Acta Biologica Plantarum Agriensis
ISSN 2061-6716 (Print), 2063-6725 (Online)
https://ojs.uni-eszterhazy.hu/index.php/ABPA
https://doi.org/10.21406/abpa.2023.11.1.4

11(1): 4–45 (2023)
Dedicated issue
Review

CHANGES IN GEOTHERMAL VEGETATION AT MYVATN, ICELAND, AND COMPARISONS TO OTHER GEOTHERMAL AREAS

Janice M. Glime*[1]*, Zen Iwatsuki[2]† & Theodore J. Bornhorst[3]

[1]*219 Hubbell St., Houghton, MI, USA 49931;* [2]*formerly of Hiroshima University, Japan;* [3]*Department of Geology and Geological Engineering, Michigan Technological University, Houghton, MI, USA 49931; *E-mail: jmglime@mtu.edu*

Abstract: We sampled 207 plots from 15 transects at the Myvatn geothermal area in Iceland in 1985, one year after the September 1984 eruption of Krafla, and again in 1987, and compared the species and community structure to that of other sites we had visited in Japan and New Zealand. We found 5 lichen, 47 bryophyte, and 28 tracheophyte species at Myvatn. Overall Shannon diversity (H') was high at 4.34, with Brillouin (information-theory-based) species diversity (H') being very similar at 4.32. The greatest diversity occurred at > 25–35°C surface temperature and the least at > 60°C. Zones are defined mostly by temperature and humidity, with Cyanobacteria closest to the vents in the hottest zones, followed by bryophytes, then lichens, then tracheophytes. *Bryum argenteum*, *Ceratodon purpureus*, and *Fossombronia* sp. 1 (probably immature *F. foveolata*) occupied the highest temperatures near the vents in 1985. Lichens tended to avoid hot soils with high humidity. Soil chemistry most likely plays a role, but with so many variables and many values at unquantifiable levels, we considered it premature to determine their individual effects. By 1987, *Bryum argenteum*, a near-vent species, had almost totally disappeared, along with the steam emissions where they had thrived. The geothermal areas in cold climates could serve as refugia for more temperate species that may have existed prior to the Ice Age, or they may simply be suitable habitats for northern extensions of the species. This study gives us a glimpse of potential vegetational changes resulting from climate changes as demonstrated in three regions of the world.

Keywords: bryophytes, lichens, plants, soil chemistry, temperature, successional changes, volcanoes

INTRODUCTION

Steaming geothermal fields are a natural laboratory of soil chemistry, humidity, and temperature variations. We know little about the mechanisms that permit plant extremophiles to evolve, survive, and reproduce under their most extreme of physical stresses (Lindgren *et al.* 2016). In Iceland and elsewhere, the geothermal ecosystems are poorly known and mostly descriptive (Elmarsdóttir *et al.* 2003).

Geothermal areas are important in consideration of the survival of life during the glaciation periods in the Earth's history (Fraser *et al.* 2014; O'Gorman *et al.* 2014; Pointing *et al.* 2014). The hypothesis is that they could serve as important refugia for cryptogamic vegetation. Although areas near the vent opening may be too hot for most life, the surrounding ground grades into the colder ground that is no longer uninhabitable, thus creating a zone of survivable temperatures within this gradation. Most studies on geothermal vegetation in glacial climates are from the Antarctic region (Broady *et al.* 1987; Halloy 1991; Convey *et al.* 2000; Bargagli *et al.* 2004; Lewis Smith 2005a, b, c; Convey and Lewis Smith 2006; Shortlidge 2014). In the Arctic, Halliday *et al.* (1974) studied the flora associated with hot springs of Greenland. More recently, Elmarsdóttir *et al.* (2003, 2015) have reported vegetation zones of 17 Icelandic geothermal areas (without listing species), including the Myvatn area, and Bjarnason and Fridriksson (1972) described the vegetation colonization of the island of Surtsey following its formation off the Icelandic coast due to a volcanic eruption beginning in November 1964. Other contributions to these cold climate studies are from alpine areas (e.g. Halloy 1991).

In 1983, Iwatsuki (*Figure 1*) and Glime began a study of the communities associated with geothermal vents in Japan, followed by visits to Iceland in 1985 and 1987 and New Zealand in 1988, to look for worldwide patterns. Since our field work, Jónasson and Einarsson (2009) have described the geothermal features of several high-temperature geothermal areas and Elmarsdóttir *et al.* (2015) have described the vegetation in five geothermal areas in Iceland. The present vegetation study in 1985 represents a geothermal area near Lake Myvatn that was not included in their study. The Krafla area had experienced earthquake movement, fissures, lava flows, and fires the previous year (4–18 September 1984) (McClelland 1984), extending over 9 lava fields and 36 km^2. This created new habitat that experienced primary succession in the area of our study. However, because of the patchy nature of volcanic flow and geothermally heated ground, it was not possible to be sure that a given quadrat was undergoing primary succession since this area already had geothermal activity. Furthermore, in contrast to our

Japanese sites, the area had steaming fissures but lacked the small vents with circular zones of temperature and vegetation around them. Our objectives were to determine the species in the vent area, to describe the associated soil chemistry, and to relate cover, diversity, and frequency to temperature, moisture, and *p*H. These descriptions permit us to compare the Myvatn geothermal area with similar areas in other parts of the world.

Figure 1. Zen Iwatsuki warming his hands at a geothermal fissure at Myvatn, Iceland (Photo by Janice Glime).

MATERIALS AND METHODS

Data for the comparison of cryptogams and tracheophytes are based on sampling in the Myvatn area of Iceland at Namafjoll and Krafla (65°40' N, 16°52' W) on 16–22 August 1985. We (Iwatsuki and Glime) re-visited Myvatn, Iceland, 24 July-10 August 1987 to reassess the vegetation and to take soil samples for analysis. Methods in Japan and New Zealand were the same as those in Iceland.

Plant Sampling

In 1985 at Myvatn, Iceland, we established random distances between 15 transects and located a 20 x 20 cm quadrat randomly in each 5–meter segment of the transect, totalling 207 quadrats; near discernable vents sampling was within every meter. Two additional transects had no plants. In 1987 we established 16 transects with a total of 195 quadrats. The number and length of transects was determined by the size of the geothermal area, with a range of 3–20 quadrats per transect. We estimated percent cover for each plant and lichen taxon and for percent visibly bare ground, initially checking our estimates of cover against that determined by using a grid (20 x 20 cm wooden frame marked off in 2 x 2 cm squares strung with rubber bands). In cases where vegetation was multilayered, the total cover could exceed 100%. The sampling procedure in Japan and New Zealand was similar (Glime and Iwatsuki 1994, 1997). Voucher specimens are deposited in the Herbarium of Hiroshima University (HIRO), Japan.

Resource Methods

We measured soil temperature at the surface and at 15 cm depth, soil *p*H, and soil and air humidity in the field as well as collected soil from each plot for laboratory analysis.

Measurements of *p*H were made on collected soil samples in distilled water within 24 hours using a digital field *p*H meter. Soil humidity was measured on a relative scale ranging 1–10 with a garden humidity meter. Some soil humidity values are missing because rainy weather made measurements meaningless.

Soil samples were collected in each quadrat visited in 1987 and stored dry until they were analyzed in 1989, but funding limited the number of samples analyzed to 80, chosen randomly. Bulk analysis of 20 elements was first accomplished using X-ray fluorescence spectroscopy, Philips AXS automated wavelength spectrometer, from Mahwah, NJ, USA, and calibrated using international geochemical reference samples for Al, Mg, K, Na, Fe, Mn, Ba, Ti, P, Si, Ca, Zr, Sr, As, Zn, Cu, Ni, Cl, V, and S (Rose *et al.* 1986). The entire dry soil sample was then soaked with room temperature distilled water and the leachate passed through a 0.45 micron filter. Substances passing 0.45 microns were considered to be dissolved. The ratio of water mass to soil mass was kept constant, thus normalizing the differing soil sample sizes. After leaching, the residual/leached soil sample was dried and homogenized, followed by repeated analysis. The soluble portion was determined to be the difference between the bulk and leached soil measurements. The data are discussed below with respect to the instrumental lower limit of reliable detection or limit of quantification/analytical level. Sulfur was also measured on the leachate and determined to be replicable compared to the subtraction method.

Species Diversity

The species diversity indices used here are based on the Shannon formula (Shannon 1948; Shannon and Weaver 1949) and the Brillouin information theory formula (Patten 1962; Glime *et al.* 1981).

Shannon

$$H' = -k\sum_{i=1}^{s} [P_i * \ln(P_i)]$$

where P_i is the probability (n_i/N) of encountering species i in a sample of one individual from a community too large to be counted, N is the number of individuals in the sample, s is the number of species, and k is a constant that permits one to convert to base 2, assuming a species is either present or absent, hence having two states (Pielou 1966).

Brillouin

$$H' = (k/N)\,[\ln(N!) - \sum_{i=1}^{s} \ln(n_i!)]$$

where n_i is the number (or cover) of individuals of species i, N is the number of individuals (or cover) in the community, and k is a constant for converting to base 2 (Brillouin 1962). This formula assumes that the entire community is known and that no extrapolation is to be made to a larger community. It is appropriate when one does not expect random distribution and the diversity is considered to be that of the sample, or in this study, that of the sum of samples.

RESULTS AND DISCUSSION

Habitat Characteristics

The surface soils at the Myvatn vents are mostly red and white clay with low *p*H near the vent, becoming pinker and greyer farther away as the *p*H rises. A thin layer of silica often covers the surface in the higher *p*H areas, presenting a rock-like surface. Although penetrable with a sharp object and some effort, it is not easily penetrated by seedlings, so it generally supports only surface plants. A more common condition is a mixture of clay and silica patches. In a few cases, the surface is a mixture of granular ash (tephra) that is mostly dry except for steam from nearby vents. There was no vegetation large enough to provide significant shade.

The surface temperature in the Myvatn study area ranged from 10 to 80°C, whereas the 15 cm range was 10 to 100°C. The *p*H ranged from 2.2 to 7.5. Moisture occurred at all 10 levels indicated by the soil moisture meter. Unlike the distinct vents at most of our previously studied Japanese sites, the Myvatn geothermal field had fissures and heated ground.

Richness, Diversity, and Cover

In the 207 plots in 1985 at Myvatn, Iceland, total richness was 5 lichens, 24 liverworts, 23 mosses, and 28 tracheophytes *(Table 1*), totalling 80 species. In 1987, we identified 3 lichens, 13 liverworts, 17 mosses, and 17 tracheophytes, totalling only 50 species. The greatest frequency in both years was that of the *Racomitrium canescens* (31, 26) and *R. lanuginosum* (37, 60). Elmarsdóttir *et al.* (2015) reported a richness of 50 tracheophyte, 30 lichen, and 10 bryophyte species from nearby geothermal areas at Namafjoll, Iceland, and 81 tracheophyte, 55 lichen, and 19 bryophyte species from Krafla, Iceland, in 2005–2008, suggesting that colonization by lichens and tracheophytes in the area was probably rapid after our study. Among the 17 Iceland site locations they studied, tracheophyte site richness ranged 0–111, lichens 7–113, and bryophytes 0–25.

Table 1. Vegetation species list, percent frequency, and mean cover at Myvatn, Iceland, in 1985 and 1987. Those with ≥ 5% frequency are in bold. (n=207 sample plots from 15 transects).

