

Bryophyte vegetation in geothermal areas in Iceland



Diplomarbeit

zur

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1 Introduction

Geothermal areas are found all around the world. Independent of the latitude and the limitations by the regions climate a special habitat is created by geological processes. Hence similar conditions are found in New Zealand and the Antarctic on the southern and Iceland, Japan or Hawaii on the northern hemisphere for example.

Providing a variety of stresses, the geothermal ground stands out as a very unusual habitat. High temperatures, constant humidity caused by steam, but also very dry patches and chemical soil conditions that range from very acid to alkaline are common. Additionally high concentrations of heavy metals and sulphur may influence the plants.

As geothermal areas are one of the few habitats that are dominated by bryophytes a multitude of questions concerning this phenomenon do arise. So far not much was written on this topic, especially the situation in Iceland. So, aim of this diploma thesis is, to try to solve several questions, like: how is the bryophyte diversity in geothermal areas? What are the specific conditions in this habitat type, concerning pH, temperature and humidity and is there a correlation to be found between these factors and the occurrence of certain species? And at last: do patterns in the distribution of the mosses and hepatics exist or is it even possible to describe communities?

1.1 *State of Knowledge*

1.1.1 Geothermal areas as a habitat for plants

Geothermal areas offer a very unusual habitat for plants: the **temperatures** are higher and more or less independent of the climate so that plants can grow out of their normal geographical range. In many areas **water vapor** escaping from geothermal steam vents offers a stable supply with moisture and also alters the microclimate. But not only water vapour escapes out of the steam vents: mercury is a relatively common constituent of geothermal gases and sometimes other **heavy metals** are found in high concentrations (Glime 1997). Often **gases** like carbon dioxide, hydrogen sulphide and hydrogen are transferred into the steam (Fridleifsson 1979). The **chemical conditions** range from very acid (especially in high temperature areas) to very alkaline (more often found in low temperature areas).

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Hydrogen sulphide in the steam tends to be oxidized by atmospheric oxygen, either into sulphuric acid or into elemental sulphur that is often deposited around the vents. Because of the sulphuric acid surface water can attain a very low pH, alter the soil and bedrock and produce a surficial zone of acid leaching. This alteration because of acid is more often found in high temperature areas in Iceland than in other parts of the world. Reasons are the higher hydrogen sulphide content of steam, the humid climate and the instable igneous minerals. The leaching process itself has also effects on the mineral content of the soil. Some elements, such as Na, K, Ca, Mg are almost completely removed. Other elements (Si, Al) increase in relative concentration (Arnórsson 1995). So, the characteristics of geothermal soils are often high acidity, low organic matter, and high contents of phosphorus, potassium, aluminium, manganese, arsenic, titanium (Given 1980).

In spite of all the disadvantageous characteristics it must be emphasized that the geothermal influence also alters the microclimate in a way that could improve the conditions for plants. The gases escaping the steam vents are often not only toxic pollutants, but also carbon dioxide. Joliffe and Tregunna (1968) discovered that with rising temperatures, a rise of the carbon dioxide and light compensation points as well as saturation points is noticeable. Hence a higher carbon dioxide concentration may be helpful to increase fixation and in this way overcome the photorespiratory losses caused by heat.

Additionally the constant warmth, if not too warm, is advantageous in the relatively cold northern summer in this latitude and in higher elevations. On the typical granular ashes and coarse-grained soil in Iceland which have a low water storage capacity (Einarsson 1994), the constant humidity near steam vents could have positive effects. Being limiting factors of photosynthesis this may facilitate the colonization of these geothermal areas for plants.

Additionally the light intensity seems to play a role in acclimation. Burr (1941) found out the compensation point of *Fontinalis spec.* depended on the light intensity. When 140 lux were present, the compensation point was reached at 20°C in contrast to 5°C with 40 lux. So, it could be assumed that the light intensity and duration of the days in the northern summer may be helpful to endure the heat.

These special chemical and physical conditions have impact on the possibilities of plants to grow in these geothermal areas.

1.1.2 Impact on plants

All the factors mentioned in the previous paragraph can be summarized as environmental stress. This stress can result in physical and chemical cellular stresses which can result in cellular lesions. This again may lead to loss of a structural or metabolic function (Schulze 2002). But what are the general impacts of soil temperature, pH and high concentrations of heavy metal and aluminium in plants and do they interact?

Temperature

Two types of high temperature stress are considered. On the one hand acute exposures to very high temperatures, on the other hand chronic exposures to temperatures just above the optimum.

Acute exposure to extreme temperatures may cause membrane disruption and thermal denaturation of cellular constituents. Repercussions of a chronic exposure to high temperatures are metabolic rate imbalances and the inactivation of very thermolabile enzymes, both resulting in metabolic dysfunction (Lange 1983).

