (22 years for Linnébreen and 18 years for Conwaybreen).

Site	Specimen ID	Species	Initial Area (mm^2)	Final Area (mm^2)	Percent Growth	ADD Growth Rate ($mm\ yr^{-1}$)
Linnébreen	1	*Pseudephebe*	244	849	247	0.69
Linnébreen	2	*Pseudephebe*	207	836	305	0.75
Linnébreen	3	*Pseudephebe*	3107	5644	82	0.99
Linnébreen	4	*Pseudephebe*	1778	3215	81	0.75
Linnébreen	5	*Pseudephebe*	85	569	569	0.75
Linnébreen	6	*Pseudephebe*	5	49	847	0.24
Linnébreen	7	*Pseudephebe*	729	1922	163	0.86
Linnébreen	8	*Pseudephebe*	583	1881	223	0.99
Linnébreen	9	*Pseudephebe*	378	1669	342	1.10
Linnébreen	10	*Pseudephebe*	207	844	307	0.75
Linnébreen	11	*Pseudephebe*	311	1281	313	0.93
Linnébreen	12	*Pseudephebe*	65	259	300	0.41
Linnébreen	13	*Pseudephebe*	363	1186	226	0.79
Linnébreen	14	*Pseudephebe*	882	2275	158	0.92
Linnébreen	D	*Rhizocarpon*	2942	3037	3	0.04
Linnébreen	E	*Rhizocarpon*	1001	1241	24	0.18
Linnébreen	F	*Rhizocarpon*	1160	1390	20	0.17
Linnébreen	G	*Rhizocarpon*	1318	1557	18	0.16
Linnébreen	H	*Rhizocarpon*	350	528	51	0.22
Linnébreen	I	*Rhizocarpon*	351	602	71	0.30
Linnébreen	A2	*Rhizocarpon*	162	277	71	0.20
Linnébreen	B2	*Rhizocarpon*	209	319	53	0.17
Linnébreen	C2	*Rhizocarpon*	85	132	56	0.12
Linnébreen	G2	*Rhizocarpon*	279	410	47	0.18
Linnébreen	H2	*Rhizocarpon*	146	193	32	0.09
Linnébreen	I2	*Rhizocarpon*	287	422	47	0.18
Conwaybreen	A	*Pseudephebe*	1632	3183	95	1.00
Conwaybreen	C	*Pseudephebe*	5054	7266	44	0.89
Conwaybreen	D	*Pseudephebe*	665	1302	96	0.65
Conwaybreen	F	*Pseudephebe*	1563	2601	66	0.72
Conwaybreen	H	*Pseudephebe*	9884	11064	12	0.36
Conwaybreen	M	*Pseudephebe*	619	1607	159	0.95
Conwaybreen	N	*Pseudephebe*	200	562	181	0.60
Conwaybreen	O	*Pseudephebe*	3821	7455	95	1.54
Conwaybreen	P	*Pseudephebe*	1841	3018	64	0.75
Conwaybreen	Q	*Pseudephebe*	26	258	912	0.69
Conwaybreen	S	*Pseudephebe*	3642	6150	69	1.13
Conwaybreen	T	*Pseudephebe*	2657	4958	87	1.18
Conwaybreen	U	*Pseudephebe*	3342	5618	68	1.07
Conwaybreen	Y	*Pseudephebe*	546	1324	142	0.82
Conwaybreen	B	*Rhizocarpon*	45	68	52	0.10
Conwaybreen	E	*Rhizocarpon*	3	7	128	0.06
Conwaybreen	G	*Rhizocarpon*	91	126	38	0.10
Conwaybreen	I	*Rhizocarpon*	99	64	−36	−0.13
Conwaybreen	J	*Rhizocarpon*	53	68	29	0.06
Conwaybreen	L	*Rhizocarpon*	100	135	36	0.10
Conwaybreen	Va	*Rhizocarpon*	78	98	25	0.06
Conwaybreen	Vb	*Rhizocarpon*	41	69	68	0.12
Conwaybreen	Vc	*Rhizocarpon*	95	172	82	0.21

lichen on surfaces of known age. The typical lichen size versus age curve obtained by measuring lichen thalli diameter on substrates of known age shows that small lichen grow fastest ("great growth phase") and larger lichen grow slower ("linear phase"). Lichen size versus age curves from a wide range of environments generated by a large group of lichenometrists show this basic pattern (Fig. 6).