Species	**1985**		**1987**	
	% Freq	**%Mean Cover**	**% Freq**	**%Mean Cover**
Percent Bare Soil	–	35.9	–	38.0
Cyanobacteria	**24**	**7.1**	**17**	**5.6**
Lichens				
Cladonia chlorophaea (Flörke ex Sommerf.) Spreng.	1	0.1	–	–
Cladonia mitis Sandst.	<1	0.0	<1	0.02
Cornicularia aculeata (Schreb.) Ach.	**7**	**0.7**	4	0.43
Peltigera canina (L.) Willd.	2	0.1	–	–
Stereocaulon Hoffm. sp.	4	0.2	2	0.05
Bryophytes				
Liverworts				
Anthelia juratzkana L. Dumort.	<1	0.0	–	–
Barbilophozia hatcheri (A.Evans) Loeske	2	0.1	1	0.21
Barbilophozia sudetica (Nees ex Huebener) L.Söderstr., De Roo et Hedd.	**12**	**3.3**	<1	0.03
Cephaloziella hampeana (Nees) Schniffn. ex Loeske	2	0.1	–	–
Cephaloziella rubella (Nees) Warnst.	3	0.3	**5**	**0.19**
Cephaloziella varians (Gottsche) Steph.	1	0.2	–	–
Endogemma caespiticia (Lindenb.) Konstant., Vilnet et A.V.Troitsky	<1	0.0	–	–
Fossombronia foveolata Lindb.	**14**	**5.3**	**20**	**4.5**
Fossombronia Raddi **sp. 1** (probably immature ***F. foveolata***)	**23**	**3.7**	1	0.13
Gymnocolea inflata (Huds.) Dumort.	<1	0.0	2	0.16
Gymnomitrion corallioides Nees	<1	0.0	–	–
Lophoziopsis excisa (Dicks.) Konstant. et Vilnet	<1	0.0	–	–
Mannia gracilis (F.Weber) D.B.Schill et D.G.Long	4	0.2	–	–
Marchantia polymorpha L.	–	–	2	0.04
Marsupella funckii (F.Weber *et* D.Mohr) Dumort	2	0.2	–	–
Mesoptychia collaris (Nees) L.Söderstr. et Váňa	<1	0.0	–	–
Nardia scalaris Gray	4	0.5	**12**	**5.8**
Odontoschisma elongatum (Lindb.) A.Evans	1	0.0	–	–
Preissia quadrata (Scop.) Nees	–	–	**13**	**3.22**
Riccia beyrichiana Hampe/***bifurca*** Hoffm.	1	0.1	**15**	**2.24**
Scapania curta (Mart.) Dumort	2	0.0	3	0.39
Scapania hyperborea Jorg.	1	0.0	–	–
Schljakovianthus quadrilobus (Lindb.) Konstant. et Vilnet	1	0.0	<1	0.005
Solenostoma gracillimum (C.Gao et J.Sun) Váňa et D.G.Long	**6**	**1.6**	3	0.52
Sphenolobus minutus (Schreb. ex D.Crantz) Berggr.	1	0.0	–	–
Mosses				
Anomobryum julaceum (Schrad. ex P.Gaertn., B.Mey. & Scherb.) Schimp.	4	0.3	–	–
Aulacomnium palustre (Hedw.) Schwägr.	–	–	<1	0.005
Barbula unguiculata Hedw.	<1	0.0	–	–
Brachythecium Schimp. sp.	<1	0.0	–	–
Bryum argenteum Hedw.	**10**	**1.5**	3	0.09
Bryum Hedw. sp.	–	–	1	0.01
Campylopus subulatus Schimp. ex J.Milde	**5**	**0.2**	–	–
Ceratodon purpureus (Hedw.) Brid.	**14**	**4.6**	**31**	**3.5**
Conostomum tetragonum (Hedw.) Lindb.	1	0.1	–	–
Dicranella Schimp.	–	–	2	0.08
Dicranum fragilifolium Lindb.	<1	0.0	–	–
Grimmia Hedw./*Schistidium* Bruch & Schimp. sp.	1	0.2	–	–
Leptobryum pyriforme (Hedw.) Wilson	<1	0.0	–	–
Oligotrichum hercynicum (Hedw.) Lam. & DC.	–	–	4	0.34
Philonotis caespitosa Jur.	1	0.0	–	–
Philonotis marchica (Hedw.) Brid.	<1	0.0	–	–
Pleurozium schreberi (Willd. *ex* Brid.) Mitt.	1	0.0	–	–
Pogonatum aloides (Hedw.) P.Beauv.	**15**	**0.7**	<1	0.005
Pogonatum dentatum (Menzies ex Brid.) Brid.	–	–	2	0.06
Pogonatum urnigerum (Hedw.) P.Beauv.	2	0.2	<1	1
Pohlia cruda (Hedw.) Lindb.	1	0.0	–	–
Pohlia nutans (Hedw.) Lindb.	–	–	<1	0.015
Polytrichastrum formosum (Hedw.) G.L.Sm.	<1	0.0	2	0.07
Polytrichastrum longisetum (Sw. ex Brid.) G.L.Sm.	–	–	**15**	**2.5**
Polytrichum juniperinum Hedw.	–	–	4	0.25
Polytrichum piliferum Hedw.	1	0.0	–	–
Psilopilum cavifolium (Wilson) I.Hagen	–	–	<1	0.005

Species	**1985**		**1987**	
	% Freq	**%Mean Cover**	**% Freq**	**%Mean Cover**
Racomitrium canescens (Hedw.) Brid.	**31**	**9.5**	**26**	**5.9**
Racomitrium fasciculare (Hedw.) Brid.	<1	0.0	–	–
Racomitrium lanuginosum (Hedw.) Brid.	**37**	**7.6**	**60**	**9.93**
Sanionia uncinata (Hedw.) Loeske	3	1.1	1	0.02
Timmia megapolitana subsp. *bavarica* (Hessl.) Brassard	<1	0.0	–	–
Tracheophytes				
Achillea millefolium L.	1	0.0	–	–
Alchemilla alpina Schinz & R.Keller	1	0.1	–	–
Arctostaphylos uva-ursi (L.) Spreng.	<1	0.1	–	–
Betula nana L.	<1	0.0	–	–
Calluna vulgaris (L.) Hull	4	0.7	–	–
Carex L.	3	0.2	–	–
Cerastium alpinum Bunge	1	0.0	**5**	**0.14**
Chromolaena collina (DC.) R.M.King & H.Rob.	3	0.1	–	–
Empetrum nigrum L.	<1	0.0	–	–
Epilobium anagallidifolium Lam.	<1	0.0	**11**	**0.49**
Equisetum arvense L.	**8**	**2.6**	**5**	**0.14**
Euphrasia frigida Pugsley	**6**	**0.2**	**5**	**0.09**
Festuca ovina L.	–	–	**5**	**0.31**
Festuca vivipara Sm.	**11**	**1.3**	–	–
Galium uliginosum Pall. ex M.Bieb	1	0.0	**5**	**0.23**
Koenigia islandica L.	<1	0.0	–	–
Luzula DC.	–	–	<1	0.005
Parnassia palustris L.	1	0.0	–	–
Persicaria vivipara (L.) Ronse Decr.	–	–	2	0.02
Poa angustifolia Elliott	**14**	**3.0**	2	0.24
Poa compressa L.	4	0.2	**8**	**2.59**
Prunella vulgaris L.	1	0.1	–	–
Ranunculus acris L.	4	0.1	<1	0.005
Sagina caespitosa Lange	**12**	**2.4**	**25**	**3.74**
Salix herbacea L.	<1	0.0	3	0.04
Scorzoneroides autumnalis (L.) Moench	1	0.0	3	0.06
Selaginella selaginoides (L.) P.Beauv. ex Schrank & Mart.	<1	0.0	–	–
Stellaria media (L.) Vill.	2	0.1	–	–
Thalictrum alpinum L.	–	–	<1	0.005
Thymus praecox* subsp. *brittanicus (Ronniger) Holub	3	**5.9**	**19**	**1.69**
Veronica fruticans Jacq.	<1	0.0	–	–
Viola palustris L.	1	0.1	–	–

At Myvatn geothermal vents the number of bryophyte taxa (47) is far greater than at the vents of Ponponyama, Japan (15 species; 20–80°C; *p*H 2.8–7.5) (Glime and Iwatsuki 1994) or Wakoto, Japan (8 species; 25–80°C; *p*H 3.5–6.0) (Glime and Iwatsuki 1997). Compared to non-vent heathland areas of Iceland, the Myvatn geothermal area has more bryophytes (47) than tracheophytes (28) (10–80°C; *p*H 2.2 to 7.5), whereas the surrounding heathland has more taxa of tracheophytes (> 100) than of bryophytes (~60) (Gunnlaugsdottir 1985). The following results illustrate the patterns that emerge and possible reasons for the differences.

With widely varying characteristics within geothermal areas, we might expect a relatively high species diversity, with various species being able to occupy the wide range of niches. The overall Shannon diversity (H’) at Myvatn vents was high at 4.34 and bryophyte diversity of 3.56, with Brillouin (information-theory-based) overall species diversity (H’) being similar at 4.32 and bryophyte H’ being

3.54. Nevertheless, the within-quadrat diversity ranged widely, with the widest range of diversity at 10–25°C (0.13 to 6.21). The overall Shannon diversity at Myvatn was highest at surface temperatures > 25–35°C and lowest at > 60–80°C (*Table 2*). Shannon diversity at Wakoto, Japan, was 2.96 (unpublished, based on Glime and Iwatsuki 1997). At five sites in Hokkaido, Japan, Shannon diversity ranged from 2.20 to 3.44 and richness from 8 to 34 in plots with surface temperatures up to 35°C (Glime and Iwatsuki unpublished). At surface temperatures between 45°C and 65°C, Shannon diversity (four sites only) ranged 1.49 to 2.58 and richness of 6 to 12.

Table 2. Shannon and Brillouin information-theory-based mean, minimum, and maximum species diversity values in five temperature zones for Myvatn, Iceland, summer of 1985. N = number of samples; M = number of species.

Temperature Range	N	M	Shannon			Brillouin		
			Mean Div	Min Div	Max Div	Mean Div	Min Div	Max Div
> 60–80°C	5	6	1.70	0.28	2.58	1.62	0.42	2.60
> 45–60°C	19	13	1.88	0.20	3.70	1.83	0.18	3.70
> 35–45°C	25	21	2.83	0.15	4.39	2.79	0.13	4.37
> 25–35°C	50	56	4.03	0.20	5.81	3.99	0.18	5.80
10–25°C	112	74	3.96	0.13	6.21	3.93	0.12	6.19

Faoro *et al.* (2010) considered a Shannon diversity of 4.12 for soil bacteria in the Southern Brazilian Atlantic Forest to be high. Compare the Myvatn geothermal overall diversity to the generally lower Shannon values in a variety of habitats from a quick search of published values for plants: 1.523–1.959 for cover species in 13 landscapes in Western Ghats in southwestern India (Nagendra 2002); 0.56–1.20 for vegetation around a paper mill in Assam, northeast India (Das *et al.* 2012); 0.25–0.77 for macrophytes in 7 unregulated and 0.08–0.68 in 7 regulated stream reaches in Denmark (Baattrup-Pedersen and Riis 1999); 2.19–2.92 for 6 riparian woody plant sites in Muscogee and Harris Counties, Georgia, USA (Burton *et al.* 2005); 0.0–3.30 for submersed bryophytes < –5 cm, 1.75–3.59 for bryophytes from water –5 cm to 5 cm above, and 1.83–4.04 for bryophytes 10–30 cm above in 11 streams in the Canadian Rocky Mountains of Alberta and British

Columbia, Canada (Glime and Vitt 1987); 2.3–2.9 for bryophyte flora and vegetation in one virgin and three managed *Picea abies* forests in southwest Sweden (Gustafsson and Hallingbäck 1988); 1.03–2.13 for bryophytes and tracheophytes in karst caves in southern China (Ren *et al.* 2021). Although most of these sites appear to be restricted to certain plant groups, they provide some perspective with which to evaluate the diversity. Perhaps part of this high diversity at the geothermal area is due to the lack of competition in the early colonization stage and a large number of suitable microniches with enough moisture for successful establishment.

Because of its recent volcanic activity, we expected that the Myvatn geothermal vegetation might bear some similarities to the vegetation of Surtsey following the 1963–1967 volcanic activity that created the island off the southern coast of Iceland. New bryophyte species appeared on Surtsey every year, starting with 2 in 1967 (Ingimundardóttir *et al.* 2014), but the nearest source of propagules was Iceland, 200 km away. In 1971, there were 36 species, but by 1972 the number had doubled to 72. By 2008, only 38 total were found, 15 of which were new. Some of the 1972 taxa are common to the Myvatn geothermal flora, including *Leptobryum pyriforme*, *Philonotis* spp., *Pohlia* spp., *Sanionia uncinata*, *Schistidium* spp. The early species on Surtsey that had expanded by 2008 include *Bryum argenteum* and *Racomitrium lanuginosum*, both of which were common at Myvatn, and *R. fasciculare* (not relocated at Myvatn in 1987), as well as *Schistidium maritimum* (Turner ex Robt.Scott) Bruch & Schimp., which might have been our unidentified *Grimmia*/*Schistidium*. Of the expanded species only *Racomitrium ericoides* (Brid.) Brid. was absent at Myvatn. When Surtsey was revisited in 2018, the total number of bryophyte taxa had increased from 43 in 2008 to 59 (Ingimundardóttir *et al.* 2022). The volcanic vent species declined as the vent activity declined.

Zonation

The surface temperatures ranged 10–80°C among the Myvatn plots. Close to the vents the soil was dominated by Cyanobacteria; these were not identified further. Out of direct reach of hot steam, bryophytes and lichens dominate, with lichens restricted to cooler, drier soils. Next is a zone of shallow-rooted tracheophytes. Outside the influence of hot soil in the root zone, larger herbaceous and small woody plants can survive.

Elmarsdóttir *et al*. (2003) found that soil **temperature** is a dominating factor in determining the distribution of species in three Icelandic geothermal sites. In those sites species diversity and composition differed between warmer and colder sites, but in addition to these were differences in *p*H and soil carbon content that influenced the species present. The total number of tracheophyte species exhibited a negative relationship with high soil temperature. Nevertheless, other factors such as location, elevation, and weather were still important in separating communities of the three sites.

Cyanobacteria

Cyanobacteria generally are the only photosynthetic organisms closest to the vents. They are only affected by temperature at the surface and are able to tolerate temperatures there up to 80°C. They also occupy soils throughout the humidity range of the vents (*Figure 2*). They occur throughout the *p*H range, from less than 3.5 up to more than 7, but their greatest cover occurs from *p*H 5 to ~8 (*Figure 2*).

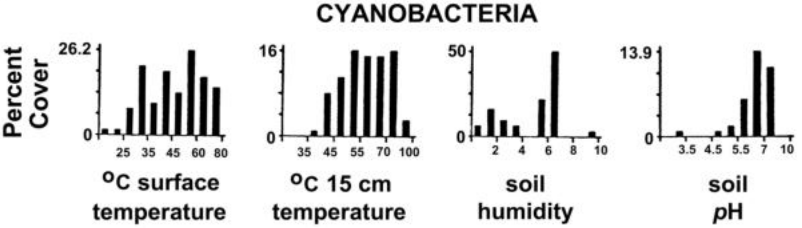


Figure 2. Cyanobacteria realized niche dimensions for temperature, humidity, and *p*H at geothermal vents in Myvatn, Iceland, in 1985, showing mean percent cover for four resources. Highest percent cover is indicated by number at top of Y axis. Numbers on X axis are boundaries of two intervals used for resource analysis.