In general there are two ways in which plants can react on heat and become in a certain way heat resistant. One way is heat avoidance that is obtained for example by reflection, isolation, cooling by transpiration or morphological features like splitting of the leave surface. Another way to cope with high temperatures is to become heat tolerant by changing the lipid composition of the membrane or via heat shock proteins (this mechanism is supposed to work at the most eight hours). A third possibility to achieve heat tolerance is to use compatible solutes like Glycerine, Proline and Betaines that are called chemical chaperones and stabilize the structure of proteins. The variation of heat tolerance between ecotypes or species can be changed by hardening, sensitization, adjustment, developmental differences, or through effects of nutrition and ions in the concerning habitat (Schulze 2002).

Additionally, there seems to be a difference between the effects of high aboveground air temperatures and high temperatures of the soil, a plant is growing in. Brady (2008) supposes that most plants are more sensible to the temperature of the soil than to aboveground air temperature.

pH

A low pH and hence a high concentration of hydrogen ions has direct and indirect effects on plants. In many cases the hydrogen ion itself is not the toxic factor which prevents basophilic plants from growing on acidic soils. Only in extremely acidic

soils with a pH below three does the ion itself seem to be the limiting factor for plant growth (Lötschert 1969). So in most cases indirect factors seem to be more important. One aspect is the influence of hydrogen ions on the nutrient ion adsorption. In most cases cation uptake is promoted and anion uptake inhibited by enhanced pH because many uptake processes are mediated by proton pumps that create the potential for ion uptake (Olsen 1953; Sutcliffe 1962; Bowling 1976). The displacement of cations from their adsorption sites on the soil particles shortens the supply of plant nutrients such as magnesium, calcium or potassium. Additionally a low pH has influence on the amounts of Al^{3+} , Fe^{3+} , Fe^{2+} and Mn^{2+} that are all toxic to higher plants. In most cases in which acid soil conditions reduce the growth of plants, the toxicity of aluminium seems to be the predominant or even the only factor. The solubility of Al depends only on the pH, in contrast to Fe and Mn, whose solubility also depends on the redox potential (Lange 1983).

Heavy metals

Although certain metal ions are required for metabolic reactions, they exhibit toxic effects when given in amounts, too high for the plant. Other metals, like Pb, Cd, and Hg are toxic in even small amounts because of their affinity to acidic and thiol groups of proteins and nucleotides and their competition with other metals like Zn or Ca within the plant cell (Lange 1983).

1.1.3 Bryophytes in geothermal areas

(Moist) geothermal habitats are dominated by bryophytes (Glime 2007). What are the advantages they have in contrast to tracheophytes?

One reason for the low competition from tracheophytes is the high root temperature. Bryophytes obtain water and nutrients not through roots out of the ground they grow on, but through the surface of the plant itself, which makes them more dependent of rain and moist air than of the water content of the soil. Instead of the soil nutrients, also nutrients carried by airborne dust can be used by bryophytes (Glime 2007). Although the optimum temperature for net-photosynthesis is between 15° and 20°C (Frahm 2001), this situation with only little or no rhizoid penetration enables bryophytes to exist only on the cooler surface, their older, lower parts die and isolate the higher, younger parts of the plant from the heat. Besides this insulation by the older parts of the plant increases the soil temperature beneath the plants and in this

way alters the conditions for the roots of tracheophytes in a harmful way. In addition, bryophytes seem to tolerate higher temperatures than many other plants (Glime 2).

Like lichens, bryophytes are poikilohydrous, which means that their metabolism is only active in the soaked state and survival of dry periods is possible by a state called anhydrobiosis (Frahm 2001). The poikilohydric behaviour has the advantage that such plants can live in environments where they become heated regularly to temperatures that would be lethal for them in an active, soaked state. But in the soaked state terrestrial cryptogams still are supposed to display a heat tolerance between 30 and 50°C. It's also striking, that the heat tolerance of bryophytes (as well as lichens and fungi) in the desiccated state, relates well to climatic regions or thermal character of the environment, respectively (Lange 1983).

Richard Stout and colleagues in Seattle are working on reasons for the heat tolerance of bryophytes from thermal areas in Yellowstone National Park (U.S.A.). So far they found out that fungal endophytes in tracheophytes seem to play an important role. Being put under stress, the endophytes produce high amounts of the soluble carbohydrate trehalose. This in turn may activate stress tolerance mechanisms in the plant that help to survive higher temperatures. This mechanism was found in a grass, but it's also possible that bryophytes do have the same or a related mechanism.