We used our direct measured *Rhizocarpon* growth results to create size versus age curves like those produced by traditional indirect studies. We used the best-fit curve formulas to calculate annual growth starting with a diameter of 1.5 mm at 3 years age. The starting lichen size was set to match the initial lichen size-age shown in the *Rhizocarpon* long-axis growth curve generated for Spitsbergen by Werner (1990) but with the colonization period subtracted to given lichen age rather than substrate age. Annual growth was summed on a year-by-year basis in a spreadsheet to determine size-age relationships. We used four different growth models, each derived from our best fit curves with statistical significance better than $p < 0.05$ (Fig. 7). These four models are comparable to models used in other published direct measured growth studies, but fit to our directly measured *Rhizocarpon* data. Model 1 is a second-order polynomial (shown in Fig. 4, b). Model 2 is a logarithmic model (Bradwell, 2010). Model 3 is a model in which growth rate is linearly proportional to size, and Model 4 is a model of constant growth independent of size. Model 3 uses a

TABLE 2

Best fit curve parameters and statistics.

Pseudephebe				
Curve Type	Equation	r^2	F-value	Significance
Linear	$y = 0.0033x + 0.711$	0.10	3.018	0.094
2nd order polynomial	$y = -0.0002x^2 + 0.0231x + 0.3814$	0.52	13.64	0.0001
Logarithmic	$y = 0.1664\ln(x) + 0.2782$	0.29	10.46	0.003
Rhizocarpon				
Curve Type	Equation	r^2	F-value	Significance
Linear*	$y = 0.0029x + 0.0956$	0.24	5.68	0.012
2nd order polynomial	$y = -0.0002x^2 + 0.0119x + 0.0202$	0.53	9.99	0.001
Logarithmic	$y = 0.0315\ln(x) + 0.0549$	0.13	2.82	0.109
Logarithmic*	$y = 0.0547\ln(x) + 0.0011$	0.36	9.92	0.006

* Excluding single largest outlier.

linear best fit to our data but with the single largest lichen thalli removed, otherwise the resulting curve is very similar to Model 4. The Model 4 constant growth rate is the average growth rate of all our measured *Rhizocarpon* thalli. Compared to Werner's (1990) growth curve, the directly measured growth rates of this study predict smaller lichen thalli for lichen ages up to 100–230 years, depending on the growth model used (see Fig. 7). Beyond this age range, the direct growth rates predict larger lichen for a given age than the Werner curve. The models predict lichen ages from diameter that vary by 50–150 years from ages predicted by the Werner curve. In terms of growth rates, the directly measured growth rates are slower for smaller lichens (up to 20–25 mm) and faster for lichens larger than 25 mm compared to the Werner (1990) growth curve.

WHY ARE DIRECTLY AND INDIRECTLY MEASURED GROWTH CURVES DIFFERENT?

The typical indirectly measured size versus age curve shows an intuitively realistic pattern of growth. They show that, like humans, lichen grow fastest during their youth, slowly reach a size plateau during middle age, and at least for some individuals, decrease in size with old age. However, the existence of the great growth period followed by limited growth does not appear to be supported by any directly measured lichen growth studies. Is either the indirect or direct approach flawed? Which approach best characterizes lichen growth? The following sections discuss possible reasons why the two approaches differ.

