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Source: *Arctic and Alpine Research*, Vol. 30, No. 2 (May, 1998), pp. 175-183
Published by: INSTAAR, University of Colorado
Stable URL: http://www.jstor.org/stable/1552132
Accessed: 03-07-2015 23:11 UTC

Arctic and Alpine Research, Vol. 30, No. 2, 1998, pp. 175–183

Frequency Distributions of *Rhizocarpon geographicum* s.l., Modeling, and Climate Variation in Tröllaskagi, Northern Iceland

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Abstract

Seven stable moraine surfaces in Tröllaskagi, northern Iceland, were sampled to produce frequency distributions of the sizes of up to 1000 *Rhizocarpon geographicum* s.l. thalli at each site. All frequency distributions showed a similar form, with patterns of disruption at the same points in the curves. In order to examine the possible cause(s) of this disruption, the structure of the observed distributions was compared with randomly generated distributions of lichen sizes. In the absence of snowpack data, temperature observations for the last 115 yr were used to produce duplicated model runs simulating the potential effects of snowkill on the lichen communities, producing results in close agreement with the observed data. It is concluded that in this area of northern Iceland, lichen growth was disrupted at four periods over the last 120 yr, and that at these periods possibly 80 to 100% of lichen thalli may have been lost. This has implications for lichenometric dating of moraines in the region, but as yet it is not possible to determine whether disruptions were solely due to climate, or to a combination of factors, including competition.

Introduction

Increasing attention has been paid in lichenometric studies to examination of the structure of lichen populations of largest lichens on boulders as a source of paleoclimatic information, especially as it relates to dating diachronous surfaces (McCarroll, 1993; Matthews and McCarroll, 1994; Bull, 1996). Less use has been made of utilizing the frequency distributions of "populations" of lichens covering large areas, although size-frequency studies by Benedict (1985), Innes (1983, 1986), Lock[e] et al. (1989) and Caseldine (1991) have demonstrated the potential of such information for dating purposes, and for identifying disturbance of "populations" by external factors (in the case of Benedict's [1996] work in the Colorado Front Range, rebuilding of game drive walls).

Examination of large samples of lichen sizes ("populations") on surfaces has engendered some debate as to the nature of the frequency distribution described. Innes (1983, 1986) has questioned the consistency with which particular distributions have been demonstrated. Having reported a true log-normal distribution for *Rhizocarpon* section *Rhizocarpon* (Innes, 1981), he argued that a range of distributions from truncated log normal to Poisson could be used for populations from Scotland and southern Norway (Innes, 1983). Andersen and Søllid (1971) also presented truncated log-normal models, although for the Indian Peaks region of the Colorado Front Range, Benedict (1985) suggested that a negative log-linear function best fitted the empirical data, perhaps because true truncated log-normal functions could only be found on "older" surfaces where communities were effectively closed. This wide variety of findings reflects a number of factors: differences in the sizes of thalli measured, differences in the growth rates and hence the maturity of the communities, and in the diversity of the environmental influences to be found operating at different locations. As a result of this diversity of opinions, and uncertainty over whether there is a "natural" mathematical form to the distribution, the present study follows Benedict (1985) who argued for the use of the best-fit curve for the particular community under observation, and only thalli >10 mm are used due to the difficulties of accurately measuring below this size.

In Iceland lichenometry has been used for dating moraine sequences (e.g. Gordon and Sharp, 1983; Caseldine, 1987; Kugelmann, 1991; Caseldine and Stötter, 1993), but there has been only one study of lichen "population" structures (Caseldine, 1991). Indirect measures of lichen growth in Iceland suggest that measureable lichens of *Rhizocarpon geographicum* s.l. cover only the last 200 yr, perhaps as a result of acid loading from the Laki eruption of 1783 (Caseldine, 1991; Kugelmann, 1991). Since this date, growth seems to have been relatively continuous with no equivalent volcanic effects, thus providing an opportunity for examining size-frequency distributions starting from a relatively recent *tabula rasa.*

Caseldine (1991), in a study initially designed to attempt to apply the frequency-distribution dating approach developed by Benedict (1985), described the existence of log-linear "populations" of *Rhizocarpon geographicum* s.l. in Tröllaskagi, northern Iceland, which showed varying degrees and forms of disturbance or disruption. These were principally on dynamic geomorphological features, debris flows, and rock glacier surfaces, with Little Ice Age terminal moraines also occasionally showing some reworking on proximal slopes after initial formation. The present study sought to develop this work and had two principal objectives: (1) to establish whether disturbed "populations" could be found on stable surfaces, moraines of believed known age; and (2) whether such disruptions could reflect non-site-specific factors, particularly snowkill, as previously demonstrated by Benedict (1990, 1993), especially as the area is known to have experienced significant variations in climate over the last two centuries (Stötter et al., in press).