Difficult for bryophytes is the combined influence of moisture and heat. Most European mosses have a heat tolerance of 39-45°C (Nörr 1974). But bryophytes that are constantly wet have a lower tolerance for continuous high temperatures (Glime 1987a, Glime 1987b). Nörr (1974) gives 42-51°C as the upper heat limit for wet bryophytes, whereas it's 85-110°C for dry plants. The reason for the death of wet mosses at temperatures above this limit is too high respiration loss (Longton 1979). But if the temperature is high but not lethal for the plant another advantage of bryophytes gets important: in contrast to most of the tracheophytes the regenerative capacity of heat-damaged moss plants is very high (Diercksen 1964). Although there has not been done much research on this topic, it seems as if there is no difference between the heat tolerance of hepatics and mosses, so far.

Like mentioned above bryophytes get their nutrients not through roots out of the earth. This is advantageously concerning the effects a low pH has on the availability of nutrients, or the toxicity of aluminium enhanced by a high concentration of hydrogen ions. Hence the harmful impact on bryophytes is much lower than it is for tracheophytes.

Besides bryophytes are heavy metals tolerant and have a high ability to absorb and accumulate heavy metal (Frahm 2001), which is an advantage on geothermal soil. Glime (2007) additionally states that some bryophytes, like tracheophytes can take a cooling advantage of transferring water from lower to upper parts and in this way prevent the younger, growing parts from heat damage. The constant humidity in many geothermal areas would allow this mechanism.

Having a look at the worldwide distribution of bryophytes in geothermal areas, cold regions seem to be the most diverse (Glime 2007).

Concerning Iceland, a total of 605 bryophytes (www.floraislands.is) is listed. According to Jóhannsson (1989-2003), around 81 taxa are common in geothermal areas. Additionally, J. M. Glime (2007) compiled geothermal bryophyte taxa with worldwide distribution, which were *Campylopus*, *Cephaloziella*, *Polytrichum*, *Racomitrium* and *Dicranella* and listed them according to the regions of the world they do occur. The finding was that Iceland has the most taxa among the listed eight countries.

1.2 Study area

1.2.1 Geology of Iceland

With an area of 103.106 km², Iceland is the third largest island in the Atlantic Ocean (Steinthórsson & Thorarinsson 1997). Lying between longitude 13°30' and 24°32' W and latitude 63°24' and 66° N, the mainland is situated only a short distance south of the Arctic Circle (Nutall 2005). The country's average elevation above sea is around 500m (Steinthórsson & Thorarinsson 1997).

Structure and plate tectonics

Iceland is situated on the Mid-Atlantic Ridge, but its special geological features can be explained with the hot spot underneath the island. Hot spots are found in the upper mantle, so under the earths' crust. Hence they are independent of the movement of the plates, which explains why the hot spots seem to move during time, although it's only the plate moving above the hot spot. In these special areas melted mantle material is rising up; this could lead to the development of new islands (for example Iceland and Hawaii) or mountains like the Tibesti Mountains in the Sahara. The hot spot beneath Iceland is active since approximately 60 million years. 25 million years ago, when the North Atlantic rift-system got right above the hot spot the creation of Iceland began. Since then the hot spot had been under continental crust of Greenland. Now, the rising mantle material could lift the crust, erupt and finally built the landmass of Iceland (Einarsson 1994).

During the geological history of Iceland a WNW drift of the North Atlantic Plate system relative to the hot spot could be observed. Today the Mid-Atlantic Ridge crosses Iceland from SW to NE and has spreading rate of approximately 1,95 cm/y. Volcanic activity and relatively new rocks, like postglacial lavas and detrital rocks, which are not older than 9-13 ka are found in this zone across the country. The further away from this median rift zone with crustal spreading and volcanism, the older the rocks are. An 0,7 Ma to about 10 ka old "palagonite formation" from the Upper Pleistocene is followed by a Plio-Pleistocene "grey basalt formation" with an age of 3,1-0,7 Ma. The outermost unit is built by Upper Tertiary "plateau basalts" that are older than 3,1 Ma (Steinthórsson & Thorarinsson 1997).

Geothermal activity

The crestal area of the Mid-Atlantic Ridge is characterized by a high heat flow. As Iceland is located entirely within this heat flow, hot springs are very abundant in the

country. But the thermal output varies greatly from one area to another. Altogether there are around 1000 geothermal localities in Iceland, but steam fields for example are confined to the active zones of rifting and volcanism that run through the country. Today, geothermal activity is divided into two types on basis of the maximum temperature in the uppermost 1 km. In so called low temperature areas this base temperature is $< 150^{\circ}\text{C}$ and water that is heated up in these areas usually has a basic pH. In contrast to this the high temperature areas show a temperature above 150°C in the depth of 1 km and are also characterized by sour thermal water (Bordas 1980).