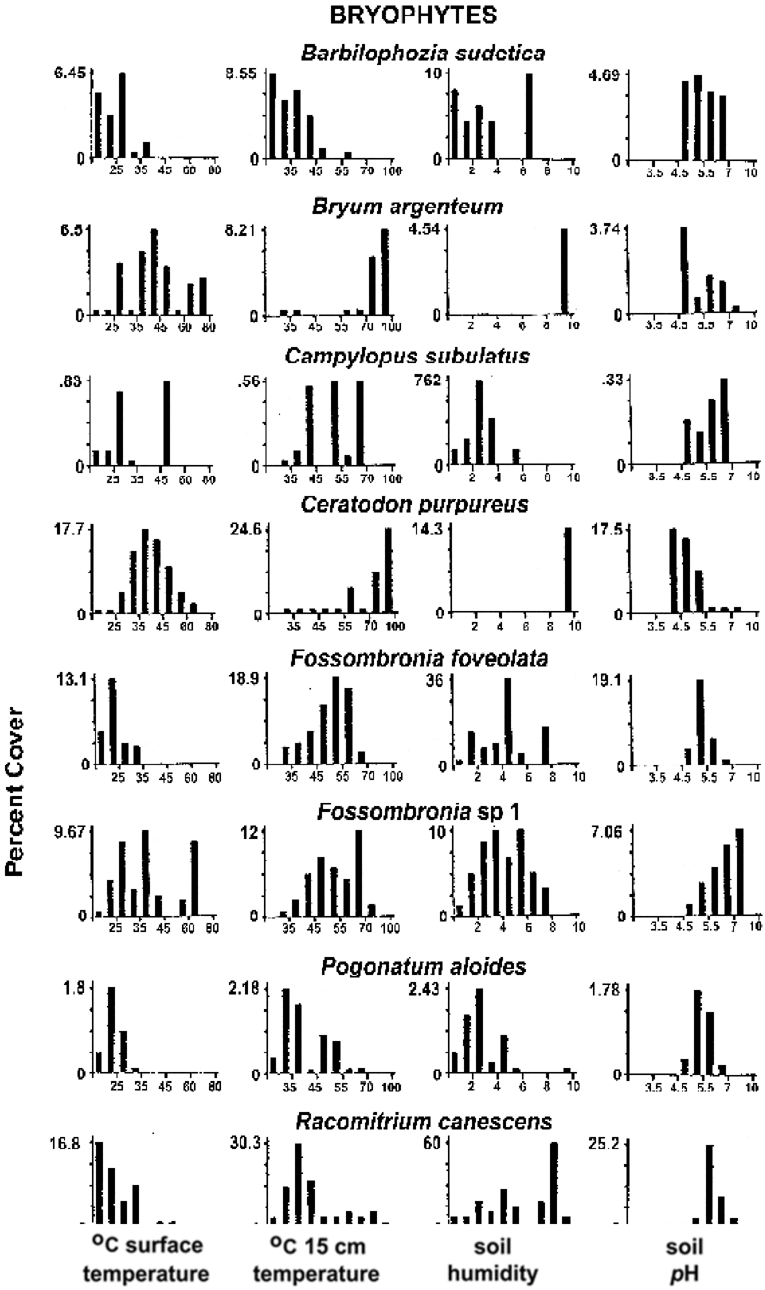
Bryophytes

The bryophytes are the predominant organisms in the next zone after Cyanobacteria and are much richer in species (47 in 1985; 30 in 1987) than the other groups. Among those with a frequency greater than 5%, in 1985, 3 are liverworts and 6 are mosses *(Figure 3). Bryum argenteum*, *Ceratodon purpureus*, and *Fossombronia* sp. 1

(probably immature *F. foveolata*) occupied ground with the highest temperatures near the vents in 1985, but were not restricted to these near-vent locations. In the 1987 plots, *Bryum argenteum* had decreased in cover, whereas the other two had increased (*Table 1*).

At Myvatn in 1985 the leafy liverworts occupied temperatures both below and above 25°C, except for *Gymnocolea inflata* (4 quadrats only) that occurred only below 25°C. Only the thallose liverworts *Preissia quadrata* (Scop.) Nees (1987 only), and *Riccia beyrichiana/bifurca* were able to occupy the hard clay soils near geothermal fissures, receiving intermittent steam from fissures. Thus, their substrate was relatively dry, but the plants received periodic wetting from the steam. By 1987, *Marchantia polymorpha* was present and *Cephaloziella rubella*, *Nardia scalaris*, *Preissia quadrata*, and *Riccia beyrichiana/bifurca* had reached > 5% frequency *(Table 1)*. *Solenostoma gracillimum* had dropped in our plots from 6% to 3% frequency.

Bryophytes are able to colonize some of the hottest sites (> 50°C at the surface) in geothermal areas worldwide, and these sites are often continually wet from steam or steam run-off (Given 1980; Kappen and Smith 1980; Smith 1981; Bargagli *et al.* 1997; Burns 1997; Glime and Hong 1997; Elmarsdóttir *et al*. 2003; Bonini *et al*. 2005; Convey and Lewis Smith 2006). Biebl (1967) found that the liverwort *Preissia quadrata*, present in Myvatn geothermal fields in 1987, had heat resistance in a range of 41–48°C, and *Dicranum scoparium* Hedw., known from geothermal fields of Greenland (Halliday *et al*. 1974) and the Queen Charlotte Islands, Canada (Glime and Hong 1997) was resistant at 45–47°C. These latter two taxa are both common in the North Temperate Zone in shaded, non-thermal habitats. Among those bryophytes with the highest dry heat tolerance when exposed for 30 minutes are such geothermal taxa as *Ceratodon purpureus* (also common at hottest Myvatn sites) and *Dicranum scoparium* (not seen at Myvatn sites) (Lange 1955). In Lassen Volcanic National Park, California, USA, Shortlidge (2014) found *Ceratodon purpureus* to be among the more common bryophytes in the most heated areas.


BRYOPHYTES
Percent Cover
Barbilophozia sudetica
6.45
8.55
10
4.69
Bryum argenteum
6.51
8.21
4.54
3.74
Campylopus subulatus
.83
.56
762
.33
Ceratodon purpureus
17.7
24.6
14.3
17.5
Fossombronia foveolata
13.1
18.9
36
19.1
Fossombronia sp 1
9.67
12
10
7.06
Pogonatum aloides
1.8
2.18
2.43
1.78
Racomitrium canescens
16.8
30.3
60
25.2
0
25 35 45 60 80
35 45 55 70 100
2 4 6 8 10
3.5 4.5 5.5 7 10
°C surface temperature
°C 15 cm temperature
soil humidity
soil *p*H

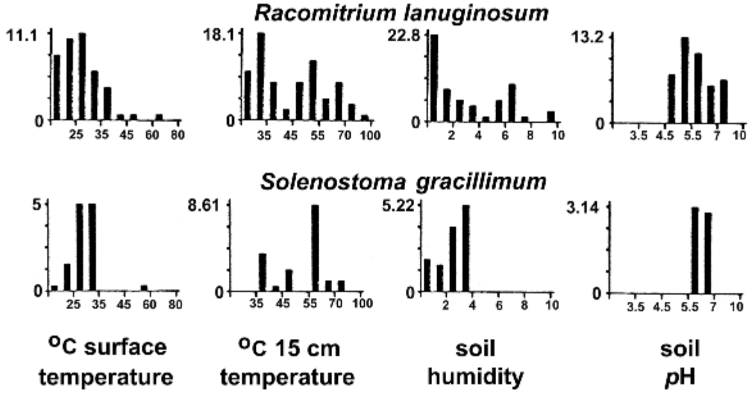


Figure 3. Mean percent cover of bryophytes and realized niche dimensions for temperature, humidity, and *p*H at Myvatn, Iceland, geothermal vents, summer of 1985, showing plants with a frequency of ≥ 5%. Highest percent cover is indicated by number at top of Y axis. Numbers on X axis are boundaries of two intervals used for resource analysis.

Most European mosses have a heat tolerance of up to 39–45°C (Scheibmair 1938; Dirckson 1964; Nörr 1974). Mosses that are constantly wet have an even lower tolerance for continuous warm temperatures (Dilks and Proctor 1975; Glime 1987a, b). Glime (1987a, b) found that the aquatic *Fontinalis* spp. became debilitated and ceased growing at temperatures as low as 20°C when submersed for extended periods of time. It is therefore likely that mosses moistened by continuous wet vapor from the vents might be unable to tolerate especially high temperatures.

Our results support those of studies elsewhere, despite the young nature of our fissures. Shortlidge (2014) found that in Lassen Volcanic National Park, California, USA, few tracheophytes can survive in geothermal soils, but mosses are often found in some of the hottest regions of geothermal systems. This same pattern prevailed in geothermal areas of Japan (Glime and Iwatsuki 1994, 1997), but was somewhat less distinct in Iceland, perhaps due to the overall cool climate and short period since volcanic disturbance.

In Yellowstone, the more acid sites with 10 cm temperatures greater than 50°C were dominated on the fine soils by the mosses *Racomitrium canescens*, *Bryum pseudotriquetrum*, and *Ceratodon purpureus* (Sheppard 1971). On more coarse soils with "steam," Sheppard found *Pohlia nutans* and *Dicranum muehlenbeckii*. The drier coarse soils had species of *Polytrichum*.

At geothermal fields at Krafla, Iceland, Buda *et al.* (2018) found only 12 bryophyte species – 5 liverworts, 7 mosses – in their habitat analysis, but their sample number was small and focussed on invertebrates. The most common bryophyte was *Racomitrium lanuginosum*. At Myvatn, this species had relatively high cover at temperatures below 40°C. In the hotter plots at Reykjanes and Olkelduhals, Iceland, Elmarsdóttir *et al.* (2003) found the bryophytes *Gymnocolea inflata* and *Campylopus* Brid. (reported here also from Myvatn in 1985 at < 25–< 49°C, but not found in 1987) to be the most abundant species at 45–49°C. But in their study the leafy liverwort *Gymnocolea inflata*, a widespread species in the northern part of the Northern Hemisphere, only occurred at high temperatures, whereas in 1987 at Myvatn we found it only in low frequency (2%) and at surface temperatures below 25°C; we found it only once in 1985.

Lichens

Only one lichen species, the bipolar *Cornicularia aculeata*, had a frequency exceeding 5%. It was absent in all plots with a surface temperature greater than 25°C (*Figure 4*), but the total lichen cover was too small to ascribe it to a particular zone. The 15 cm soil temperature had little effect on it. It occurred at the lower end of the humidity scale and a soil *p*H range of 4.5–7.

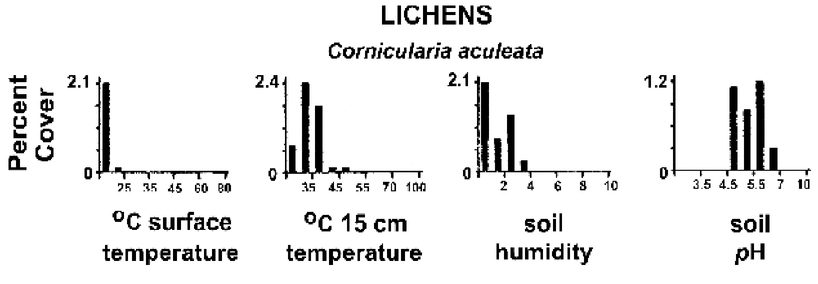


Figure 4. Mean percent cover and realized niche dimensions for temperature, humidity, and *p*H for lichens at Myvatn, Iceland, geothermal vents, summer of 1985, showing the only lichen species with a frequency of 5% or greater. Highest percent cover in a quadrat is indicated by number at top of Y axis. Numbers on X axis are boundaries of two intervals used for resource analysis.

The greatest lichen abundance was that of *Cornicularia aculeata* on cool soils (*Figure 4*), which differs from the findings of Elmarsdóttir *et al*. (2003) in three different geothermal areas of Iceland. They found that *Peltigera canina* was the most common lichen species in both the hot and cool plots. Its frequency in our 1985 plots was < 5%, and it was not found in the 1987 plots.

Lichens were less common at the Myvatn vents than in other geothermal areas we have studied. Early successional heat coupled with moisture may be responsible for their scarcity. When Kappen and Smith (1980) subjected two Hawaiian steam vent *Cladonia* species to a series of temperatures at 2°C intervals from 32°C to 52°C for 30 minutes, *Cladonia oceanica* Vain, which grew on *Campylopus*, was tolerant to a soil surface temperature of 37.5°C and *Cladonia skottsbergii* H.Magn. to 35.5°C. In the field the limit for *Cladonia oceanica* was 27.2°C, but even this resulted in stunted growth. A maximum of 23°C permitted healthy, ramified growth. Short-term tolerances can be much greater than long-term temperature tolerance in geothermal lichens, especially while hydrated (Glime and Iwatsuki 1990).

The low diversity of lichens at Myvatn may also be due to a longer arrival time than that required for dispersal of bryophytes, although Marshall (1996) found lichen soredia to be quite common in traps at 1 m above the surface on Signy Island in the Antarctic. However, there is no indication how far they travelled. Tapper (1976) found that 50% of the dispersal of soredia from two epiphytic lichens to be a maximum of 26–27 m. Bryophyte spores, on the other hand, are easily dispersed long distances (Patiño and Vanderpoorten 2018). Heinken (1999) found that fragments from among five species of *Cladonia* were dispersed a maximum of 68 cm 15 days after trampling; those dispersed by animals travelled a maximum of 9.7 m. Bonde (1969) found that thallus fragments of *Cornicularia aculeata* were numerous in propagule traps on Mary's glacier, Colorado, USA. Thus, it could be that establishment on moist, heated ground is the greatest barrier to lichen presence. Long-term experiments are needed to determine these effects on lichen establishment.