Field Observations

Fieldwork in 1995 by the authors followed the same sampling methodology as that of Caseldine (1991). Where possible

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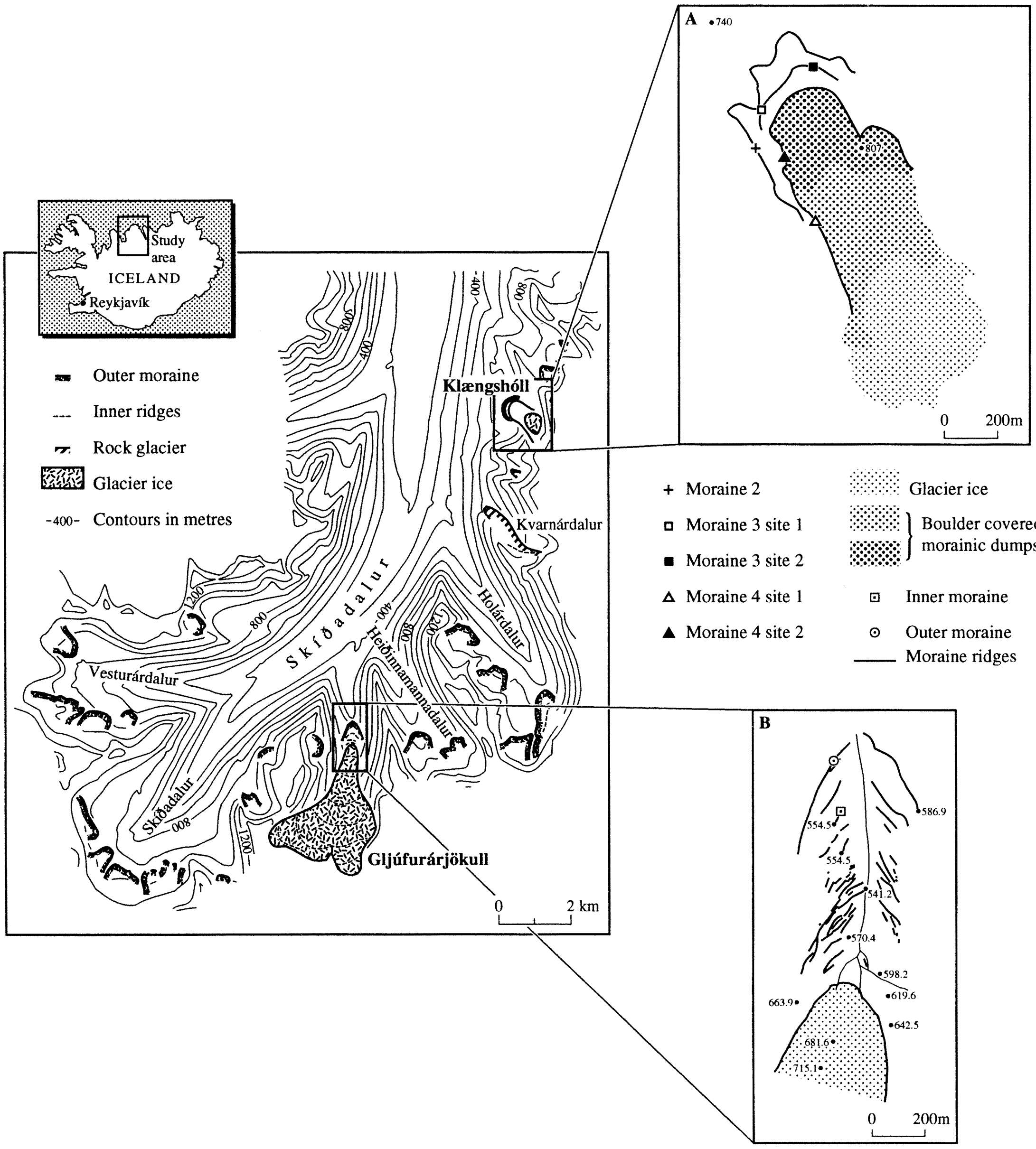

FIGURE 1. Location map showing details of moraines studied. Altitudes are in meters.

measurements of the long axes of up to 1000 thalli of *Rhizocarpon geographicum* s.l. ≥10 mm were made on stable moraine surfaces at two glaciers, Klængshóll (65°47′N, 18°35′W) and Gljúfurárjökull (65°43′N, 18°40′W) (Fig. 1, which also shows the location of the sample sites). Measurements were accurate to within 0.5 mm, care was taken to avoid coalesced thalli but all measurable thalli were included. Measurements were restricted to moraine crests, in particular avoiding "green zone" areas at the base of moraine slopes. Distances covered along the moraine crests varied depending on the size of the moraine and the available surface area for lichen growth. Similarly in order to achieve sufficient measurements on smaller moraine areas there was no control for boulder size. (A limited analysis of the relationship between maximum lichen size, longest axis, and longest axis length of boulders for 50 thalli at each of three moraine sites at Klængshóll, produced correlation (*r*) values between 0.32 and 0.39, suggesting at best a very weak positive relationship.) Data from 1989 used in the later analyses were corrected to 1995 by application of a growth rate of 0.42 mm yr^{-1} (Caseldine and Stötter, 1993).