POPULATION SAMPLING DIFFERENCES

Indirectly determined growth curves are based on the single largest lichen thallus on a surface or feature of known age, which by design, is the oldest and fastest growing specimen. Some indirect studies use an average of a fixed number of the largest lichen (e.g., Innes, 1985b) but this variation still makes a non-random selection of largest lichen from the general population. Directly measured growth curves in contrast, are generated by measuring a wide range of lichen sizes without regard to their ages. Direct growth samples may not be truly randomly selected, but since a wide range of lichen sizes are measured, the direct approach is not intentionally biased to the fastest growing lichens. Therefore, direct growth curves represent more average growth rates. Since it is clear that lichen grow at different rates even on the

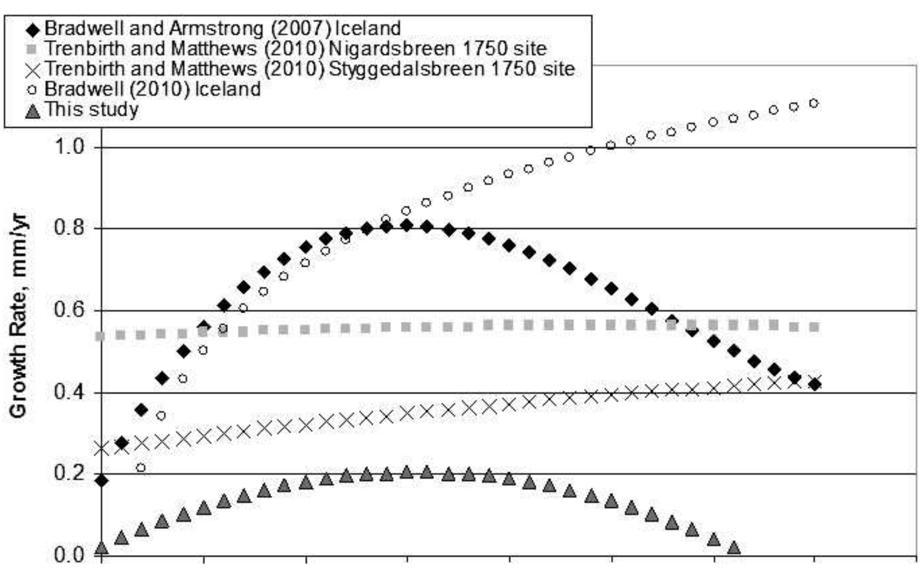

FIGURE 5. Comparison of directly measured *Rhizocarpon* growth rates. Bradwell and Armstrong (2007) measured 41 *Rhizocarpon* section *Rhizocarpon* thalli for 5 years, Bradwell (2010) measured 23 *Rhizocarpon* section *Rhizocarpon* for 5 years, and Trenbirth and Matthews (2010) measured 2795 thalli consisting of *Rhizocarpon* section *Rhizocarpon* and *Rhizocarpon* section *Alpicola.*

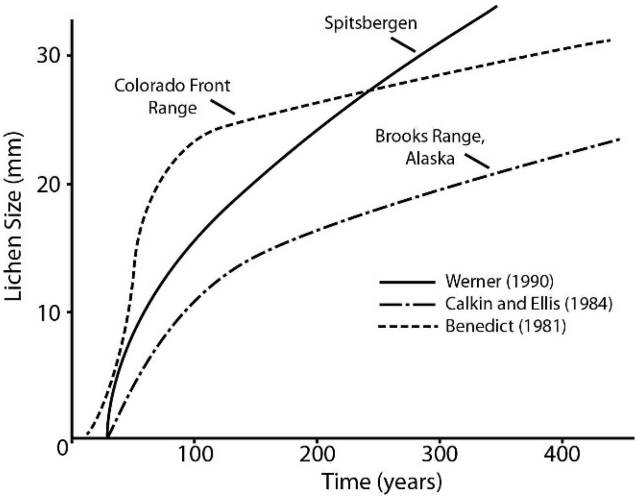

FIGURE 6. Examples of *Rhizocarpon* long axis growth curves generated by indirect measurements. From Werner (1990).

same rock surface (e.g., the scatter in any direct growth rate plots), we must accept that lichen vary in their growth rates, perhaps due to localized microenvironments and/or genetic differences. Therefore, indirectly determined growth curves represent *optimal* growth rates and the direct measure approach represents average, and therefore slower, growth rates.