This leads to the question where the origin of this water is. In Iceland heavy precipitation can be found due to the humid air from the surrounding ocean. Measurement of the deuterium content also supports that the source water of geothermal areas is supposed to be shallow groundwater of meteoric origin. The precipitation flows along fissures down into the hot bedrock in the highland areas, where it's heated up. The heat of the bedrock has two ultimate sources: on the one hand the general heatflux of the volcanic zone and on the other hand the shallow level intrusions in the centre of the high temperature areas. Afterwards, this hot water flows along faults and pervious horizons in direction of the lowlands, withdrawing heat from the regional heat flow along its way. There is to be found a distinct correlation between the flow direction and the general geological strike (Fridleifsson 1979). In **high temperature areas** the water only travels along relatively short distances, ascends and may flash to steam at a depth of 1 km or even less. Often gases like carbon dioxide, hydrogen sulphide and hydrogen are transferred to the steam (Bordas 1980). Hydrogen sulphide, the oxygen in the atmosphere and water may react to sulphuric acid, which alters the ground. Other surface manifestations of the approximately 20-30 high temperature areas in Iceland are steam holes and boiling mud pools (Arnórsson, 1995).

In the **low temperature areas**, erosional features like fjords and valleys are nearly parallel to the main geological strike. Hence the hot water can flow through the same permeable horizons all the way from the high- to the lowlands (in contrast to regions like the Eastern fjords which are devoid of hot springs because of erosional features that are nearly perpendicular to the direction of the geological strike). The water in low temperature areas usually only contains nitrogen and small amounts of hydrogen sulphide. The number of low temperature areas in Iceland is estimated at 250 (Einarsson 1994; Fridleifsson 1979).

1.2.2 Description of the examined areas

The main criteria for choosing these areas are a minimum size, the occurrence of temperatures that are high enough to influence the vegetation and the possibilities to reach the areas by bus/car or a one day's walk, respectively.

- Area 1: **Mývatn** (Plots 1-4, Plot 7)
- Area 2: **Krafla/Leirhnúkur** (Plot 5)
- Area 3: **Landmannalaugar** (Plots 8-11)
- Area 4: **Hveragerði** (Plots 12-19)
- Area 5: **Reykjanes** (Plots 20-23)
- Area 6: **Dyngjufjöll** (Plots 25-26)
- Area 7: **Haukadalur** (Plots 27-28)
- Area 8: **Hveravellir** (Plots 30-31)

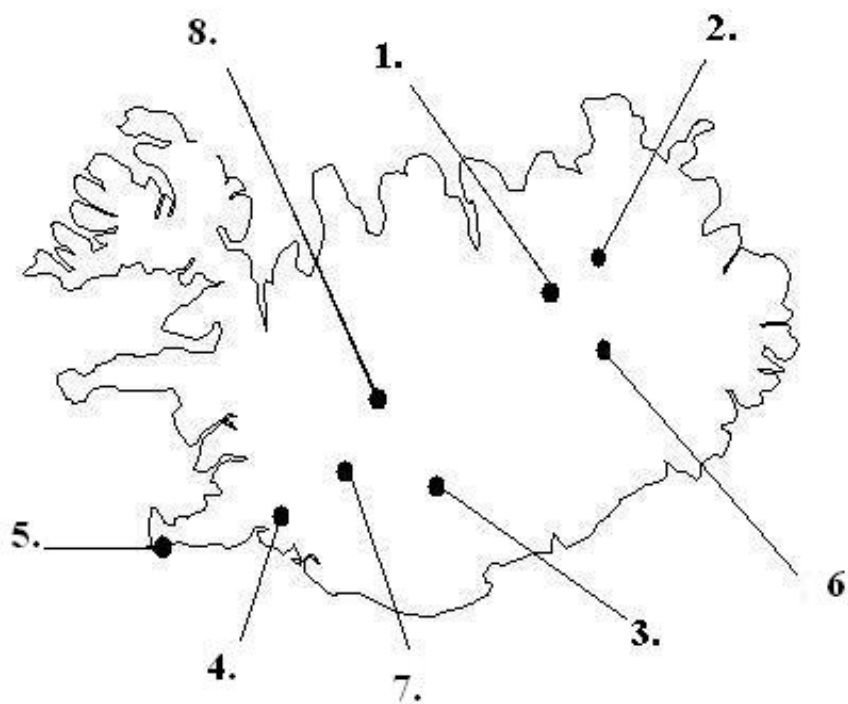


Figure 1-1. Examined areas in Iceland

1.2.2.1 Area 1: Mývatn

Mývatn (the “Lake of the midges”) is located in the northern zone of postglacial volcanism and was created about 2500 years ago. The shallow and eutrophic lake is famous for its diverse duck population, lake balls (marimo), a rich diatom flora

(which is utilized) and a surrounding that's characterized by volcanic activity (Einarsson 2005). Besides strange lava formations and pseudocraters geothermal ground with steam vents is found only a few hundred meters east of the lake near the ringroad to Egilstaðir. Both north of the ringroad next to a factory that uses the silica-rich sediments and south of the road, where clefts with escaping steam pass through a hilly landscape covered with volcanic ashes.

Plot1: overlapping rocks above a steam vent with a thin humus layer mainly overgrown with bryophytes.