A range of moraine ages were used from mid- to late-Holocene to 19th century. These are shown in Table 1 where minimum ages are quoted based either on tephras identified in the overlying soil profile, or on lichenometric (largest single lichen) dating. All moraine surfaces are at least 150 yr old, and although the more recent ones may not be as old as the Laki eruption, it should be emphasized that the lichenometric dates are minimum ages, and the real ages may be older (see discussion below).

Data from the sites are presented in Figures 2 and 3. Both individual frequency distributions (sorted into 3 mm class intervals) and the combined data for the two glacier forelands (Fig. 4) conform in general to a log-linear relationship (statistically the best fit to the data of any of the functions discussed in the introduction). Previous studies had showed little effect from varying the class interval sizes between 5 to 2 mm (Innes, 1986; Caseldine, 1991), so 3 mm was selected as a compromise be-

TABLE 1

Site details for the observed frequency distributions

Sites	Sampler	Year[a]	Number of lichens	Minimum age
Gljúfurárjökull				
Inner Moraine	CC	1988	1000	1850s[b]
	AB	1995	1000	
Outer Moraine	CC	1989	1000	1850s[c]
	AB	1995	1000	
Klængshóll				
Moraine 2	AB	1995	1000	>2800 BP[d]
Moraine 3: Site 1	AB	1995	1000	2800–1000 BP[e]
Site 2	AB	1995	500	
Moraine 4: Site 1	AB	1995	1000	1840s[f]
	CC	1989	1000	
Site 2	AB	1995	1000	

[a] Data collected in 1988 and 1989 was corrected to 1995 sampling sites by assuming a growth rate of 0.42 mm yr^{-1}.

[b] Lichenometric date, resurvey 1995.

[c] Lichenometric date.

[d] Tephrochronological date, presence of Hekla 3 in the soil profile.

[e] Tephrochronological date, absence of Hekla 3 but possible Landnám tephra.

[f] Lichenometric age based on largest lichen for 1995 resurvey.

tween having too many classes with too few observations in them, and adequately covering young sites with enough intervals >10 mm in size. In view of the estimated field error of ±0.5 mm, the smallest size used in the statistical analysis was 11 mm, due to the difficulty of getting an unbiased sample around 10 mm in size. As in the previous study by Caseldine (1991), the number of lichens in the higher size classes, above 40 to 50 mm, proved highly irregular, especially at the individual site level, emphasizing the uncertain accuracy of using the single largest observed thallus for dating.

Visual examination of Figure 4 reveals the apparent occurrence of a number of breaks or discontinuities in the graph, several of which can be seen at the site level (Figs. 2, 3). Three breaks in particular stand out, dated according to the largest lichen growth curve: 23 ± 1.5 mm (A.D. 1944–1937); 38 ± 1.5 mm (A.D. 1908–1901); and 47 ± 1.5 mm (A.D. 1887–1879), with a possible fourth at 32 ± 1.5 mm (A.D. 1922–1915). For sizes greater than about 50 mm the observations are too irregular to reveal recurrent features. Attempts to define these breaks statistically proved difficult due to the highly subjective nature of determing the values involved in statistically significant break points. While this is clearly a weakness in the analysis, the consistency of the position of the visual breaks is considered the most important finding. The later modeling exercise demonstrates a way in which such breaks can be produced, and underlines the high degree of variation in survival/recruitment that is required to produce comparable visually distinctive discontinuities.

The comparability of the results for the two forelands suggests a regional, or at least a non-site-specific cause for the disruptions in the lichen "population" structure. A number of potential causes can be postulated:

(1) *Disease*: Although a potentially significant factor, especially in communities under stress, this would be difficult to test retrospectively, and may have been an additional element, rather than the sole cause of lichen death.

(2) *Competition*: Competition between and within lichen species is clearly of major importance in the development of lichen covers on surfaces such as moraines, as a number of studies have shown (e.g. John and Dale, 1989; John, 1990). For young moraines in Iceland (i.e. deposited over the last century), the availability of space for successful recruitment is assumed not to have been a limiting factor. For older moraines this would certainly not be the case, and is probably the cause of the highly dispersed distribution of thallus sizes in the larger size intervals. The fact that the principal breakdown in the linear relationships generally occurs above 35 to 40 mm perhaps demonstrates the size, and hence age, at which competition becomes significant. Studies by Meyer and Venzke (1985) at Klængshóll showed the presence of up to 12 lichen species on the moraines under study. On the youngest moraine (Moraine 4) only two were identified as occurring at above occasional levels, *Rhizocarpon geographicum* and *Aspicilia* sp. (*alpina*?), yet as Figure 2 shows both observed distributions demonstrate breaks. Thus while not tested in this analysis the problem of competition, especially on the older surfaces, must remain a possible contributor of importance to the observed size-frequency distributions. This seems likely to be true for surfaces in excess of 100 yr (i.e. with a maximum lichen size of 40 mm), but unlikely for more recent surfaces.

(3) *Volcanic activity*: For Iceland volcanic activity is a possible cause, but although eruptions can be found within the break periods they are few and relatively small, and there are more potentially effective eruptions outside the periods (Simkin and Siebert, 1994).