Tracheophytes

Only five species of tracheophytes had a frequency ≥ 5% in 1985 (*Figure 5*). Except for *Sagina caespitosa*, they did not occur at surface temperatures above 35°C. For *p*H, *Poa angustifolia* had a bimodal distribution, having greater cover toward the extremes of its *p*H range where most other tracheophyte species were absent or had little cover. *Thymus praecox* subsp. *brittanicus* had only a 3% frequency in the vent area, but had the highest mean cover (5.9%) of all tracheophytes (*Table 1*), mostly at < 25°C (*Figure 5*). In 1987 we found a frequency of 19%, but a cover of only 1.69%.

In Iceland geothermal areas, small herbs such as *Sagina caespitosa*, *Epilobium*/*Chromolaena* spp. and grasses such as *Festuca* spp. and *Poa* spp. form most of the tracheophyte flora (*Table 1*). Sheppard (1971) found that mosses in Yellowstone National Park made it possible for grasses (*Agrostis rudis* Roem. & Schult.) to grow in very hot areas by providing a moist substrate above the hot soil. At Myvatn, *Thymus praecox* subsp. *brittanicus* and the horsetail *Equisetum arvense* are species that are typically more deeply rooted than the moss-like *Sagina caespitosa*. *Thymus* has higher cover than any other species at locations with cooler root temperatures (*Figure 5*), but both *Thymus* and *Equisetum* are able to occupy root zone (15 cm) temperatures up to 70°C (*Figure 5*). On the other hand, *Equisetum arvense* is abundant only at surface temperatures below 29°C. Sheppard (1971) found it as a pioneer on sulfurous clay soils as well as fields of fine volcanic rock. In their study of Icelandic geothermal vegetation, Elmarsdóttir *et al.* (2003) found some tracheophytes in the hot zones, including *Agrostis stolonifera* L., *Alchemilla alpina*, *Thymus praecox*, and the fern *Ophioglossum azoricum* C.Presl. Of these, *Alchemilla alpina* and *Thymus praecox* (< 33°C) occurred in our 1985 plots at Myvatn, but *Alchemilla* had a frequency of only 1% in 1985 and was not found in 1987.

The geothermal sites in Japan and New Zealand had different tracheophyte species from those at Myvatn. Geothermal areas at Yellowstone follow a zonation pattern similar to that at Myvatn, with grasses becoming more common when the root zone cools to 30–50°C (Sheppard 1971). At Myvatn, *Festuca* occurred where 15 cm temperatures reached 80°C, and some *Poa* lived where the 15 cm temperature exceeded 70°C.

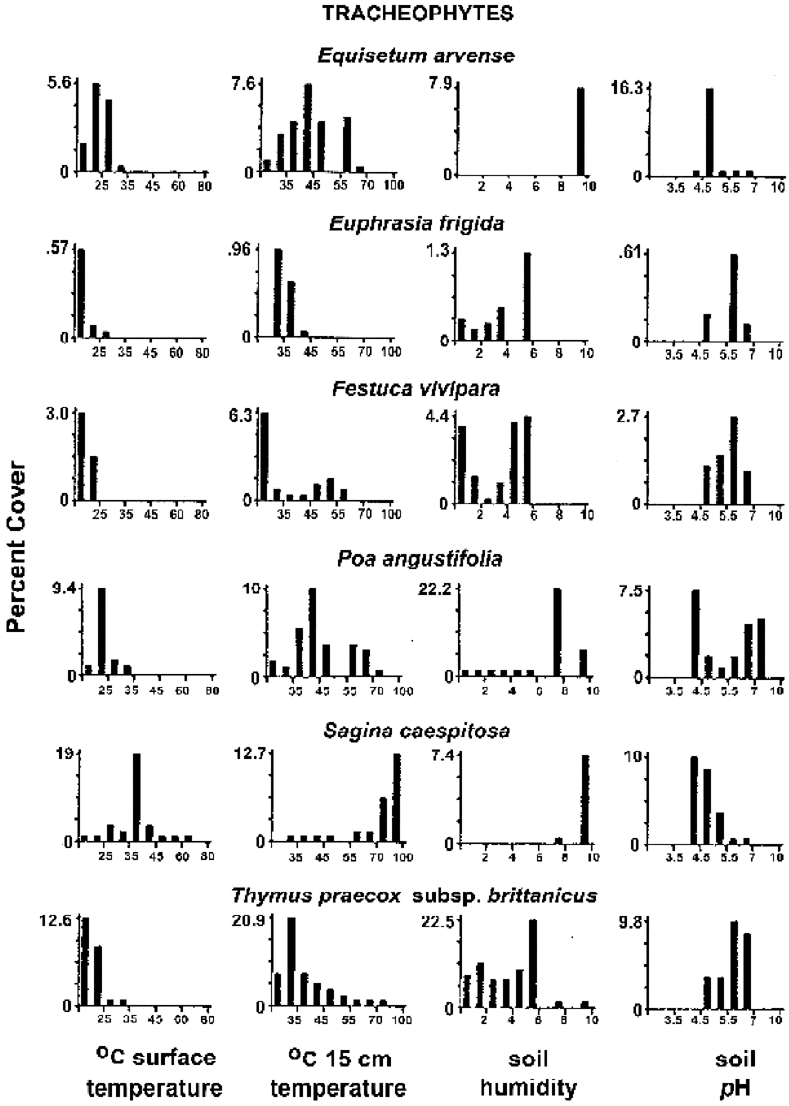


Figure 5. Mean percent cover for tracheophyte realized niche dimensions for temperature, humidity, and *p*H at geothermal vents in Myvatn, Iceland, in 1985, showing plants with a frequency of 5% or greater, plus *Thymus praecox* subsp. *brittanicus* with the highest mean percent cover in cool plots. Highest percent cover is indicated by number at top of Y axis. Numbers on X axis are boundaries of two intervals used for resource analysis.

Overall

Surface plants such as algae, lichens, and bryophytes occupy areas with high temperatures at 15 cm soil depth, sometimes exceeding 80°C (*Figure 4*). This was especially evident for the mosses *Bryum argenteum* and *Ceratodon purpureus* at Myvatn, perhaps due to a lack of tracheophyte competition at these temperatures and the buffering effect of the dense moss cushions to protect the growing tips. Bryophytes have greater cover than do tracheophytes at higher surface temperatures in both Iceland and Japan (*Figure 6*). In Japan, most of the lichens are restricted to cool surface temperatures, while bryophytes occupy surface temperatures as high as 65°C (Glime and Iwatsuki 1990). The patterns are the same, but the Myvatn site has greater cover of both tracheophytes and surface bryophytes. Could this be because the site is too young for competition to play a role?

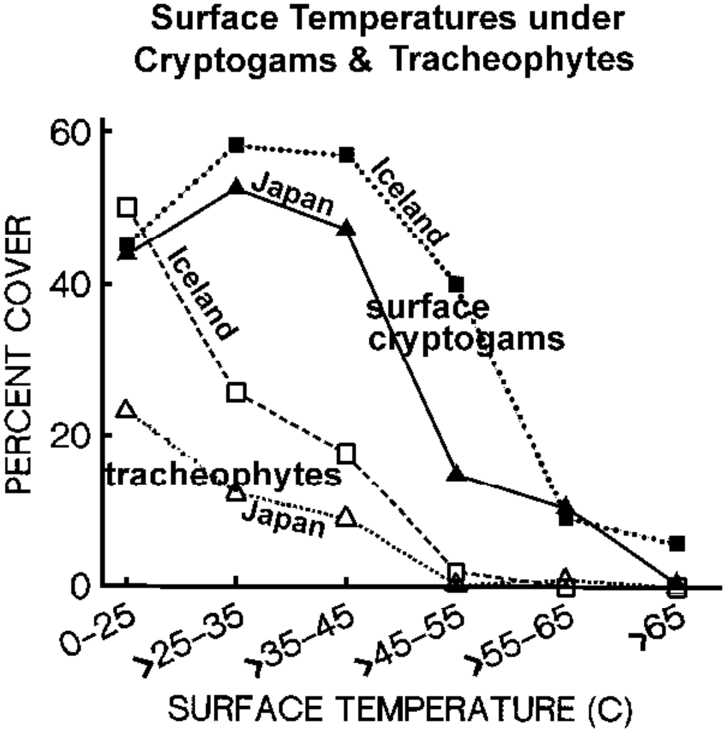


Figure 6. Comparison of cryptogams and tracheophytes in Japan and Iceland at various surface temperatures in geothermal areas. Based on Iwatsuki and Glime unpublished data from five sites in Hokkaido, Japan, and several sites in Iceland.

Climate change models predict changes in rainfall patterns, greater drought in some areas, and more extremes of both high and low temperatures (United Nations 2023). Understanding the dynamics of geothermal communities and the stressors that prevent habitation in near-vent areas can help us in predicting and planning for climate change effects on vegetation. Laboratory experiments don't allow for the randomness of dispersal, the interactions of species, or the changes from day to day and year to year that are available to the geothermal communities.

Thermal Limits

The foregoing results demonstrate that in the zones closest to the vents, cryptogams are more numerous than tracheophytes, often to the exclusion of tracheophytes. Within the geothermal area, tolerance levels vary considerably. A species with a wide temperature tolerance might have a narrow moisture tolerance or *p*H tolerance range (*Figures 2–5*). These combinational differences lead to the patchwork of communities observed.

The zonation pattern at Myvatn is the same as that at all the geothermal areas we have studied around the world. Faber (1925), reporting on Java geothermal vents, concluded that geothermal sites were first colonized by lichens and mosses and then by shallow-rooted ericaceous (heath) plants, but ericaceous plants are of little importance in the systems we have studied. In New Zealand Given (1980) identified a zonation pattern at Karapiti, correlating with soil temperature profiles, comparable to those of Java (Faber 1927), Katanuma, Japan (Naito *et al*. 1970), Ponponyama, Japan (Glime and Iwatsuki 1994), and Wakoto, Japan (Glime and Iwatsuki 1997). In New Zealand Muukkonen (2005) found that canopy height and species richness correlated with ground temperature and soil *p*H. Burns and Leathwick (1995) likewise found that in their New Zealand studies canopy height and species richness decreased with increasing temperature. This was concurrent with a change from a ground cover of leaf litter to one of bryophyte mats toward the vents.

The upper thermal limit for cell metabolism generally lies between 45°C and 55°C (Konis 1949; Langridge 1963). Matsuura (1961) found that the root parenchyma of *Miscanthus sinensis* Anderson, a grass in the Japanese vent community, was the most likely tissue to show injury when compared with roots of *M. sinensis* plants farther from the vent center. Given (1980) showed that at Karapiti in New Zealand the limits of active root development correlate very closely with the 50°C isotherm position in the soil.

One reason for the high temperature tolerance of geothermal mosses may be their own insulating ability. If we assume that the bryophytes and lichens serve as an insulating layer that retains the surface heat, then lower temperatures within the 45–55°C range were probably present at the time of their establishment. However, as the moss grew, the temperature increased at the soil surface, but the same insulation by plant tissue that raises the surface soil temperature insulates the growing tip of the moss from that temperature. Thus, as older, lower parts of the moss die, insulation by those lower parts makes it possible for the younger apical parts to continue to live. We have measured a 9°C drop in soil surface temperature when we removed the covering of *Campylopus* at Waimangu, N. Z. Kappen and Smith (1980) have measured temperatures at various soil depths and inside the moss cushions. They have shown that a 40°C temperature at the detritus layer below the moss diminishes to 33°C 4 cm above the detritus in the moss cushion, and to 24°C at the surface of the moss. Under a lichen thallus, the temperature diminished from 39°C at the detritus layer to 22.6°C at the lichen surface. This insulating effect would further reduce competition from tracheophytes by making both the root and surface zones under bryophytes and lichens too hot for invading roots.

Lange (1969) has found that desert lichens are photosynthetically active only when the temperatures are below 25°C. Therefore, geothermal lichens are likely to have a lower temperature maximum than do desert lichens because they must endure these temperatures during all hours of the day and all seasons, often in a hydrated state, whereas the desert lichens will experience lower temperatures in some seasons and in some weather events. This would prevent geothermal lichens from ever having photosynthesis because the high temperature prevails during their wet state, whereas the desert lichens take advantage of the cool morning temperatures coupled with morning dew for their photosynthetic period. This is supported by lichen distribution at geothermal sites in Japan (Glime and Iwatsuki 1990).

We have found small patches of *Racomitrium canescens* at a surface temperature of 80°C (Kogen Spa, Hokkaido, Japan), but ordinarily it was restricted to a maximum of about 44°C. Finding a moss at such a high temperature can indicate a change in thermal activity since the time the moss became established, or may be a recent transplant by a visiting animal.

Soil Moisture

Moisture is difficult to measure with any consistency because of changes in the weather. However, on a given day, one can assume that measurements within a given vent system can be compared. The importance of the moisture, and perhaps the heat, are evident on the Icelandic island of Surtsey (Bjarnason and Fridriksson 1972). The sand-covered lava around the crater, where there was still an emission of heat and steam, had a cover of 40–50% mosses, whereas moss cover in areas away from vent influence never exceeded 10%. In less mossy areas, small caverns or vent steam influence seemed to be important to the location of mosses.

Frequent alternations between wet and dry can be detrimental to bryophytes (Oliver and Bewley 1984). The three most common bryophytes in the geothermal communities of Lassen Volcanic National Park, California, USA, were significantly affected by temperature, light, and relative humidity (Llaneza-García *et al*. 2009; García *et al*. 2016). In these studies, the wetland moss *Aulacomnium palustre* (Hedw.) Schwägr. was intolerant of drying and never recovered its optimal photosystem II (PSII) efficiency after rewetting. *Campylopus introflexus* (Hedw.) Brid. was able to maintain optimal values of PSII efficiency at 50% water loss for 48 hours, recovering completely after rewetting. Hence, physiological adaptations of geothermal bryophytes can differ widely.