Plot2: next to a factory that works with diatomaceous slurry. Hilly ground with several steam vents, bare rock around the vents, elsewhere layer of volcanic ashes. Sparse vegetation.

Plot 3: on the opposite (southern) side of the ring road as Plot 2. Hills with black coarse grained ashes. Steam emerging out of clefts. Dense vegetation (mainly bryophytes) only near the cleft.

Plot 4: samples from a natural grotto with hot water.

Plot 7: same location like Plot 2.

1.2.2.2 Area 2: Krafla/ Leirhnúkur

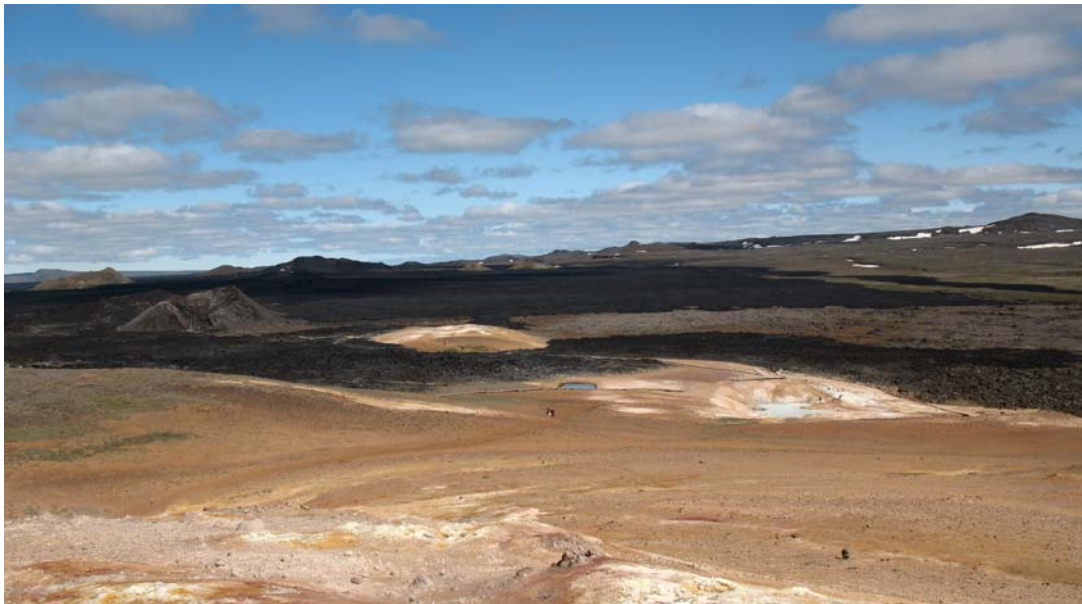


Figure 1-2. Hills of altered soil in young lavafields at Leirhnúkur

The Krafla volcanic system in Northeast Iceland consists of the Krafla central volcano and a 100km long transecting fissure swarm (Rymer 1997). This area north

east of lake Mývatn underwent a series of eruptions in the 1720s and after some calm decades in the Krafla system a major rifting episode took place which led to nine eruptions and a spreading of five meters (Jóhannesson 1997). It was last active between 1975 and 1984 (Rymer 1997). Krafla is one of 35 rifts in a chain that draw magma from a central reservoir fed by up flowing magma from great depths (Ritchie 2001). Sæmundsson (1991) identified this reservoir as an 8km x 10km measuring caldera. Within this caldera there is a high temperature geothermal field that is exploited by a power plant (Stafansson 1981). The examined area was at Leirhnúkur, a volcanic fissure that is part of the Krafla volcanic system. It's a vast area of new lava (the last eruption was in 1984) and several hills that are strongly altered by sulphuric acid that in some places has dissolved the soil to mud pools. Not many plants seemed to be able to survive on the thin and hot soil. Remarkable is that the patches with vegetation often were near steam vents.

Plot 5: on a hill with loamy soil, presumably altered by sulphur. Only little steam emerging from approximately 20 cm deep depressions in the ground. Vegetation limited to these depressions and to few patches on the very hot ground.

Plot 6: loamy depression, with little steam.

1.2.2.3 Area 3: Landmannalaugar

Landmannalaugar is located at the foot of Laugahraun, a rhyolitic lava stream in the southern part of the central highland. Laugahraun itself is located at the northern border of the Torfajökull area, a central volcano with a diameter of 20km. Laugahraun, which consists of many single lava streams, had its last eruption in 1480. Now it's in a period of subsiding activity, visible in numerous hot springs and solfataras (Schutzbach 1976). A hot stream emerging out of the lava, as well as the most popular hiking trail Laugavegur make Landmannalaugar a highly frequented spot for tourists. The plots were on the margins of Laugahraun, often only few metres away from the hiking trail to Hrafninnusker.