(4) *Climate*: Survival of lichen species in severe climatic environments is well established (e.g. Kappen, 1993), but Benedict (1990) has shown how lichen growth can be affected by snowkill. In the Colorado Front Range it appears that where the average annual snow-free period is less than 10 to 12 wk for at least 5 to 8 yr all crustose lichen species will die. Thus, given the appropriate climatic conditions it is possible that considerable disturbance of lichen populations can take place. Direct comparisons between Colorado and Iceland are difficult due to greater day length in the latter, and possible winter snowpack differences, but climatic disruption remains a possible influence on the observed size-frequency distributions.

Given the range of possible explanatory factors for the size-frequency distributions and the field data currently available it was decided to attempt to test the likelihood of the alternative explanations through modeling. The purpose of the modeling was twofold: (1) to see if it was possible to reproduce the observed distributions; (2) if so, to identify the degree of lichen loss likely to have occurred.

Testing for a disease-related cause over the last 200 yr is not possible without epidemiological data suggesting the impact on distributions of sizes. Thus while it cannot be ruled out, it remains a very difficult factor to test. Similarly, although competition would have played a part in determining the observed distributions, it would be necessary to carry out much more detailed field surveys of the moraine surfaces to elucidate whether the relationships established elsewhere, as for instance in Alberta (John and Dale, 1989), are applicable in northern Iceland, and whether they outweighed other influences such as climate. The existence of undisturbed "populations" from a 1920s debris flow in the current study area at a lower altitude (Caseldine, 1991), would tend to support the idea of competition only becoming significant with time, in this case not within the last 70 yr, as less surface area is available for colonization. As far as volcanic activity is concerned, as stated above there is no obvious relationship between Icelandic eruptions and the postulated break dates, and the impact would have to be almost as severe as the

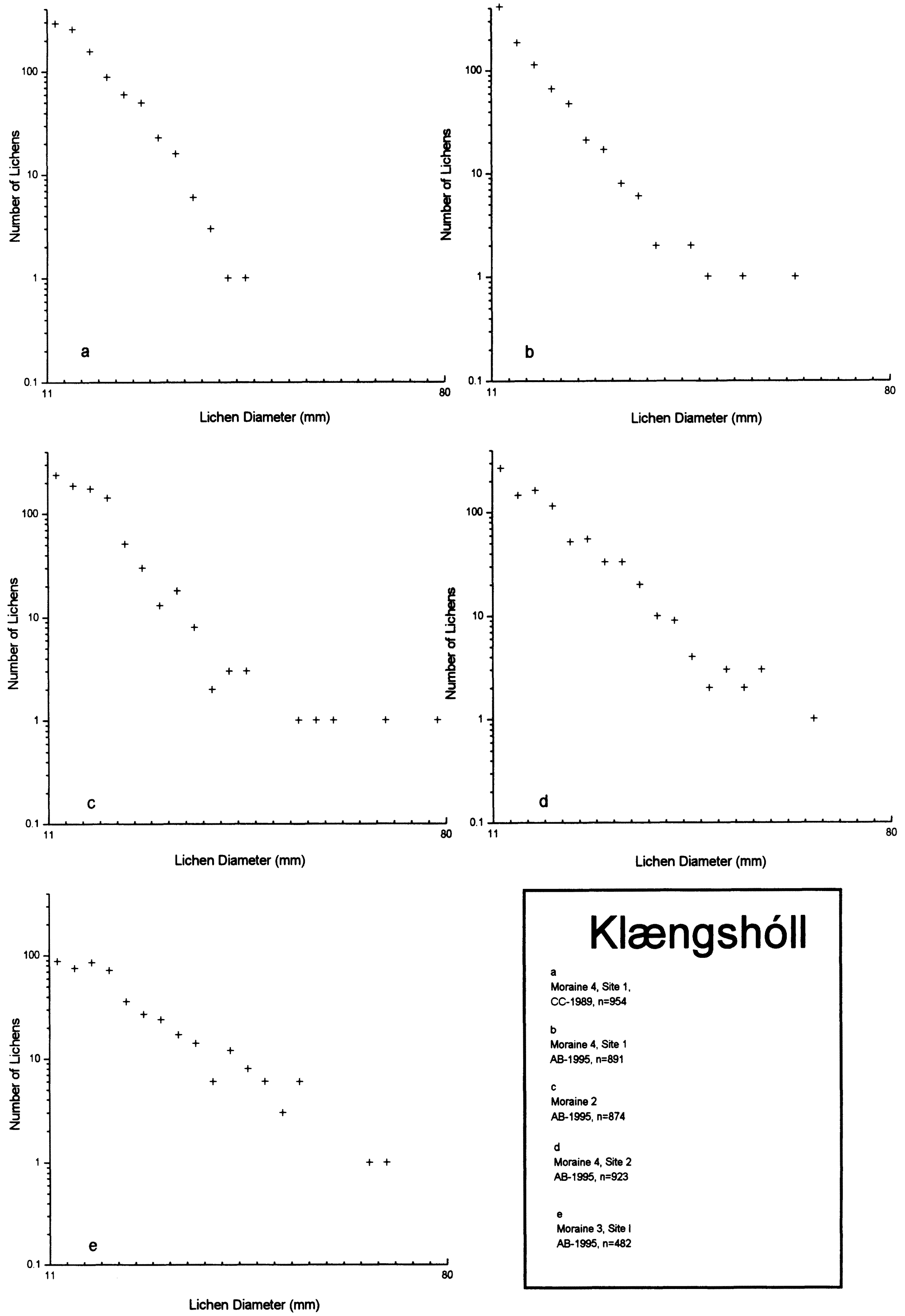

FIGURE 2. Size-frequency distributions for individual moraines at Klængshóll. Lichen diameters are in millimeters with a class interval of 3 mm. See text and Table 1 for details of individual sites.