Soil Chemistry

Most geothermal soils are low in *p*H, organic matter, phosphorus, potassium, and aluminum, but they are high in metals (especially iron) and trace elements such as manganese, arsenic, and titanium (Faber 1925; Grimmett and McIntosh 1939; Lotschert 1956; Given 1980). To give the Myvatn data perspective, we have compared levels in several other ecosystems. Our data provide a basis for hypotheses to be tested by future researchers.

Lange (1973), working in Iceland, suggested that high humidity, high temperatures, and water/soil chemistry all play a part in determining the species of bryophytes at each geothermal site. Grimmett and McIntosh (1939) considered the vegetation associated with geothermal sites in New Zealand to be associated with *p*H and toxic elements in the soil. In Yellowstone National Park, USA, Sheppard (1971) considers soil temperature, *p*H, and humidity to be the controlling factors.

In 1985, the *p*H in Myvatn quadrats ranged from 2.2 to 7.5. No vegetation occurred at a *p*H of 3.6 or lower except for algae in one plot at 2.7. Elmarsdóttir *et al*. (2003) found that cover and richness of tracheophytes in Icelandic geothermal areas decreased at low **soil *p*H**. At Myvatn the Cyanobacteria are most common at *p*H 5.5–7.5 (*Figure 2*) and in Ponponyama and Wakoto, Japan, at *p*H >3.5–< 5.0 (Glime and Iwatsuki 1994, 1997). Most vents in Iceland are higher in *p*H than the surrounding soil, whereas those in Japan are usually lower in *p*H than the surrounding soil. Perhaps this relationship reflects the absence of competition and presence of a continuously moist atmosphere, as well as the tolerance of Cyanobacteria for higher temperatures that occur with the extremes of *p*H in the vent zones.

Most of the samples had few quantifiable soluble elements, with only 5 (Al, Sr, Cl, V, S) out of 20 being reliably detectable in at least 30 of the 80 samples. Most plants occurred where the elements were in the low end of quantifiable levels for that element or where they were unquantifiable, with some notable exceptions. Using this method, numbers at the high end also typically have a wide variance, so only generalities are possible.

Ba, **Ni**, and **Zn** were below quantifiable limits of 90, 5, and 5 ppm respectively in the soluble fraction of all 80 samples. **Zr** was reliably detectable (> 5 ppm) in only 1.

Soluble **phosphorus** was reliably detectable ($\geq$ 150 ppm) in only 9 of the 80 analyzed soil samples, ranging up to 600 ppm (although the error range is large). The quantifiable levels in the geothermal soils at Myvatn were exceptionally high. Arp and Knause (1984) found a range of 469 ppm total P in interior forest soils to 1086 ppm in wetlands in New Brunswick, Canada, compared to a range of < 150–2720 ppm total P at Myvatn. In tropical forest soils, one of the lowest P systems known, Li *et al*. (2013) found the highest level of available (soluble) P to be 2.45 ppm in their Chinese study.

Hou *et al*. (2018) reported 0.14–1.14 ppm for water-soluble P in Chinese tropical forest soils. At Myvatn 71 of 80 samples had less than the detectable levels of 150 ppm soluble P. Some of the Myvatn P levels were high enough for its phosphates to interfere with uptake of N and other anions. Some plots with the high levels had no or little vegetation. *Equisetum arvense* and *Euphrasia frigida* occurred only below the reliable detection level (≤ 150 ppm). *Racomitrium lanuginosum* had the broadest tolerance among the bryophytes and *Sagina caespitosa* among the tracheophytes (both at < 150–600 ppm).

Soluble **sulfur** was detected in all samples, ranging 70–25,900 ppm and ranging 100 to 25,900 ppm in one transect. Most of the species occurred at intermediate levels of sulfur (> 200–1600 ppm), but *Racomitrium lanuginosum* and *Racomitrium canescens* had the greatest cover at ≤ 20 ppm, although they displayed the widest tolerance range of any plants, up to the 800–1600 ppm range. *Ceratodon purpureus* had the greatest cover at concentrations ≥ 1600–3500 ppm. *Sagina caespitosa* occurred at ≤ 600 ppm, but had its greatest cover at levels approaching 3500 ppm. This is consistent with the *Ceratodon purpureus* findings of Carvey *et al.* (1977) on mine spoils that often contained high levels of sulfur; the species was both a colonizer and abundant stayer, surviving low levels of *p*H.

Sodium in soluble form ranged < 2000 to 3470 ppm and was detected in all samples of some transects while being completely undetectable in others. The two *Racomitrium* species exhibited the widest range for Na, occurring up to 3470 ppm.

Chlorine, indicating the presence of salts, was reliably detected in 49 samples and ranged from ≤ 20 to 164 ppm. Most species existed throughout the available range; only *Gymnocolea inflata* was restricted, occurring only at < 20 ppm, but only present in 1 plot in 1985 and 4 plots in 1987.

Soluble **aluminum** was reliably detected in 32 samples, ranging from ≥ 1500 to 20,450 ppm. No vegetation occurred in the three plots that had Al > 4000 ppm. Hou *et al*. (2018) found 2.6–13 ppm Al in tropical rainforest soil in China, whereas our reliably detectable level for Myvatn was ≥ 1500 ppm; nevertheless, 32 samples at Myvatn had soluble levels above 1500 ppm.

Soluble **arsenic** ranged < 10 to 23 ppm and was reliably detectable in 11 samples. It was tolerable throughout this range to *Preissia quadrata* (present only in 1987 quadrats), *Chromolaena* *collina*, *Euphrasia frigida*, *Racomitrium canescens*, *Racomitrium lanuginosum*, and *Thymus praecox* subsp. *britannicus*.

Soluble **titanium** was reliably detected in 27 samples, ranging < 300 to 2300 ppm, with *Nardia scalaris*, *Fossombronia cf. foveolata*, and *Festuca ovina* occurring throughout the < 300–2300 ppm range.

Soluble **vanadium** was reliably detected in 57 samples and ranged < 5 to 170 ppm. *Nardia scalaris* occurred at ≤ 80 ppm, but was most abundant at levels near 80 ppm. *Racomitrium lanuginosum* occurred up to 170 ppm, but occurred mostly at ≤ 20 ppm. The essential role of vanadium in plants is still under debate, and it appears that it can benefit some plant processes while being toxic to others (Imtiaz *et al*. 2015).

Soluble **calcium** was reliably detectable (≥ 1500 ppm) only 3 times in 80 samples, **copper** (≥ 5 ppm) in 6, **magnesium** (≥ 1500 ppm) in 2, **potassium** (≥ 800 ppm) in 1, **silica** (≥ 5000 ppm) in 2, and **strontium** (≥ 5 ppm) in 6. Quantifiable soluble **iron** (≥ 3500 ppm) occurred in only 10 samples, ranging < 3500 to 9790 ppm. Only two of these had vegetation (*Festuca ovina* and *Fossombronia cf. foveolata*) in plots with higher levels of iron, both at 9500–9790 ppm. Both species had their highest cover at that level; *Fossombronia cf. foveolata* had a mean cover of 60% in that range.

In three Chinese tropical rainforest soils, Li *et al*. (2013) found the highest level of **potassium** to be 90.52 ppm and lowest at 30.81 ppm, whereas at Myvatn the one sample where it was detectable (≥ 800 ppm) had 10,500 ppm, a level that is likely to have a wide error range.

Manganese in soluble form ranged < 40 to 1530 ppm and was reliably detectable (≥ 40 ppm) in only 10 of the 80 soil samples, typically not more than one sample in a transect. All five taxa (Cyanobacteria and bryophytes *Fossombronia cf. foveolata*, *Barbilophozia sudetica*, *Nardia scalaris*, *Riccia beyrichiana*/*bifurca*) that occurred at the highest levels also occurred at or below the lowest detectable.

Iron and aluminum are toxic at low soil *p*H levels such as those at Myvatn, whereas phosphorus, nitrogen, and calcium are unavailable at low *p*H (Truog 1951). These conditions can inhibit the growth of tracheophytes that might be tolerant of the moderately high soil temperatures. On the other hand, bryophytes and lichens depend little on soil nutrients and can survive on nutrients carried by windborne dust. Nevertheless, those soluble airborne elements carried in the vapors arising from the vents can rest on soil and become available to rooted plants as well.

Rajsz *et al*. (2021) found that geothermal plants in Iceland were enriched with metals compared with those in non-geothermal control sites. These included Cd, Co, **Cu**, **Fe**, and **Ni** in *Calluna vulgaris*, Cd, **Mn**, and **Ti** in *Empetrum nigrum*, Hg and Pb in *Festuca vivipara*; *Thymus praecox* had the highest bioaccumulation factor for **Ti** and **Zn** (those in **bold** were included in analysis in this study).

Pippuci *et al*. (2015) found that in a geothermal field in Italy, only *Calluna vulgaris* among the tracheophytes was able to grow near the geothermal sources, withstanding vapor with CO_2, H_2S, CH_4, H_3BO_3, SO_4^{-2}, and NH_4^+. In our experience, the soil quickly becomes warmer near the vents, probably accounting for the observations of Pippuci and coworkers of lower PSII efficiency, higher oxidative damage to membranes, and lower stomatal conductance than the same species further from the vent.

We are hesitant to draw any broad conclusions from the soil chemistry data other than that the relationships are complicated. Rather, the observed relationships and apparent limits should be used to form hypotheses for new research. Skewed and discontinuous distributions for vegetation related to any given element can be affected by the excess or limited quantities of other elements, *p*H and temperature affecting solubility, growth temperature or humidity extremes, random dispersal and distance to source of the vegetation resulting in low frequency, or greater competition at some levels from other vegetation species that do best at those levels. Although 80 samples is a large number, the number of contributing resource variables is likewise large and for all but five elements (Al, Sr, Cl, V, S), fewer than 30 samples had the soluble form of the element at detectable levels using the analytical methods we used in 1989 for our 1987 samples. These relationships appear to be interesting, but they require much more data on soluble elements. More importantly, we need experiments and observations on the nutrient levels associated with bryophytes in nature. Most of what we know for this group of organisms is based on culture conditions.

Changes in 1987

An eruption in 1984 undoubtedly altered the temperature, moisture, and community structure as seen in 1985 and 1987, but with no mapping of the previous vegetation and conditions, we could not ascertain exactly where these changes had occurred. At least some of the soil was obviously undergoing primary succession, but the disruption was patchy. There were large areas where any existing propagules could be buried. We have no reason to believe that any existing live propagule banks were exposed. With all the geothermal activity on Iceland, propagule sources are never far away, so it is likely that most colonizers came from recent transport from other Icelandic locations.

By 1987 the number of species in our sampling had decreased from 80 to 50 (*Table 1*). The missing species were almost all species that had a frequency of ≤ 1% in 1985. Two were probably misidentifications in one of the two years. It is likely that populations identified in 1985 as *Anomobryum julaceum* were young *Ceratodon purpureus.* It is also possible that we misidentified the species of *Festuca* in one of the two years.

The identified lichen species dropped from five to three and remained infrequent.

Twelve species were not relocated in 1987. Liverworts, in particular, had a notable changeover. *Barbilophozia sudetica* dropped from a frequency of 12% to < 1%. On the other hand, the liverwort *Preissia quadrata*, with a 1987 frequency of 13% and mean cover of 3.2%, was present in our quadrats for the first time in 1987, as was *Marchantia polymorpha*, with a frequency of 2% and a mean cover of 0.04%. Both have been present in other geothermal studies (e.g. Kennedy 1996 in the Antarctic). *Nardia scalaris* increased from 4% to 12% frequency in the two years. *Riccia beyrichiana/bifurca* went from 1% frequency in 1985 to 15% in 1987.

Among the mosses, *Campylopus*, the common geothermal inhabitant in Japan, New Zealand, and the Antarctic, with a 1985 Myvatn frequency of 5%, was not relocated in the 1987 quadrats. *Bryum argenteum* had a frequency of 10% in 1985, but only 3% in 1987 (*Table 1*). Most of its disappearance coincided with notable changes in the geothermal area, with open fissures disappearing where it had been most abundant.

Eight new species of mosses occurred in the 1987 quadrats, whereas 14 were not relocated. *Ceratodon purpureus* continued to colonize new areas, going from 14% to 31% frequency. The advance of Polytrichaceae by 1987 is also noteworthy. While the frequency of *Pogonatum aloides* diminished from a frequency of 15% in 1985 to only one occurrence (< 1% frequency) in 1987, the number of Polytrichaceae species increased from 4 to 8. Among these, *Polytrichum longisetum*, not found in 1985, had reached a frequency of 15% and mean cover of 2.5% by 1987.

Among the tracheophytes, the grasses *Festuca ovina* (but possibly it or *F. vivipara* was misidentified) and the Polygonaceae *Persicaria vivipara* were also new. All of the species with a frequency $\geq$ 5% occurred in the 1987 quadrats as well. *Epilobium anagallidifolium* increased in frequency from < 1% to 11% with a cover in 1987 of 0.49%; *Sagina caespitosa* increased from 12% to 25%, and *Thymus praecox* subsp. *brittanicus* from 3% to 19% frequency in the sampled quadrats. However, the frequency of *Poa angustifolia* dropped from 14% to 2% between the 1985 and 1987 samples, whereas that of *Poa compressa* increased from 4% to 8% frequency and a 1987 cover of 2.59%.

Surprisingly, the percent bare soil in sampled plots actually increased in 1987 from 35.9% in 1985 to 38% (*Table 1*).

Although there were many quadrats with 100% cover, there were eight with no cover and some entire transects lacked cover or had less than 5% in most quadrats. It is unclear if this increase is due to new geothermal activity or to the randomness of the transects and quadrats.