Another sampling issue was described by Loso and Doak (2006). They argued that the apparent reduction in growth rates of larger lichen observed from indirect measurement studies can arise from the interaction of lichen mortality and sampling efficiency. That is, on older surfaces, the initial lichen colonists will be increasingly rare and hard to find. If smaller, younger lichen are measured and assumed to be initial colonizers, a reduced growth rate for large lichens will incorrectly be calculated. Loso and Doak (2006) argued that this sampling bias is sufficient to explain the differences between direct and indirect growth curves. While they may be correct, we argue that the additional factors we discuss in this paper also contribute to the differences between direct and indirect growth curves.

LONGITUDINAL VERSUS CROSS SECTIONAL SAMPLING

A growth curve that is constructed by measuring a wide range of individuals of known but different ages at a single time is a "cross sectional" survey. A growth curve constructed by measuring the change in size of the same individuals over time is a "longitudinal" survey. While both provide information about growth rates, results from the two types of studies are based on different assumptions and highlight different aspects of growth within the population. In the field of childhood growth studies, the differences between longitudinal and cross sectional studies have been extensively analyzed (e.g., Cole, 1994; Wei et al., 2006). Longitudinal studies of children's growth tend to underestimate the extremes since the population sampling tends to be smaller. Similar results and concerns are found in other types of surveys (e.g., Edwards, 2000; Rindfleisch et al., 2008), which show that results of longitudinal studies are not directly comparable with cross sectional studies.

CHANGING GROWTH CONDITIONS OVER TIME

As pointed out by Armstrong and Bradwell (2010) and Trenbirth and Matthews (2010), another major difference between the indirect and direct approaches is that the growing conditions of the past 5–25 years are not the same as the conditions that the lichen experienced over the time span used for indirect studies. Indirectly determined