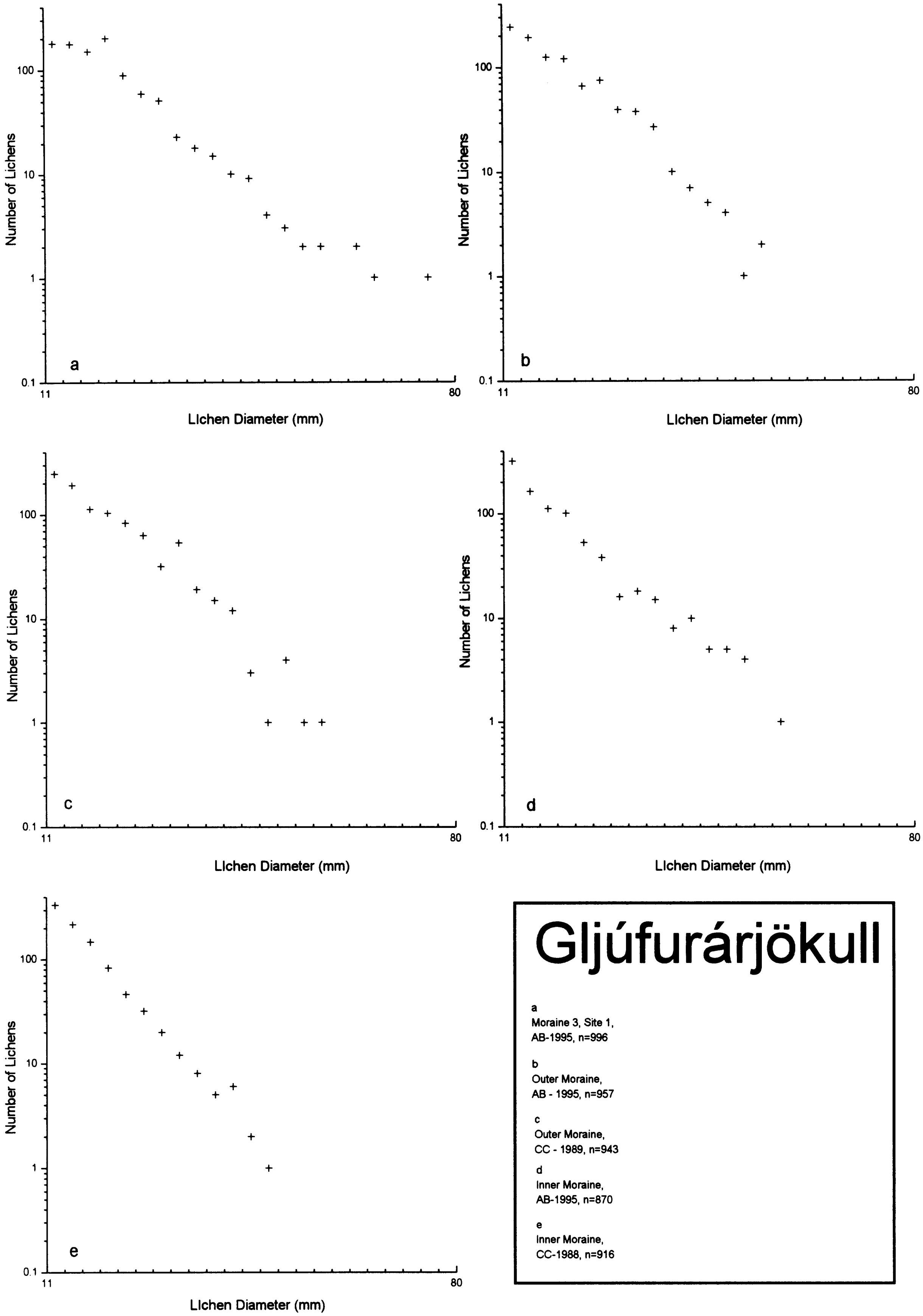

FIGURE 3. Size-frequency distributions for individual moraines at Gljúfurárjökull. Lichen diameters are in millimeters with a class interval of 3 mm. See text and Table 1 for details of individual sites.