Dissemination

Kennedy (1996) suggested that the presence of the temperate species *Campylopus introflexus*, *Marchantia polymorpha*, and *Philonotis acicularis* (Müll.Hal.) Kindb. in geothermal areas of the maritime Antarctic indicates that dormant propagules minimize initial delays in colonization of newly warmed areas. Convey and Lewis Smith (2006) commented on the ability of bryophytes to be transported as viable propagules into the Antarctic, a characteristic that must apply to Icelandic geothermal bryophytes as well. One of the factors that determines the expansion of areas covered by plants in geothermal areas is their ability to produce any sort of diaspore.

Although grasses seem to bloom normally, few of the bryophytes produce capsules and spores; none were present at Myvatn. Thus, expansion should be easier for those cryptogams capable of producing special asexual reproductive structures, such as gemmae (*Marchantia* L.), bulbils (*Bryum argenteum*), or deciduous branches (*Campylopus* spp.). Of the mosses we have found in geothermal areas, only *Trematodon* Michx. commonly has capsules, a genus not present at Myvatn. Instead of specialized reproductive structures, many of these mosses are capable of rapid colonization by fragments (Giles 1971). We dried and pulverized *Campylopus* from New Zealand and found that all three species grew rapidly from these tiny fragments in greenhouse pots (Glime and Iwatsuki, unpublished data).

The first liverwort to arrive on the newly created, geothermal Surtsey was *Marchantia polymorpha* (Magnússon and Fridriksson 1974); it was first located at Myvatn in 1987. Among the leafy liverworts, *Cephaloziella*, *Scapania*, and *Solenostoma* arrived first at Surtsey, but species identification was uncertain. These three genera were also present at Myvatn in 1985.

Bryophyte propagules must be preadapted to tolerate the geothermal conditions where they land (Lewis Smith 1984). Lewis Smith suggests that some of the species on the Antarctic islands may have remained as dormant spores among the ashes for years, germinating when volcanic activity warmed their location. Van Zanten and Pócs (1981) found that some moss spores could germinate after 20 years of dry storage, with spores of acrocarpous mosses having more drought tolerance than those of pleurocarpous mosses. But Van Zanten and Pócs considered that liverwort spores have less longevity and tend to have larger spores that are unable to travel as far as smaller spores. However, the majority (17/24) of liverwort species from the Myvatn geothermal area have spores < 20 µm in diameter (Schuster 1969; Vojtkó 1993; Newsham 2010; BFNA 2011). *Riccia beyrichiana/bifurca*, with a spore size of 90–125 µm, occurred only twice at Myvatn in 1985, but increased to 15% frequency in 1987 plots. *Mannia gracilis* (spores 58–65 µm) had a frequency of 4% in 1985 but was not relocated in 1987; *Fossombronia foveolata* (38–54 µm) had a 14% frequency in 1985, with another 23% frequency of immature plants that were probably that species, decreasing to 20% in 1987. *Solenostoma gracillimum* (spores 10–12 µm) likewise reduced in frequency in 1987 plots, from 6 to 3%. *Preissia quadrata*, with spores 60–80 µm, was first found in our 1987 plots. These size differences suggest that small spores arrive at the vents before large ones.

Although we are aware of no studies that have examined seed germination on thermal soils, we know from non-vent studies that many temperate and northern forest seeds require cold stratification to germinate (Salisbury and Ross 1978; for examples see Vandelook *et al*. 2009, Fetouh and Hassan 2014; Walck *et al*. 2011). Such a cold period is unavailable to seeds dispersed to the heated ground of geothermal areas. For plants lacking a vegetative means of reproduction, this need might prevent colonizing. Stolons and rhizomes of grasses can slowly invade the warm ground, provided there is sufficient soil depth with temperatures below 50°C – the upper limit for roots to survive (Salisbury and Ross 1978). Studies on the germination temperatures of the vent area grasses might further explain the zonation pattern.

On Deception Island in the Antarctic *Funaria hygrometrica* was the first to colonize ash-laden areas – and to produce capsules (Lewis Smith 1984). This was its first known appearance in the Antarctic, necessitating long-distance dispersal. It was here on heated ground that, by 1981, *Ceratodon purpureus* and *Leptobryum cf. pyriforme*, the latter also reported from the Antarctic for the first time, were producing capsules profusely. Both species were also present at the Myvatn sites in 1985, but with no capsules. Other early arrivals on Deception Island included *Marchantia polymorpha* L./ *berteroana* Lehm. et Lindenb. (thallus shape indicated that they were grown from gemmae), *Tortula* Hedw./*Syntrichia* Brid., *Campylopus* cf. *introflexus*, *Bryum pseudotriquetrum* (Hedw.) P.Gaertn., B.Mey. & Scherb., *B. argenteum* (at Myvatn in 1985, diminishing in 1987), and *Polytrichum juniperinum* Hedw. (1 quadrat at Myvatn in 1987). These Antarctic colonizers seemed to prefer the cooler parts of the geothermal field, attesting most likely to their Antarctic origin. In the Antarctic, geothermal bryophytes typically survive, sometimes by mutation, and spread by vegetative growth and dispersal (Skotnicki *et al*. 2002).

Marchantia s.s. was notably absent at the Myvatn site in 1985, despite the occurrence of *M. polymorpha* in non-geothermal areas of Iceland. Absence of this rapid colonizer might be due to its mode of invasion. Its rapid appearance after fire appears to be from gemmae in the diaspore bank (During 2001). However, in geothermal areas, heat and soil chemistry, often including low *p*H, are not conducive to the long-term survival of gemmae, being further unfriendly to propagule survival due to extreme heat during the eruption. It is likely that it arrives there by spores, which are small [10–15 µm (Schuster 1969)].

Ceratodon purpureus is among the worldwide geothermal inhabitants, including Myvatn, and can be a weed in open habitats in the temperate zone. Shortlidge (2014) explored the biology behind its presence and survival in geothermal areas in the Antarctic. She found a correlation between within-population genetic diversity of the moss and microarthropod abundance. Furthermore, Shortlidge (2014) found greater genetic diversity within populations than among them. Cronberg *et al*. (2006) and Rosentiel *et al*. (2012) had already shown that mites and springtails can carry sperm of this species from males to females. Shortlidge (2014) found evidence of environmental desiccation tolerance in moss sperm. She also found evidence that with less stress, sexual reproduction is increased. The greatest genetic diversity of *Ceratodon purpureus* occurred at the mid-point of the temperature gradient and had a positive correlation with invertebrate diversity, fungal biomass, and soil organic matter. Eppley *et al*. (2011) found that at Lassen Volcanic National Park, California, USA, the number of sporophytes per shoot in this species is positively correlated with distance from geothermal emission locations. Furthermore, transplantation of geothermal populations of *Pohlia nutans* to mesic conditions resulted in high numbers of gametangia and sporophytes (Rosenstiel and Eppley 2009; Eppley *et al*. 2011). In their experiments, Rosenstiel and Eppley (2009) found that 20% of the sperm of *Pohlia nutans* were still viable after 100 hours, and that longevity was not affected by temperatures of 22–60°C. However, life span of sperm was significantly shortened at temperatures above 75°C.

In contrast with the diversity within the populations of *Ceratodon purpureus* in Antarctica (Shortlidge 2014), Skotnicki *et al*. (2002) found low levels of genetic diversity in the *Pohlia nutans* population on Mt. Rittmann in the Antarctic region, suggesting that it arrived there by a single dispersal event, increasing in cover through vegetative growth.

Disjuncts

The warm temperatures of geothermal areas in cold regions permit the growth of species that often are greatly disjunct from their primary distribution. Lewis Smith (2005a, c) found that the volcanic Deception Island in the Antarctic had only 36 (44%) moss and 6 (32%) liverwort species in common with the bryophyte flora of Signy Island, out of 81 and 19, respectively, total for the two islands. He found that mosses and liverworts can exist within only a few centimeters of the geothermal vents that have temperatures reaching 90–95°C.

Of the species of Antarctic colonizers, *Bryum argenteum* [Deception Island (Lewis Smith 1984)], *Ceratodon purpureus* [Antarctic (Shortlidge 2014)], *Pohlia nutans* [Mt. Melbourne, Antarctica, (Bargagli *et al*. 2004); only 1 quadrat at Myvatn in 1987; also on Surtsey (Ingimundardóttir *et al.* 2014)], and *Polytrichum juniperinum* [Deception Island (Lewis Smith 2005a); Myvatn in 1987 only, rare] were present at the Myvatn site, where we also found *Polytrichum piliferum* and *Polytrichastrum formosum*. When Bargagli *et al*. (2004) found *Pohlia nutans* in geothermal areas of Mt. Melbourne, Antarctica, the nearest known population that was most closely genetically related was 110 km north at the geothermal area of Mt. Rittmann.

It is interesting that some of the same genera (different species) occur in geothermally heated areas on the Antarctic Islands and in the Myvatn area, including *Sanionia* [South Sandwich Islands (Convey and Lewis Smith 2006)], *Campylopus* [Deception Island (Lewis Smith 1984)], and *Cephaloziella* [Victoria Land (Broady *et al*. 1987); three species at Myvatn in 1985; *Cephaloziella varians* was in both Myvatn and Deception Island and is the most widespread and abundant liverwort in Antarctica (Newsham 2010)]. The genus *Campylopus* is widespread and common at geothermal vents in both hemispheres. In the Myvatn geothermal area of Iceland we found *Campylopus subulatus*, but only in 1985. Bargagli *et al*. (2004) found *Campylopus* in geothermal areas of Mt. Melbourne, Antarctica. On Deception Island in the Antarctic, Lewis Smith (1984) found *Campylopus introflexus*. *Campylopus introflexus* is one of the most tolerant plants to high temperatures, occurring at 40–47°C surface temperatures on the South Sandwich Islands (Convey and Lewis Smith 2006). These mosses endured in areas where soil temperatures reached a maximum of 75°C at only 2.5–5 cm. Bryophytes such as *Campylopus* and *Cephaloziella* in the Antarctic form cushions over the warm ground (14–31°C) in northern Victoria Land (Broady *et al*. 1987), thus providing insulation bolstering below ground heat. At Ponponyama, Japan, *Campylopus japonicus* was one of only three species that survived at temperatures above 53°C (Glime and Iwatsuki 1997). In New Zealand we found that *Campylopus introflexus* had a surface temperature distribution similar to that of *C. clavatus*, with both ranging up to 45°C, whereas *C. capillaceus* was present throughout the entire range to 65°C (unpublished data).

Convey and Lewis Smith (2006) found that bryophytes on the South Sandwich Islands in the maritime Antarctic were associated with particular temperature profiles. The greatest bryophyte richness on the islands occurred in the geothermal areas. Only 4 mosses out of 35 species on the island never occurred on heated ground. On the other hand, 8 of the 9 liverwort species and 50% of the mosses occurred only on currently or recently heated ground. Convey *et al*. (2000) found both maritime and sub-Antarctic taxa on the heated ground of the South Sandwich Islands.

In New Zealand, Muukkonen (2005) similarly found that geothermal areas include disjuncts from warmer climates in communities mixed with representatives of the surrounding communities with species that were able to endure high-stress conditions with respect to temperature and soil minerals. The same relationship can be seen in alpine geothermal areas, where the warm ground permits the presence of species that do not otherwise occur in the area. In Sasso Pisano, Italy, 16 mosses and 3 liverworts were present in the geothermal area (Bonini *et al*. 2005). *Campylopus pyriformis* (Schultz) Brid., *Leucobryum juniperoideum* (Brid.) Müll.Hal., and *Odontoschisma denudatum* (Mart.) Dumort. occurred in this area and were not known elsewhere in Tuscany.

At 6000 m asl in the Andes, both mosses and liverworts thrive on the heated ground overlying temperatures of 22 to 31°C at 10 cm depth (Halloy 1991), sharing the warmth with lichens, algae, and fungi. As many as 36 bryophyte and lichen taxa were reported from a mere 400 m^2 of vegetation. Warm temperatures are certainly important in permitting warm habitat mosses to grow at high elevations or high latitudes. In high latitudes, thermal areas have perennially unfrozen soil and maintain species as disjuncts from regions that have warmer climates.

Climate Change

Leblans (2016) suggested that Iceland presents "unique" environments that can help us clarify long-term global change in carbon dynamics. Many of the same stressors found in geothermal areas are of concern where human interference is altering natural ecosystems. The geothermal areas have advantages over experiments because of their long-term persistence. Thus, the geothermal fields can serve as models to help us predict what sorts of ecosystems may prevail if our changing climate, soil, and atmospheric conditions begin to mimic these unusual habitats.

Hao and Chu (2021) demonstrated that bryophytes from tropical ecosystems in Hong Kong were well-acclimated to their current temperature regimes, but that increases of only 1.5 and 3°C caused a significant negative effect on health, photosynthetic rate, and growth of the bryophytes in their test. These bryophytes included *Hypnum plumaeforme* Wilson, a moss we found to be common at geothermal vents of Wakoto, Japan (Glime and Iwatsuki 1997).

Bryophytes are not only important as indicators of vegetation changes we might expect with climate change, they serve as homes for a variety of invertebrates that also will be affected by climate change. Buda *et al*. (2018) described 4 tardigrades and 2 oribatid mites, as well as nematodes and rotifers, from bryophytes of steaming lava fields at Krafla, Iceland – the same general area as in our study. They found one to six invertebrate species in individual bryophyte collections with a mean density of 13.1 individuals g^{-1} and a maximum of 40.8 individuals g^{-1} calculated per dry material. Elmarsdóttir *et al.* (2003) found 103 to 146 invertebrate species in the three Icelandic geothermal areas they studied, demonstrating a rich community that can help us to understand the ecosystem interactions and dynamic changes that can result from climate change.