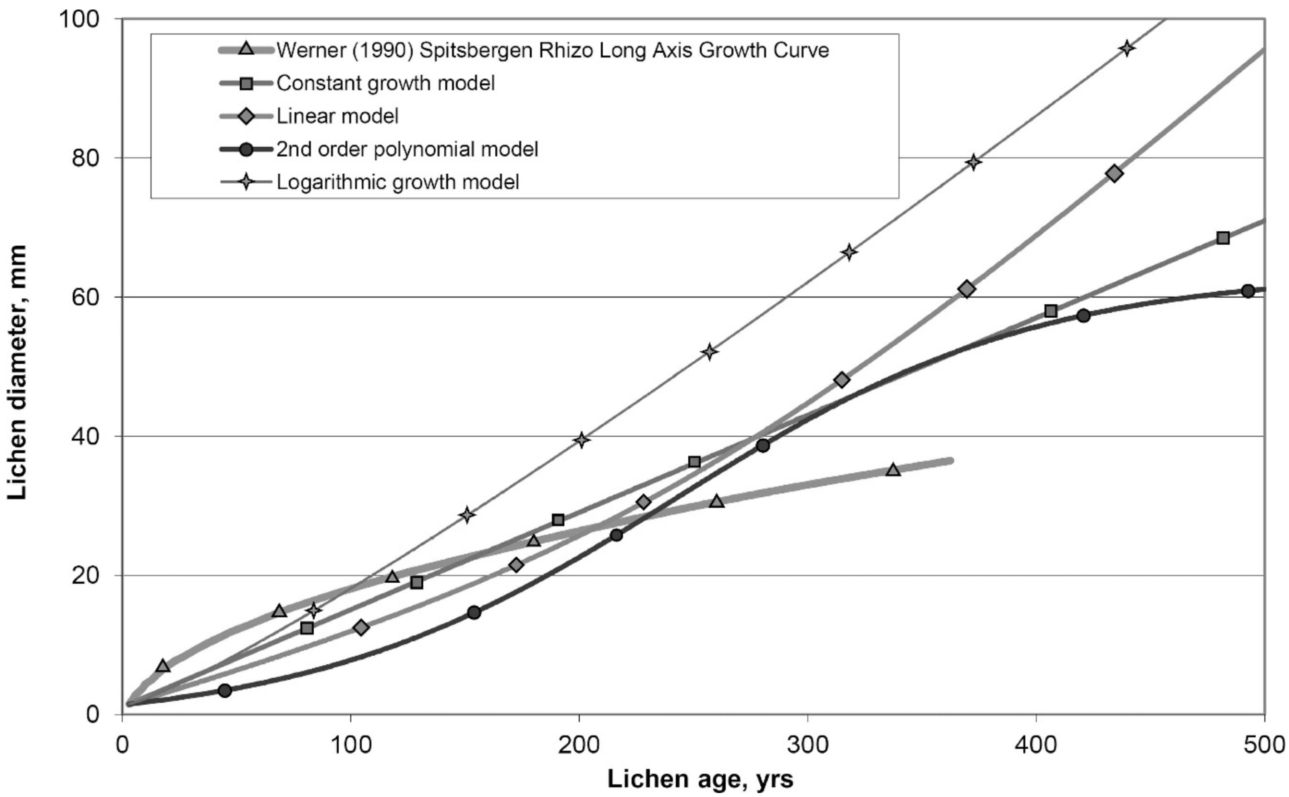

FIGURE 7. Size versus age curves generated for *Rhizocarpon* by several different growth models based on the direct-measured growth rates. See text for explanation of the models.

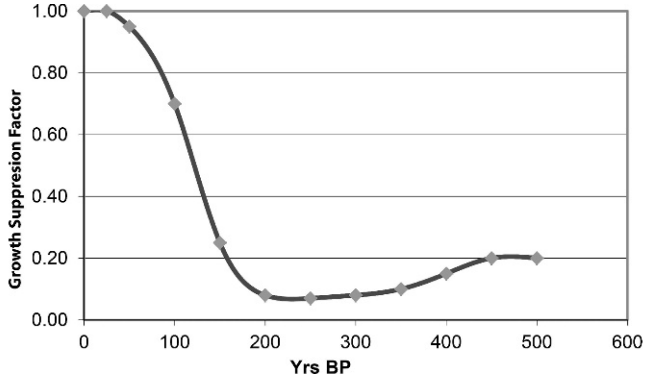

FIGURE 8. Assumed climate-related lichen growth suppression over the past 500 years. Lichen growth suppression is expressed as a reduction in growth rate from the latest 20th century.

lichen growth curves integrate the growing conditions since the lichen started growing, which may be 500 years or more. Specifically, the largest lichen used in indirect studies grew up during the relatively tough years of the Little Ice Age (LIA) and therefore likely experienced slower growth during their youth compared to the youthful lichen of today (totally consistent with your parents' frequent phrases like "you kids have it easy today; back when I was growing up …"). Beschel (1961, p. 1048) wrote, "An indirect measurement treats the old and large thalli as if they had the same environment, especially the same climate in their youth many centuries ago, as the small thalli on a much more recently exposed substratum experienced in the most recent past." How valid is this assumption?