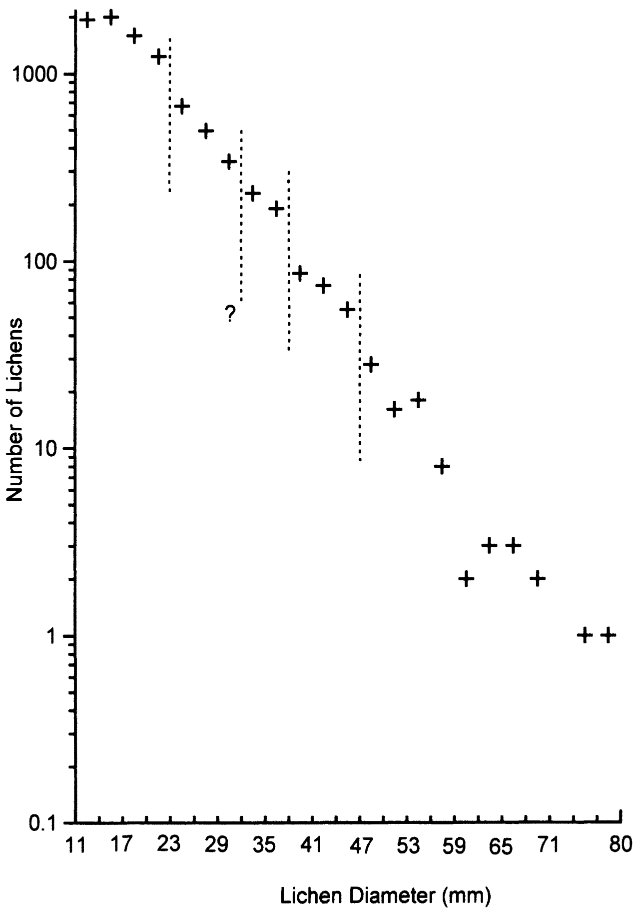

FIGURE 4. Data for all moraine sites combined in a single graph. Vertical dashed lines define the breaks in the total "population." Lichen diameters are arranged in 3 mm classes.

1783 Laki eruption to alter the distributions (see later modeling discussion). The presence of the recent undisturbed "population" record also argues against a volcanic explanation.

Of all the likely factors climate is probably that which can be examined most effectively at this preliminary level of analysis. This is, however, not without problems. In order to test rigorously a possible snowkill hypothesis, data on snowlie and snowpack thickness would be required. Such observations are extremely rare, hence the need for using some form of proxy data. The nearest suitable meteorological data are from Akureyri, approximately 20 km from the sample locations, at an altitude of 5 m a.s.l. Extrapolation to the altitude and location of the study sites is difficult, but if it is only severe climatic events that could be responsible for altering lichen populations to the extent observed, it is likely that these should be registered in the meteorological record. In view of this, we decided to attempt to evaluate a possible climatic link using the available meteorological data.

Theoretical Modeling

To examine whether climatic data could be used to suggest a possible influence on the structure of the lichen "populations" investigated, we decided to model the structure of lichen communities based on albeit simplified assumptions of their population dynamics, growth rate, and the climate in the region over the last 200 yr.

The basic model assumptions are the following:

(1) That optimal lichen growth rate for the region is 0.42 mm yr^{-1}, with a 10-yr colonization period (from Caseldine and Stötter [1993], see discussion above).

(2) That undisturbed lichen communities will eventually assume a normal distribution (Benedict, 1985), and that the standard deviation of the population around the mean will be 21%. The latter value is seen as a conservative approximation as there are no studies confirming the actual values to be used, except perhaps that of Innes (1986), in which generally lower values were obtained.

(3) That lichen communities were totally killed off at the time of the Laki fissure eruption in 1783.

(4) That climate can cause lichen death in the form of snowkill. This will occur if the snow-free period is less than 12 wk, and it is assumed that between 50 and 90% of all lichens will die (derived from empirical data in Benedict [1990]).

Climate data in the form of monthly mean temperatures were used to calculate the probable snowkill years. Data from 1882 to 1995 were corrected for an altitude of 750 m by assuming a temperature gradient of 0.65°C 100 m^{-1}; this is presented in Figure 5. Years in which the number of snow-free weeks was less than 12, assuming that a snow-free month occurred when monthly mean temperature was greater than 1.0°C, were assumed to be years in which significant lichen kill would occur. Temperature data are available from 1846 by use of correlation with the Stykkishólmur record, but only post-1882 data was used as the correlation between Akureyri and Stykkishólmur, especially on a monthly basis, although statistically significant is relatively weak (Sigfúsdóttir, 1969; Stötter et al., in press). Although winter precipitation is clearly of significance for snow cover the available meteorological data is not good enough to be able to put into the model. Precipitation data from Akureyri are only available from autumn 1927 onwards and extrapolation back using Stykkishólmur is not possible (Stötter et al., in press), hence the need to use temperature as the best available proxy.

Model runs were undertaken using Minitab version 10 for Windows by generating an initial lichen community in 1794 (10-yr colonization period after Laki) of 10,000 randomly generated lichens with a normal distribution of mean size determined by the growth rate curve, and a standard deviation of 21%. At every snowkill event a proportion of these lichens were killed with no size bias, and replaced with a fresh population. The model was run under varying assumptions:

(1) Lichen kill would occur in any year where mean monthly temperature was greater than 1.0°C for less than 3 mo. Where consecutive years of high snow cover occurred within the 10-yr lichen colonization period, models were run assuming no lichen growth at all during that period (i.e. growth occurs only 10 yr after the last snow-cover event), and also allowing for limited growth (e.g. a percentage of lichens will survive each event and will survive the 10-yr colonization period). This emphasizes the importance of the cumulative effect of closely occurring events.