Plot 8: dry and steep slope without steam vents; in a lava field with a thin soil layer.

Plot 9: slope at the edge of a lava field. Numerous steam vents. Uneven ground with many rocks.

Plot 10: slope at the edge of a lava field. Steam emerging from clefts in the rock. Relevés on the moderately warm ground nearby the steam vent.

Plot 11: like Plot 10 but closer to the cleft.

1.2.2.4 Area 4: Hveragerði



Figure 1-3. One relevé of plot 13 near Hveragerði

Hveragerði is a small city near the south coast of Iceland, where steam fields in the city centre give evidence of the geothermal activity and the energy is used on large scale to heat greenhouses. In the hinterland of Hveragerði the Hengill high temperature field is located.

The examined areas are the Reykjadalur and the Grænidalur, two valleys that are only a few km north of Hveragerði.

The vegetation consists mainly of meadows and heath land and is interrupted by relatively small patches of hot ground, often accompanied by steam vents and solfataras.

Plot 12: slope at the end of the Reykjadalur. No visible steam vents but patches with bare and strongly altered soil with yellowish depositions. Very dry and stony ground.

Plot 13: along the bank of the around 40°C warm stream in Reykjadalur. Plot is influenced by steam from the stream and the soil itself is moderately warm.

Plot 14: Bryophyte vegetation very close to the stream. Steep overhang with constant humidity.

Plot 15: Very dry slope with fine grained soil and intermittent stones. No steam and a very gappy vegetation.

Plot 16: near Plot 15 and with similar conditions.

Plot 17: spot without vegetation. Soil extremely hard and altered, among other things presumably by sulphur (yellowish colour). Highest temperatures (111°C in a depth of 3cm) and lowest pH (1,04) measured compared to other plots.

Plot 18: same type like Plot 15/16.

Plot 19: slope with a medium thick layer of soil and no steam vents. Vegetation sparse and influenced by erosion.

1.2.2.5 Area 5: Reykjanes



Figure 1-4. Geothermal field at the south-western cape of Reykjanes

The Reykjanes Peninsula is located in the south-west of Iceland. It's a geological active area with relatively young bedrock like in the centre and the north-east of the country. In the Peninsula there is continuous aseismic slip between the Eurasian and the North American plate (Steinthórsson & Thorarinsson 1997). At the cape of the peninsula there is a geothermal field only few hundred metres away from the shore and utilized by a neighbouring power plant. A special feature of the Reykjanes field is that its one of the two geothermal areas being infiltrated by sea water (the other one being Svartsengi). The resulting fluids are brines. This approximately one km²

big area also hosts Gunnuhver a famous mud pool which was reactivated in an earthquake in 1967 (Fridleifsson 1979). The vegetation is very sparse due to the relatively young lava streams that cover the area.

Plot 20: thick layer with (bryophyte-) vegetation interrupted by steam vents surrounded by bare ground. Soil altered, but apparently no sulphur.

Plot 22: near Plot 20; same conditions.

Plot 23: many steam vents, but less bare ground and less altered soil.

Plot 24: no vegetation; soil with a reddish brown colour. Temperature above 100°C.

1.2.2.6 Area 6: Dyngjufjöll

The Askja volcanic system with a length of 150 km and a width of 5-10 km is located in the central rift zone. The Dyngjufjöll mountain complex, a central volcano, is part of this volcanic system. The Dyngjufjöll massif contains three calderas. The main one measuring 45 km² is named Askja. It's approximately 10.000-20.000 years old and still active. The smallest and youngest caldera is Öskjuvatn, Iceland's deepest freshwater lake (Guðmundsson). The last eruption took place in 1961 and was accompanied by earthquakes, geysers and solfataras (Ritchie 2001).

The investigated area is located near the south eastern shore of Öskjuvatn. It was hilly, nearly without vegetation and the ground seemed to be clay with a thin layer of pumice. On this ground there were approximately 2 m² big patches that seemed to be warmer than the surrounding areas (not covered with snow) and that were covered with gappy bryophyte vegetation. The number of samples for this area is limited because of the constant bad weather conditions.

Plot 25: slope with no steam, loamy soil and sparse vegetation.

Plot 26: same as Plot 25, but at the foot of the hill.

1.2.2.7 Area 7 Haukadalur



Figure 1-5. Vegetation and hot pools near Geysir

Haukadalur is located in the south east of Iceland and especially famous because of the Great Geysir, which gave name to all the geysirs around the world and the smaller geysir named Strokkur which still erupts. The area around Geysir and Strokkur offers a variety of geothermal surface manifestations like steam vents, boiling water pools and patches of hot and highly altered ground. Due to the special chemistry of the soil and its heat almost only bryophytes were able to cope with the conditions, only few tracheophytes were growing in this part of the area.

Plot 27: flat area with no steam vents. Ground with a thin and stony, coarse-grained soil layer and gappy vegetation.