To assess the impacts of changing climate conditions on long-term lichen growth, we created a simple model that simulates lichen growth over time using the four growth models presented above. We calculated the growth of lichen each established 50 years apart over the last 500 years. Lichen growth was calculated year-by-year in a spreadsheet using the growth model relationships between lichen size and growth rate, with an assumed starting diameter of 1.5 mm at age three years. To simulate the impacts of the colder LIA climate, a growth suppression factor that varies over time was also applied on a year-by-year basis (Fig. 8). We based our crude growth suppression factor on LIA reconstructions from Bradley and Jones (1993) and Isaksson et al. (2003), which are based primarily on ice core records from Svalbard but are consistent with our own temperature reconstructions from the Kapp Linné area (Nelson, 2010; Vaillencourt, 2010). We assumed that lichen growth suppression due to climate has a range similar to the lichen growth factor presented by Beschel (1961), who wrote, "The effect of the climate is of paramount importance and the difference in the constant speed of the diameter increase between a humid and an arid region may be a factor of twenty". This conclusion has been confirmed by Ten Brink (1973) and Hansen (2010). Thus our model suppresses growth rates down to 7% of modern growth rates (a reduction factor of 15) during the height of the LIA 250 years ago as shown in Figure 8. We readily admit that neither our assumed LIA climate nor the growth suppression factor is well constrained, however our simple model illustrates that changing climate can alter the size versus age patterns predicted by direct measured studies (Fig. 9). In all cases, the diameters of the older lichen are reduced from what would be predicted by direct growth rate measurements made over the past few decades. Growth rates of small, young lichen maintain the high growth rates observed from the direct measurement studies. The resulting age versus size growth curves resemble the typical curve generated by indirect growth studies. The "great growth period" is explained by the more favorable growing conditions of the recent past and the "linear phase" is a result of the older lichen experiencing harsher growing conditions during previous centuries.

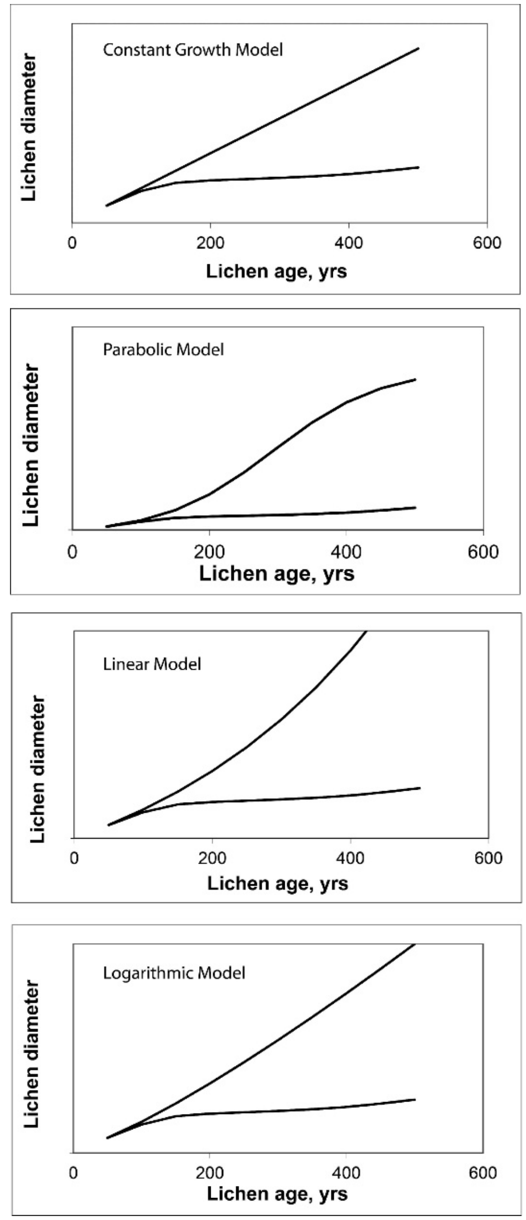

FIGURE 9. Modeled lichen growth showing no growth suppression due to climate change (upper line in each plot) and with assumed growth suppression due to harsher Little Ice Age (LIA) climate.