(2) Kill percentage was varied between 50 and 80% (that observed by Benedict [1990]).

(3) The kill percentage was varied with respect to the severity of the events. Since 1882 was the only year with a more severe snowkill i.e. only 1 snow-free month, this year was modeled to have a higher lichen mortality potential.

The characteristics of the model runs are presented in Table 2. Figure 6 shows the two best comparisons of simulated and actual data, and represent a remarkable correlation between the model results and the observed dataset for stable sites in the region. Of particular importance is the fact that the exponential decay structure of the population is accurately simulated, and

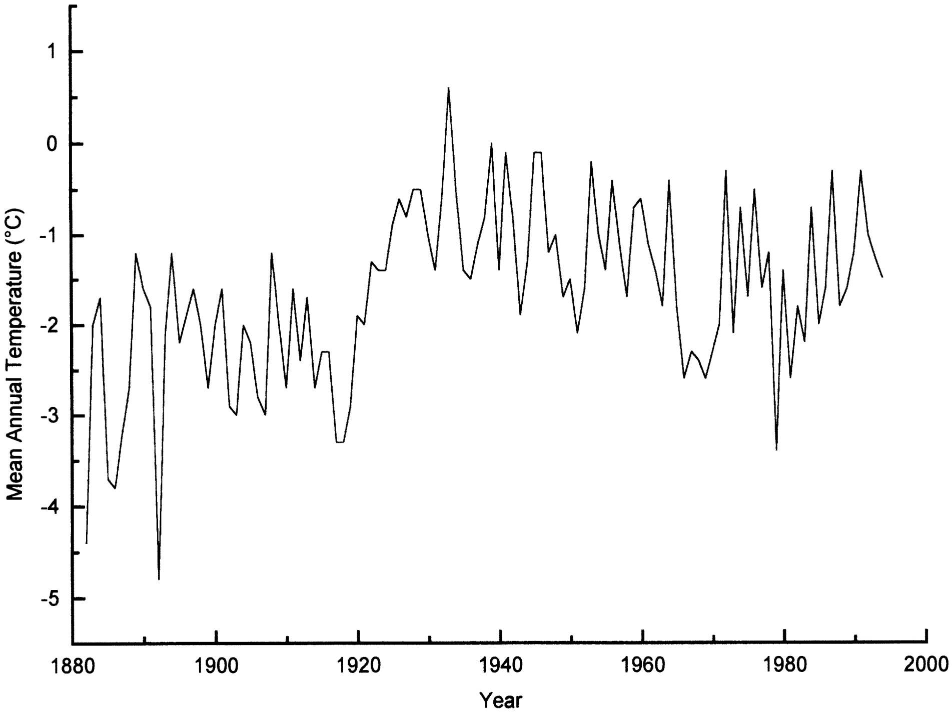

FIGURE 5. Estimated mean annual temperatures for 1882–1995 at 750 m, based on observations at Akureyri and corrected using a lapse rate of 0.65°C 100 m^{-1}.

that disturbances in the structure do correlate with those observed. A good fit is obtained with run 3 (assuming an 80% kill rate for all snowkill events), but the best fit is obtained if the 1882 severe snowkill event is assumed to kill all existing lichens (run 6, Table 2).

One feature of the modeling that is revealed is the problem of assuming a continuous normal distribution. As this is asymptotic the modeling generates theoretical lichen thalli well in excess of the maximum possible size assuming lichen growth rates represent optimal growth. Thus in Figure 6 sizes well in excess of the maximum possible assumed size of 90 mm (212 yr at 0.42 mm yr^{-1}) are predicted. In effect therefore the modeling really needs to assume that the distribution is a truncated normal distribution whereby the probability of a particular large size is used as the cutoff. The best estimate of this probability has not yet been defined, but from the data presented here it would appear to be close to 1 in 1–2000, i.e. 0.001 to 0.0005.

Of particular importance from the modeling, irrespective of the validity of a climatic influence, is the degree of lichen loss required to produce comparable breaks—80% for one event in run 3, and 100% for run 6, a virtually complete loss of lichens around 1882. Thus, whatever the reason for the pattern of observed lichen size-frequency curves, they must reflect quite major disturbances in growth at more than one occasion over the last 120 yr.

TABLE 2

Lichen "population" model runs[a]

Model runs	1794	1892	1913	1936	1959	Total
Run 1	100%/100	99%/625	50%/1250	50%/2500	50%/5525	10000
Run 2	100%/10	99.9%/270	70%/900	70%/2100	70%/6720	10000
Run 3	100%/16	99.8%/80	80%/400	80%/1600	80%/7904	10000
Run 4	100%/15	90%/117	75%/469	75%/1875	75%/7624	10000
Run 5	100%/13	98%/320	60%/480	80%/1200	60%/7987	10000
Run 6	—	100%/80	80%/320	80%/1280	80%/8320	10000

[a] Figures in each cell are the percentage number of lichens killed by the event 10 yr preceding the date (assuming a 10 yr colonization period), together with the number of lichens surviving from that colonization period after all subsequent kill events.