CONCLUSIONS

Cyanobacteria are common near the vent in the hottest and most acid areas. Bryophytes dominate the ground cover near the vents where the 15 cm soil temperature is above 50°C, but the surface temperature is usually below 65°C. Lichens are common slightly farther from the vent and are tolerant of low *p*H and high temperatures but avoid areas that are both hot and wet. *Bryum argenteum* and several Icelandic bryophyte genera are common worldwide in geothermal areas: *Campylopus*, *Cephaloziella, Ceratodon*, *Pogonatum* / *Polytrichastrum* / *Polytrichum*, *Pohlia*, *Racomitrium*, *Sanionia*, or in warmer climates away from geothermal areas.

Geothermal habitats support vegetation representative of warmer climates and, especially in new geothermal areas, provide a natural laboratory that can help us to understand some of the effects to expect from climate changes in their natural habitats instead of a laboratory, including a wide range of heavy metals, temperature gradients, moisture gradients, *p*H gradients, rate of arrival, species interaction effects, and rate of change.

Acknowledgments – The 1987 research was funded by National Geographic Research, Grant Number 3469–86, to J.M. Glime and Z. Iwatsuki. Tatsuwo Furuki (Natural History Museum and Institute, Chiba, Japan), Toru Matsui (Deceased, formerly of Faculty of Science and Technology, Kochi University, Japan), and Hiromi Miyawaki (professor emeritus at Saga University, Japan) helped with identification of liverworts. The manuscript has been strengthened by suggestions from reviewers Nils Cronberg and Vadim Bakalin.

REFERENCES

ARP, P.A. & KRAUSE, H.H. (1984). The forest floor: Lateral variability as revealed by systematic sampling. *Canadian Journal of Soil Science* **64**: 423–437. https://doi.org/10.4141/cjss84-043

BAATTRUP-PEDERSEN, A. & RIIS, T. (1999). Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology* **42**: 375–385. https://doi.org/10.1046/j.1365-2427.1999.444487.x

BARGAGLI, R., CATENI, D., NELLI, L., OLMASTRONI, S. & ZAGARESE, B. (1997). Environmental impact of trace element emissions from geothermal power plants. *Archives of Environmental Contamination and Toxicology* **33**(2): 172–181. https://doi.org/10.1007/s002449900239

BARGAGLI, R., SKOTNICKI, M. L., PEPI, M., MACKENZIE, A. & AGNORELLI, C. (2004). New record of moss and thermophilic bacteria species and physico-chemical properties of geothermal soils on the northwest slope of Mt Melbourne (Antarctica). *Polar Biology* **27**: 423–536. https://doi.org/10.1007/s00300-004-0612-6

BFNA (2011). Bryophyte Flora of North America. *Provisional Publication, Missouri Botanical Garden, BFNA*, 6 Vols. https://www.mobot.org/plantscience/BFNA/bfnamenu.htm

BIEBL, R. (1967). Temperaturresistenz tropischer Urwaldmoose. *Flora oder Allgemeine botanische Zeitung. Abt. B, Morphologie und Geobotanik* **157**: 25–30. https://doi.org/10.1016/S0367-1801(17)30049-2

BJARNASON, A.H. & FRIDRIKSSON, S. (1972). Moss on Surtsey, Summer 1969. *Surtsey Research Society, Surtsey Research Progress Report* **6**: 9–10.

BONDE, E.K. (1969). Plant disseminules in wind-blown debris from a glacier in Colorado. *Arctic and Alpine Research* **1**(2): 135–139. https://doi.org/10.2307/1550020

BONINI, I., CASINI, F., CHIARUCCI, A. & DOMINICIS, V.D. (2005). The bryophyte flora of the geothermal field of Sasso Pisano (Pisa, Italy). *Cryptogamie Bryologie* **26**: 291–299.

BRILLOUIN, L. (1962). *Science and Information Theory* (2nd edition). Academic Press, New York, 351 pp.

BROADY, P., GIVEN, D., GREENFIELD, L. & THOMPSON, K. (1987). The biota and environment of fumaroles on Mt Melbourne, Northern Victoria Land. *Polar Biology* **7**(2): 97–113. https://doi.org/10.1007/BF00570447

BUDA, J., OLSZANOWSKI, Z., WIERZGOŃ, M. & ZAWIERUCHA, K. (2018). Tardigrades and oribatid mites in bryophytes from geothermally active lava fields (Krafla, Iceland) and the description of *Pilatobius islandicus sp. nov.* (Eutardigrada). *Polish Polar Research* **39**: 425–453. https://doi.org/10.24425/118755

BURNS, B. (1997). Vegetation change along a geothermal stress gradient at the Te Kopia steamfield. *Journal of the Royal Society of New Zealand* **27**: 279–293. https://doi.org/10.1080/03014223.1997.9517539

BURNS, B. & LEATHWICK, J.R. (1995). *Geothermal Vegetation Dynamics* (Vol. 18). Wellington: Department of Conservation, 26 pp.

BURTON, M.L., SAMUELSON, L.J. & PAN, S. (2005). Riparian woody plant diversity and forest structure along an urban-rural gradient. *Urban Ecosystems* **8**(1): 93–106. https://doi.org/10.1007/s11252-005-1421-6

CARVEY, K., FARRAR, D.R. & GLENN-LEWIN, D.C. (1977). Bryophytes and revegetation of coal spoils in Southern Iowa. *The Bryologist* **80**: 630–637. https://doi.org/10.2307/3242421

CONVEY, P. & LEWIS SMITH, R.I. (2006). Geothermal bryophyte habitats in the South Sandwich Islands, maritime Antarctic. *Journal of Vegetation Science* **17**: 529–538. https://doi.org/10.1111/j.1654-1103.2006.tb02474.x

CONVEY, P., LEWIS SMITH, R.I., HODGSON, D.A. & PEAT, H.J. (2000). The flora of the South Sandwich Islands, with particular reference to the influence of geothermal heating. *Journal of Biogeography* **27**: 1279–1295. https://doi.org/10.1046/j.1365-2699.2000.00512.x

CRONBERG, N., NATCHEVA, R. & HEDLUND, K. (2006). Microarthropods mediate sperm transfer in mosses. *Science* **313**: 1255.

https://doi.org/10.1126/science.1128707

DAS, P., JOSHI, S., ROUT, J. & UPRETI, D.K. (2012). Shannon Diversity Index (H) as an ecological indicator of environmental pollution – a GIS approach. *Journal of Functional and Environmental Botany* **2**: 22–26. https://doi.org/10.5958/J.2231-1742.2.1.003

DILKS, T.J.K. & PROCTOR, M.C.F. (1975). Comparative experiments on temperature responses of bryophytes: Assimilation, respiration and freezing damage. *Journal of Bryology* **8**: 317–336. https://doi.org/10.1179/jbr.1975.8.3.317

DIRCKSON, A. (1964). *Vergleichende Untersuchungen zur Frost-, Hitz- und Austrocknungsresistenz einheimischer Laub- und Lebermoose unter besonderer Beruechsichtigung jahreszeitlicher Veraenderungen.* Diss Goettingen.

DURING, H.J. (2001). Invited essay – new frontiers in bryology and lichenology. Diaspore banks. *The Bryologist* **104**: 92–97.

ELMARSDÓTTIR, Á., INGIMARSDOTTIR, M., HANSEN, I., OLAFSSON, J.S. & OLAFSSON, E. (2003). *Vegetation and invertebrates in three geothermal areas in Iceland*. Proceedings from International Geothermal Conference, Reykjavík, Sept. 2003, pp. 49–55.

ELMARSDÓTTIR, Á., VILMUNDARDÓTTIR, O.K. & MAGNÚSSON, S.H. (2015). *Vegetation of high-temperature geothermal areas in Iceland.* Proceedings of the World Geothermal Congress 2015, Melbourne, Australia, 19–25 April 2015, pp. 1–11.

EPPLEY, S.M., ROSENSTIEL, T.N., GRAVES, C.B. & GARCÍA, E.L. (2011). Limits to sexual reproduction in geothermal bryophytes. *International Journal of Plant Sciences* **172**: 870–878. https://doi.org/10.1086/660884

FABER, F.C. VON. (1925). Untersuchungen uber die physiologie der Javanischen solfataren pflanzen. *Flora oder Allgemeine Botanische Zeizung* **118–119**: 89–110.

FABER, F.C. VON. (1927). *Die Kraterpflanzen Javas in physiologisch-ökologischer Beziehung.* (Vol. 1.) Arbeiten aus dem Treub-Laboratorium. Landsdrukkerij, Weltevreden, 119 pp.

FAORO, H., ALVES, A.C., SOUZA, E.M., RIGO, L.U., CRUZ, L.M., AL-JANABI, S.M., MONTEIRO, R.A., BAURA, V.A. & PEDROSA, F.O. (2010). Influence of soil characteristics on the diversity of bacteria in the Southern Brazilian Atlantic Forest. *Applied and Environmental Microbiology* **76**: 4744–4749. https://doi.org/10.1128/AEM.03025-09

FETOUH, M.I. & HASSAN, F.A. (2014). Seed germination criteria and seedling characteristics of *Magnolia grandiflora* L. trees after cold stratification treatments. *International Journal of Current Microbiology and Applied Sciences* **3**: 235–241.

FRASER, C.I., TERAUDS, A., SMELLIE, J., CONVEY, P. & CHOWN, S.L. (2014). Geothermal activity helps life survive glacial cycles. *Proceedings of the National Academy of Sciences* **111**: 5634–5639. https://doi.org/10.1073/pnas.1321437111

GARCÍA, E.L., ROSENSTIEL, T.N., GRAVES, C., SHORTLIDGE, E.E. & EPPLEY, S.M. (2016). Distribution drivers and physiological responses in geothermal bryophyte communities. *American Journal of Botany* **103**: 625–634. https://doi.org/10.3732/ajb.1500422

GILES, K.L. (1971). Differentiation and regeneration in bryophytes: A selective review. *New Zealand Journal of Botany* **9**: 689–694. https://doi.org/10.1080/0028825X.1971.10430231

GIVEN, D.R. (1980). Vegetation on heated soils at Karapiti, central North Island, New Zealand, and its relation to ground temperature. *New Zealand Journal of Botany* **18**: 1–13.

GLIME, J.M. (1987a). Temperature optima of *Fontinalis novae-angliae*: Implications for its distribution. *Symposia Biologica Hungarica* **35**: 569–576.

GLIME, J.M. (1987b). Phytogeographic implications of a *Fontinalis* (Bryopsida) growth model based on temperature and flow conditions for six species. *Memoirs of the New York Botanical Garden* **45**: 154–170.

GLIME, J.M. & HONG, W.S. (1997). Relationships of geothermal bryophyte communities to soil characteristics at Thermal Meadow, Hotsprings Island, Queen Charlotte Islands, Canada. *Journal of Bryology* **19**: 435–448. https://doi.org/10.1179/jbr.1997.19.3.435

GLIME, J.M. & IWATSUKI, Z. (1990). Niche characteristics of *Cladonia* lichens associated with geothermal vents in Japan. *Ecological Research* **5**: 131–141. https://doi.org/10.1007/BF02348468

GLIME, J.M. & IWATSUKI, Z. (1994). Geothermal communities of Ponponyama, Hokkaido, Japan. *The Journal of the Hattori Botanical Laboratory* **75**: 133–147. https://doi.org/10.18968/jhbl.75.0_133

GLIME, J.M. & IWATSUKI, Z. (1997). Niche partitioning of plant taxa associated with geothermal vents at Wakoto, Hokkaido, Japan. *The Journal of the Hattori Botanical Laboratory* **82**: 123–141. https://doi.org/10.18968/jhbl.82.0_123

GLIME, J.M. & VITT, D.H. (1987). A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. *Canadian Journal of Botany* **65**: 1824–1837. https://doi.org/10.1139/b87-252

GLIME, J.M., TRYNOSKI, S.E. & SHORT, F.T. (1981). Bryophyte diversity: Case studies using the Brillouin Index to describe epiphytes and an alkaline marsh. *The Journal of the Hattori Botanical Laboratory* **50**: 179–190.

GRIMMETT, R.F.R. & MCINTOSH, I.G. (1939). Occurrence of arsenic in soils and water in the Waiotapu Valley and its relation to stock health 1. *New Zealand Journal of Science and Technology*, *Section A* **21**: 137–145.

GUNNLAUGSDOTTIR, E. (1985). Composition and dynamical status of heathland communities in Iceland in relation to recovery measures. *Acta Phytogeographica Suecica* **75**: 1–56.

GUSTAFSSON, L. & HALLINGBÄCK, T. (1988). Bryophyte flora and vegetation of managed and virgin coniferous forests in south-west Sweden. *Biological Conservation* **44**(4): 283–300. https://doi.org/10.1016/0006-3207(88)90021-3

HALLIDAY, G., KLIIM-NIELSEN, L. & SMART, I.H.M. (1974). Studies on the flora of the North Blosseville Kyst and the hot springs of Greenland. *Meddelelser om Grønland* **199**: 1–49.