Plot 28: in the vicinity of a steam vent, nearly no gaps in the vegetation.

Plot 29: at the edge of a boiling water pool; vegetation influenced by uprising steam.

1.2.2.8 Area 8: Hveravellir

Hveravellir, which means “plain of the hot springs”, is in the central highland in between the glaciers Langjökull and Hofsjökull. The geothermal area is at a height of around 640m. Many phenomena, like solfataras, hot springs and steam vents give evidence of the volcanic activity in this region.

All examined plots were near a warm bathing pool next to a tourist hut. Most other potential geothermal sites were without vegetation, or dominated by tracheophytes.

Plot 30: flat area without steam vents, but with a warm stream in the vicinity. Thin and hard soil layer with a whitish colour.

Plot 31: like Plot 30, but dryer and soil more coarse-grained.

2 Material and methods

Field work was carried out in July and August 2007. 56 different bryophyte species were sampled in a total of 177 relevés in eight regions.

2.1. *Material*

2.1.1 pH-Meter

To determine the soil pH a pH electrode combined with a pH meter in one device was used. The pH electrode consists of a reference electrode constructed around a hydrogen ion-sensing glass membrane electrode. The difference between the hydrogen ion activities in the suspension of the soil and in the glass electrode gives rise to an electrometric potential which is related to the soil solution pH. Then the pH meter measures the electronic potential in millivolts and converts them into pH readings (Brady 2008).

2.1.2 Infrared thermometer

An infrared thermometer is a non-contact thermometer, the temperature can be measured from a distance and a laser helps to aim at the subject. It measures the temperature by using the blackbody radiation (the amount of infrared energy) that is emitted by the object, in this case the surface of the bryophyte cover. The energy is converted to an electrical signal by a detector and is displayed.

2.1.3 Soil thermometer

A common soil thermometer with a metallic bar sensor and a digital display was used. The sensor that had to be inserted to a certain degree into the earth, in order to reduce influences from the aboveground air temperature.

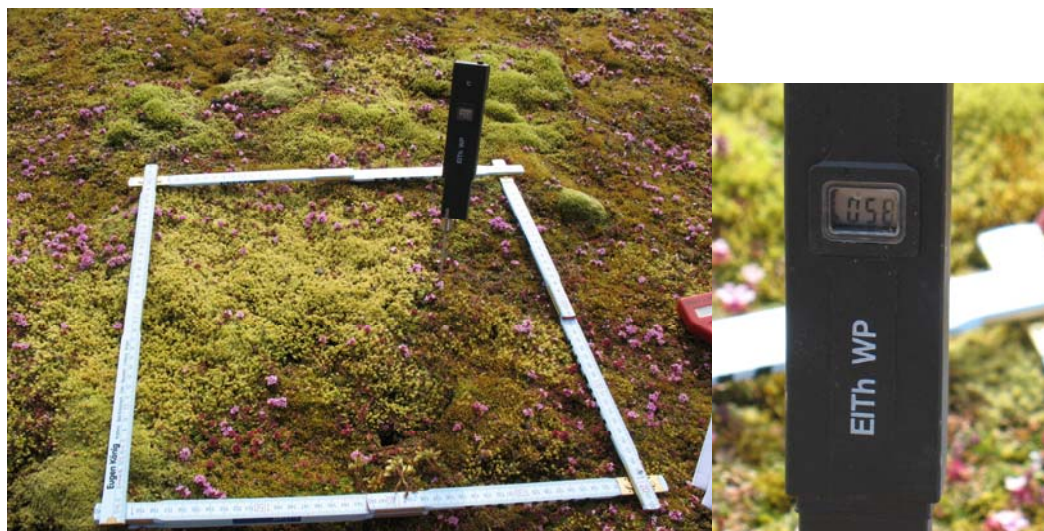


Figure 2-1. Measurement of the soil temperature in a relevé at Leirhnúkur

2.1.4 Statistical treatment

Excel and Statistica 7.1 were used for the evaluation.

2.2 Methods

In order to describe bryophyte communities and find correlations between the occurrence of species, the temperature and pH of the soil, assessments of the vegetation were made and the pH of the soil as well as the temperature were measured. Additionally the amount of steam influencing the relevé was estimated.

2.2.1 Recording methods

First a minimum area analysis was made. Therefore a test area is doubled systematically while the number of species is counted every time. The minimum area is determined, when the number of species/size of area ratio is more or less stable (Trempe 2005). For the first area near Mývatn the minimum area was 40x40 cm and this size was used for all areas in order to keep the data comparable.

The choice of the area to be examined was mainly influenced by the size of the vegetation patterns on the geothermal ground. The patches were in most cases relatively small (around 2 m²), so areas located more in the middle of the patches or near the opening of the steam vent respectively, were chosen.