Conclusions

The observations and modeling described above raise a number of issues:

(1) Four periods of disruption of growth of the lichen *Rhizocarpon geographicum* s.l. have been identified in the study area, during which observed lichen "populations" are consistent with up to 80% mortality taking place, and even theoretically 100% around 1882. Through using temperature as a proxy for snow-free months it is possible to suggest snowkill as a mechanism to explain the loss, but the proxy nature of the climatic data, and the absence of contemporary evidence from Iceland on the behavior of *Rhizocarpon geographicum* s.l. under such conditions, mean that such a link remains hypothetical.

(2) The lichen modeling, and especially the unlikely survival of lichen thalli from earlier Little Ice Age colonization shows the inherent weakness of using single, or even mean of 5 or 10, largest lichen thalli as accurate indicators of surface age. For northern Iceland this suggests that for any Little Ice Age moraines older than the mid-19th century, an age anywhere between 1783 (Laki) and the 1850s would be possible, perhaps even earlier if the Laki eruption were responsible for a major breakdown of the soil/vegetation system in the moraines. The presence of low annual temperature series in the earlier half of the 18th century, at least as severe as in the early 1880s, in the Stykkishólmur record (Sigurðsson and Jónsson, 1995), further emphasizes this point, with very few, if any thalli from the late 18th and early 19th century likely to survive at altitude.

(3) It remains possible that the Laki fissure eruption was not the single limiting event on maximum lichen size in Iceland, at least at high-altitude moraine sites, but that the recurring severe climate conditions in the mid-19th century, were the major influence, particularly extensive periods of snow cover, leading

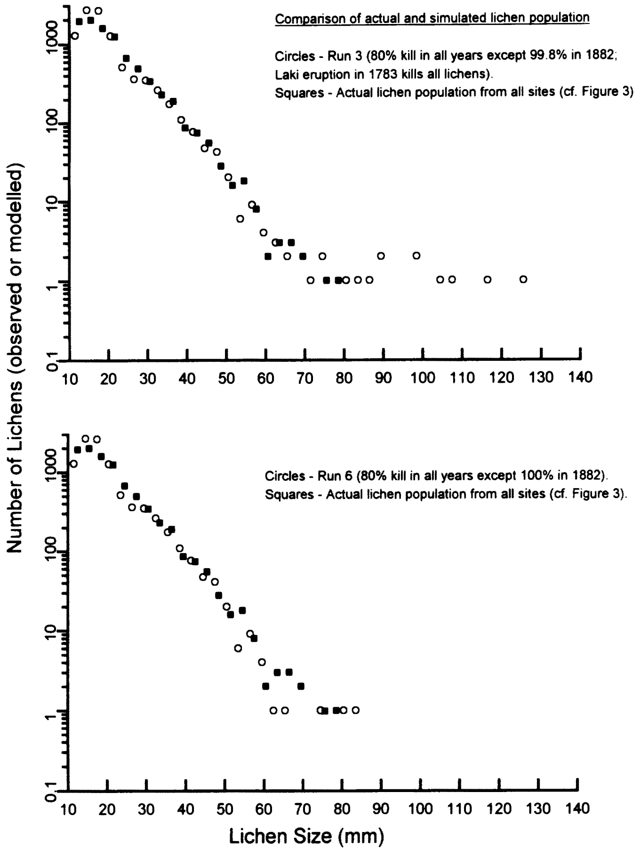

FIGURE 6. Comparison of simulated model runs and observed distribution shown in Figure 4.

to high lichen mortality. With the recent improvement in knowledge of the geochemical and toxological conditions pertaining to the Laki fissure eruption (Fiacco et al., 1994), it would be interesting to test the sensitivity of *Rhizocarpon geographicum* s.l. to simulated Laki volatiles.

(4) For areas of Iceland away from meteorological stations, especially those with only short 20th century records, the use of lichen population studies offers a way of establishing further climatic information for the last 200 yr. For other arctic-alpine environments with slower lichen growth rates this method provides an additional variant on current approaches to identifying possible short-term climatic and nonclimatic impacts.

(5) There is clearly a need for a much more detailed analysis of the questions raised here, firstly to determine the altitudinal and spatial scale of the observed distributions, and secondly, to examine current lichen ecology in Tröllaskagi with a view to establishing the likelihood of other factors being influential, in particular competition and disease.

Acknowledgments

The authors wish to thank Phil Wookey and Mark Berisford for field assistance, Hans Stötter and Maria Wastl for logistical support and valuable discussions, Danny McCarroll for comments on an earlier draft with apologies for not fully following his guidance, and James B. Benedict, William W. Locke, and an anonymous reviewer for their comments. We are particularly grateful to Lene Zachariassen and Óskar Gunnarsson for their hospitality in Iceland.

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Ms submitted December 1996
Revised ms submitted November 1997