HALLOY, S. (1991). Islands of life at 6000 m altitude: the environment of the highest autotrophic communities on Earth (Socompa Volcano, Andes). *Arctic and Alpine Research* **23**: 247–262. https://doi.org/10.1080/00040851.1991.12002843

HAO, J. & CHU, L.M. (2021). Short-term detrimental impacts of increasing temperature and photosynthetically active radiation on the ecophysiology of selected bryophytes in Hong Kong, southern China. *Global Ecology and Conservation* **31**: e01868. https://doi.org/10.1016/j.gecco.2021.e01868

Heinken, T. (1999). Dispersal patterns of terricolous lichens by thallus fragments. *The Lichenologist* **31**: 603–612. https://doi.org/10.1006/lich.1999.0219

Hou, E., Tang, S., Chen, C., Kuang, Y., Lu, X., Heenan, M. & Wen, D. (2018). Solubility of phosphorus in subtropical forest soils as influenced by low-molecular organic acids and key soil properties. *Geoderma* **313**: 172–180. https://doi.org/10.1016/j.geoderma.2017.10.039

Imtiaz, M., Rizwan, M.S., Xiong, S., Li, H., Ashraf, M., Shahzad, S.M., Rizwan, M. & Tu, S. (2015). Vanadium, recent advancements and research prospects: A review. *Environment International* **80**: 79–88. https://doi.org/10.1016/j.envint.2015.03.018

Ingimundardóttir, G.V., Weibull, H. & Cronberg, N. (2014). Bryophyte colonization history of the virgin volcanic island Surtsey, Iceland. *Biogeosciences* **11**: 4415–4427. https://doi.org/10.5194/bg-11-4415-2014

Ingimundardóttir, G.V., Cronberg, N. & Magnússon, B. (2022). Bryophytes of Surtsey, Iceland: Latest developments and a glimpse of the future. *Surtsey Research* **15**: 61–87. https://doi.org/10.33112/surtsey.15.6

Jónasson, K. & Einarsson, S. (2009). *Jardminjar á háhitasvaedum Íslands. Jardfraedi, landmótun og yfirbordsummerki jardhita.* (Geothermal features at high-temperature geothermal areas in Iceland). The Icelandic Institute of Natural History, NÍ-09012. (In Icelandic)

Kappen, L. & Smith, C.W. (1980). Heat tolerance of two *Cladonia* species and *Campylopus praemorsus* in a hot steam vent area of Hawaii. *Oecologia* **47**: 184–189. https://doi.org/10.1007/BF00346818

Kennedy, A.D. (1996). Antarctic fellfield response to climate change: A tripartite synthesis of experimental data. *Oecologia* **107**: 141–150. https://doi.org/10.1007/BF00327897

Konis, E. (1949). The resistance of maquis plants to supramaximal temperatures. *Ecology* **30**: 425–429. https://doi.org/10.2307/1932445

Lange, B. (1973). The *Sphagnum* flora of hot springs in Iceland. *Lindbergia* **2**: 81–93.

Lange, O.L. (1955). Untersuchungen über die Hitzeresistenz der Moose in Beziehung zu ihrer Verbreitung. I. Die Resistenz stark ausgetrockneter Moose. *Flora oder Allgemeine Botanische Zeitung* **142**: 381–399. https://doi.org/10.1016/S0367-1615(17)33089-6

Lange, O.L. (1969). Experimentell-oekologische Untersuchungen an Flechten der Negev-Wueste. I. CO_2-Gaswechsel von *Ramalina maciformis* (Del). Bory unter kontrollierten Bedingungen im Laboratorium. *Flora oder Allgemeine Botanische Zeitung. Abt. B, Morphologie und Geobotanik* **158**: 324–359. https://doi.org/10.1016/S0367-1801(17)30221-1

Langridge, J. (1963). Biochemical aspects of temperature response. *Annual Review of Plant Physiology* **14**: 441–462. https://doi.org/10.1146/annurev.pp.14.060163.002301

Leblans, N.I. (2016). *Natural gradients in temperature and nitrogen: Iceland represents a unique environment to clarify long-term global change effects on carbon dynamics.* Doctoral dissertation, University of Antwerp, 229 pp.

Lewis Smith, R.I. (1984). Colonization by bryophytes following recent volcanic activity on an Antarctic island. *The Journal of the Hattori Botanical Laboratory* **56**: 53–63. https://doi.org/10.18968/jhbl.56.0_53

LEWIS SMITH, R.I. (2005a). The bryophyte flora of geothermal habitats on Deception Island, Antarctica. *The Journal of the Hattori Botanical Laboratory* **97**: 233–248. https://doi.org/10.18968/jhbl.97.0_233

LEWIS SMITH, R.I. (2005b). Bryophyte diversity and ecology of two geologically contrasting Antarctic islands. *Journal of Bryology* **27**: 195–206. https://doi.org/10.1179/174328205X69940

LEWIS SMITH, R.I. (2005c). The thermophilic bryoflora of Deception Island: Unique plant communities as a criterion for designating an Antarctic Specially Protected Area. *Antarctic Science* **17**: 17–27. https://doi.org/10.1017/S0954102005002385

LI, Y., YANG, F., OU, Y., ZHANG, D., LIU, J., CHU, G., ZHANG, Y., OTIENO, D. & ZHOU, G. (2013). Changes in forest soil properties in different successional stages in lower tropical China. *Plos One* **8**(11): e81359. https://doi.org/10.1371/journal.pone.0081359

LINDGREN, A.R., BUCKLEY, B.A., EPPLEY, S.M., REYSENBACH, A.L., STEDMAN, K.M. & WAGNER, J.T. (2016). Life on the edge – the biology of organisms inhabiting extreme environments: An introduction to the symposium. *Integrative & Comparative Biology* **56**: 493–499. https://doi.org/10.1093/icb/icw094

LLANEZA-GARCÍA, E., GRAVES, C.B., ROSENSTIEL, T.N. & EPPLEY, S.M. (2009). *Desiccation tolerance and interspecific competition in geothermal bryophytes.* In: The 94th ESA Annual Meeting, 2–7 August 2009, Albuquerque, New Mexico, PS 65–97.

LOTSCHERT, W. (1956). Temperatur-und pH-studien in Salvadorenischen solfataren und thermen. *Deutsche Botanischen Gesellschaft Berlin* **69**: 21–31.

MAGNUSSON, S. & FRIDRIKSSON, S. (1974). Moss vegetation on Surtsey. *Surtsey Research Soc., Surtsey Research Progress Report* **7**: 45–57.

MARSHALL, W.A. (1996). Aerial dispersal of lichen soredia in the maritime Antarctic. *New Phytologist* **134**: 523–530. https://doi.org/10.1111/j.1469-8137.1996.tb04370.x

MATSUURA, S. (1961). Ecological study of salfatara (sic) on Owakidani, Hakone. (Part 1). *Bulletin of the Natural History Society Hakone* **1**: 1–6.

MCCLELLAND, L. (ed.). (1984). Global Volcanism Program, 1984. Report on Krafla (Iceland). Smithsonian Institution. *Scientific Event Alert Network Bulletin* **9**: 8. https://doi.org/10.5479/si.GVP.SEAN198411-373080

MUUKKONEN, P. (2005). Geotermisten alueiden kasvillisuus Uuden-Seelannin Pohjoissaarella. *Terra* **117**(4): 265–278.

NAGENDRA, H. (2002). Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Applied Geography* **22**(2): 175–186. https://doi.org/10.1016/S0143-6228(02)00002-4

NAITO, T., SUGAWARA, K., IIZUMI, S. & YAMANE, I. (1970). On the relationship between vegetation and soil at the solfatara field of Katanuma, Miyagi Prefecture. *Japanese Journal of Ecology* **20**: 198–203.

NEWSHAM, K.K. (2010). The biology and ecology of the liverwort *Cephaloziella varians* in Antarctica. *Antarctic Science* **22**(2): 131–143. https://doi.org/10.1017/S0954102009990630

NÖRR, M. (1974). Hitzresistenz bei Moosen. (Heat resistance of Mosses). *Flora* **163**: 388–397. https://doi.org/10.1016/S0367-2530(17)31762-0

O'GORMAN, E.J., BENSTEAD, J.P., CROSS, W.F., FRIBERG, N., HOOD, J.M., JOHNSON, P.W., SIGURDSSON, B.D. & WOODWARD, G. (2014). Climate change and geothermal ecosystems: natural laboratories, sentinel systems, and future refugia. *Global Change Biology* **20**: 3291–3299. https://doi.org/10.1111/gcb.12602

OLIVER, M.J. & BEWLEY, J.D. (1984). Plant desiccation and protein synthesis. IV. RNA synthesis, stability, and recruitment of RNA into protein synthesis during desiccation and rehydration of the desiccation-tolerant moss, *Tortula ruralis*. *Plant Physiology* **74**: 21–25. https://doi.org/10.1104/pp.74.1.21

PATIÑO, J. & VANDERPOORTEN, A. (2018). Bryophyte biogeography. *Critical Reviews in Plant Sciences* **37**: 175–209. https://doi.org/10.1080/07352689.2018.1482444

PATTEN, B.C. (1962). Species diversity in net phytoplankton of Raritan Bay. *Journal of Marine Research* **20**(1): 57–75.

PIELOU, E.C. (1966). Shannon's formula as a measure of specific diversity: Its use and misuse. *The American Naturalist* **100**: 463–465. https://doi.org/10.1086/282439

PIPPUCCI, A., LORENZI, R., SPANÒ, C. & SORCE, C. (2015). Stress-induced changes to the flora in a geothermal field in central Italy. *Acta Physiologiae Plantarum* **37**(10): 198. https://doi.org/10.1007/s11738-015-1953-1

POINTING, S.B., BOLLARD-BREEN, B. & GILLMAN, L.N. (2014). Diverse cryptic refuges for life during glaciation. *Proceedings of the National Academy of Sciences* **111**: 5452–5453. https://doi.org/10.1073/pnas.1403594111

RAJSZ, A., WOJTUŃ, B., SAMECKA-CYMERMAN, A., WĄSOWICZ, P., MRÓZ, L., RUDECKI, A. & KEMPERS, A.J. (2021). Metals in *Calluna vulgaris*, *Empetrum nigrum*, *Festuca vivipara*, and *Thymus praecox* ssp. *arcticus* in the geothermal areas of Iceland. *Environmental Science and Pollution Research* **28**: 67224–67233. https://doi.org/10.1007/s11356-021-15046-3

REN, H., WANG, F., YE, W., ZHANG, Q., HAN, T., HUANG, Y., CHUA, G., HUIC, D. & GUO, Q. (2021). Bryophyte diversity is related to vascular plant diversity and microhabitat under disturbance in karst caves. *Ecological Indicators* **120**: 106947. https://doi.org/10.1016/j.ecolind.2020.106947

ROSE, W.I., BORNHORST, T.J. & SIVONEN, S.J. (1986). Rapid, high-quality major and trace element analysis of powdered rock by X-ray fluorescence spectrometry. *X-Ray Spectrometry* **15**(1): 55–60. https://doi.org/10.1002/xrs.1300150111

ROSENSTIEL, T.N. & EPPLEY, S.M. (2009). Long-lived sperm in the geothermal bryophyte *Pohlia nutans*. *Biology Letters* **5**: 857–860. https://doi.org/10.1098/rsbl.2009.0380

ROSENSTIEL, T.N., SHORTLIDGE, E.E., MELNYCHENKO, A.N., PANKOW, J.F. & EPPLEY, S.M. (2012). Sex-specific volatile compounds influence microarthropod-mediated fertilization of moss. *Nature* **489**: 431–433. https://doi.org/10.1038/nature11330

SALISBURY, F.B. & ROSS, C.W. (1978). *Plant Physiology*. Wadsworth Publishing Company, Belmont, California. 682 pp.

SCHEIBMAIR, G. (1938). Hitzeresistenzstudien an Mooszellen. *Protoplasma* **29**: 394–424. https://doi.org/10.1007/BF01602538

SCHUSTER, R.M. (1969). *The Hepaticae and Anthocerotae of North America* (6 Volumes). Columbia University Press, NY & London.

SHANNON, C.E. (1948). A mathematical theory of communication. *Bell System Technical Journal* **27**: 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x

SHANNON, C.E. & WEAVER, W. (1949). *The mathematical theory of communication*. University of Illinois Press, Chicago, 117 pp.

SHEPPARD, J.S. (1971). *The influence of geothermal temperature gradients upon vegetation patterns in Yellowstone National Park.* PhD dissertation, Colorado State University, 157 pp.

SHORTLIDGE, E.E. (2014). *Testing the Ecological and Physiological Factors Influencing Reproductive Success in Mosses.* Doctoral dissertation, Portland State University, 311 pp.

SKOTNICKI, M.L., BARGAGLI, R. & NINHAM, J.A. (2002). Genetic diversity in the moss *Pohlia nutans* on geothermal ground of Mount Rittmann, Victoria Land, Antarctica. *Polar Biology* **25**: 771–777. https://doi.org/10.1007/s00300-002-0418-3

SMITH, C.W. (1981). Bryophytes and lichens of the Puhimau geothermal area, Hawaii Volcanoes National Park. *The Bryologist* **84**: 457–466. https://doi.org/10.2307/3242553

TAPPER, R. (1976). Dispersal and changes in the local distribution of *Evernia prunastri* and *Ramalina farinacea*. *New Phytologist* **77**: 725–734. https://doi.org/10.1111/j.1469-8137.1976.tb04667.x

TRUOG, E. (1951). *Mineral nutrition of plants.* University of Wisconsin Press, Madison, 469 pp.

UNITED NATIONS (2023). Climate Action. (Accessed 19 March 2023) https://www.un.org/en/climatechange/what-is-climate-change

VANDELOOK, F., BOLLE, N. & ASSCHE, J.A. VAN. (2009). Morphological and physiological dormancy in seeds of *Aegopodium podagraria* (Apiaceae) broken successively during cold stratification. *Seed Science Research* **19**(2): 115–123. https://doi.org/10.1017/S0960258509301075

VOJTKÓ, A. (1993). The spore morphology of Hepaticae species. *Acta Biologica Szegediensis* **39**: 59–69.

WALCK, J.L., HIDAYATI, S.N., DIXON, K.W., THOMPSON, K. & POSCHLOD, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology* **17**: 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x

ZANTEN, B.O. VAN & PÓCS, T. (1981). Distribution and dispersal of bryophytes. *Advances in Bryology* **1**: 479–562.

(submitted: 20.11.2022, accepted: 27.03.2023)