In addition to changing climate over the lifespan of older, larger lichen, several other aspects of growing conditions have changed since the early 20th century. In particular, anthropogenic pollution has become widespread even in the remotest area of the Arctic. From their analyses of two ice cores from Svalbard, Isaksson et al. (2003) reported that levels of sulfate, nitrate, and acidity show a pronounced increase since the 1950s. Recent studies show that lichens and bryophytes appear to be sensitive to increased nitrogen inputs (Nash and Gries, 1995; Bobbink et al., 2010, and references therein). Ultraviolet levels in the Arctic have also increased in recent decades due to decreased stratospheric ozone concentrations (McKenzie et al., 2003), although the effects on lichen growth are as yet contradictory (e.g., Lud et al., 2001; Rozema et al., 2005). Other recent environmental changes documented in the Arctic that may influence recent lichen growth rates include increased heavy metal deposition (Sun et al., 2006) and acid precipitation (Lechowicz, 1982; Mahaney et al., 1995). The impacts of these potential stressors have not been studied for the lichens typically used by lichenometrists, but it is well known that lichen do not tolerate industrial pollutants very well (Nash, 1976; Seaward et al., 1993; Nash and Gries, 1995). Van Herk et al. (2002) documented that since 1980 in the Netherlands, arctic lichen species are declining in abundance whereas subtropical and tropical lichen are increasing. Their analyses attribute these shifts to increases in temperature, and secondarily, increasing ammonia (NH^3) and, due to recent pollution control, decreasing sulfate (SO_4). It may also be relevant that numerous studies of arctic lake ecosystems have shown dramatic changes in productivity in the recent decades (Birks et al., 2004; Holmgren et al., 2009; Wolfe et al., 2006; Rühland et al., 2003; Axford et al., 2009).

In summary, there are many factors that influence lichen growth rates. The cumulative impacts of changing climate and other environmental influences on lichen growth rates are not well constrained. Yet there are ample reasons to reject the assumption that growth conditions for lichen have remained constant over the past 500 years. The long-term, indirectly determined growth rates measured by lichenometrists, however, do take into account the changing environmental conditions over the long life span of the lichens. Directly measured lichen growth will remain a critical tool for lichenologists striving to understand physiological processes within the complex symbiotic lichen ecosystem, but these relatively short-term studies represent only modern growth conditions. The lichenometrist must continue to rely on carefully compiled time-integrating indirectly determined growth measurements for the purposes of dating late Holocene landforms.

Conclusions

Directly measured lichen growth rates from Svalbard made over a 20-year interval using photographic measurements show that *Pseudephebe* ADD growth rates ranged from 0.2 to 1.5 mm yr^{-1} and *Rhizocarpon* ranged from 0.05 to 0.30 mm yr^{-1} in ADD. Growth rates are positively correlated to thallus size with some evidence for a reduction in growth in the largest specimens. Like other recent directly measurement studies, our derived growth versus size curves differ significantly from the traditional growth curves generated by indirect measurement studies.

More work needs to be done to better understand the growth mechanisms and rates of slow growing crustose lichens. Since all lichen grow very slowly, we encourage researchers to use digital photographic analyses to measure changes in lichen size over time—characterizing lichen size by measuring area provides more accurate results than measuring linear dimensions. (Note, however, that for indirect growth studies that measure hundreds to thousands of lichen just a single time each, a diameter measurement is adequate as long as identical measuring techniques are used for the calibration curve and the unknown surfaces.)

Lichen growth over recent decades is different than pre-21st century growth rates due to changing climate and other anthropogenic influences. Directly measured lichen growth rate studies can be very useful to elucidate modern lichen growth processes, but these short-term studies represent only modern growth conditions. Indirectly determined growth curves, which integrate lichen growth rates over the life span of the lichen, are better for dating prehistoric surfaces. Because of late Holocene and modern climate change, anthropogenic nutrient fluxes, etc., growth curves established by indirect methods must be the final arbiter of lichen growth rates for the application to dating Quaternary landforms.

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