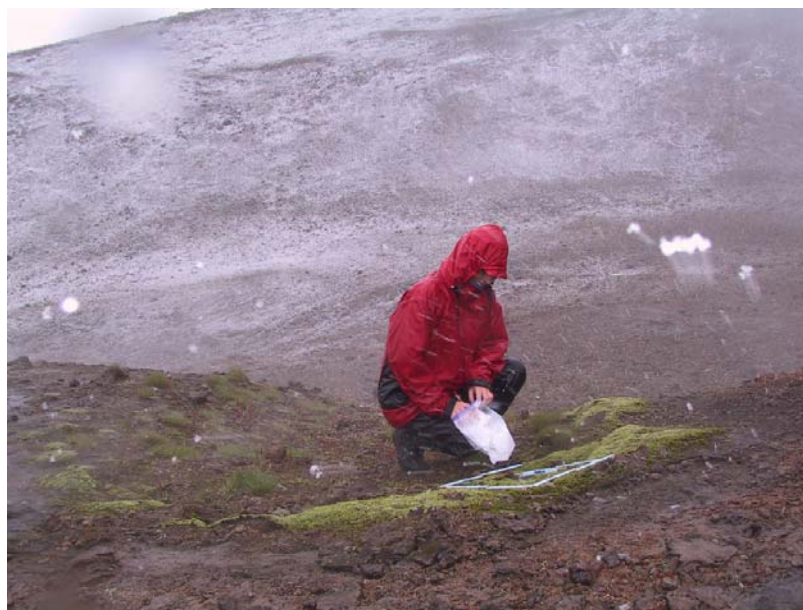


Figure 2-2. Vegetation assessment at Askja

In every relevé the bryophyte species were sampled and their cover estimated. For this the modified scala of Frey (1933 in Klement 1955) was used which was especially established for recording bryophytes and lichens.

Scale	Cover (%)	Average cover (%)
+	≤ 1	0,5
1	>1-6	3,5
2	>6-12,5	9,3
3	>12,5-25	37,5
4	>25-50	37,5
5	50-100	75,0

The sampled bryophytes were later identified under the microscope. Literature that was used for identification: Damsholt, K. 2002, Frahm, J.P.; Frey, W. 2004, Frey, W.; Frahm, J.P.; Fischer, E.; Lobin, W., Frey, W.; Lösch, R. 1998, Hesselbo, A., Jóhannsson, B. 1983, Jóhannsson, B. 1989-2003 and Nyholm, E. 1954.

Vascular plants were not taken into account, only their occurrence was noted.

2.2.2 Analysis of phytosociological data

The data was transferred into gross tables. During the rest of the analysis the tables for the certain areas were treated separately. The constancy (frequency of occurrence) of the different species in one area was worked out.

The constancy classes are according to Dierschke (1994):

V	>80-100	I	>10-20%
---	---------	---	---------

IV	>60-80%	+	>5-20%
III	>40-60%	r	- 5%

Then the species were arranged according declining constancy. The resulting constancy tables were sorted manually. Especially species with a medium constancy were taken into account, in order to arrange groups of species that usually were found together in one relevé. To improve the clearness of the vegetation tables below, similar relevés in one area are summarized in units. Additionally the ecological differences were compared to habitat parameters recorded during field work.

2.2.3 Determination of soil pH

The pH of soil is defined as the negative logarithm of the hydrogen ion activity (concentration) of a soil (Brady 2008). The pH was measured during fieldwork. First a small amount of soil from the middle of the respective 40x40 cm square was mixed with distilled water at a ratio of 1:2. The pH was measured once in every relevé in an area. In between every single measurement the electrode and beaker were cleaned with distilled water.

2.2.4 Measurement of temperature

The temperature of the soil was measured in a depth of approximately 3 cm under the soils surface as well as on the surface of the bryophytes.

The temperature was measured in 3 cm depth because problems with the reliability of other methods occurred. Planed, was to determine the temperature on the surface of the soil itself because this presumably is the most important temperature influence on the bryophytes. The problem with the soil thermometer was that it had to be inserted some cm into the soil otherwise the influence of the aboveground air temperature seemed to be too strong. The same problem occurred with the infrared thermometer during the measurement of the soil as well as of the bryophyte surface. During field work, day temperatures varied between approximately -5 and 20° C and the influence of the sun was strong, too. Additionally the hot water vapour coming out of the steam vents was not a constant influence on the surface temperature because it changed its direction with the wind and its intensity seemed to change, influenced by processes underground.

2.2.5 Humidity

The amount of steam altering the microclimate of the relevé was estimated.

Explanations for the abbreviations:

- n.s.:** no steam/ steam vent was visible near the relevé.
- s0:** vent was visible, but no steam escaped out of the vent.
- s1:** steam from a vent in the proximity of the relevé increased humidity slightly.
- s2:** relevé near a vent with medium amount of steam.
- s3:** relevé near a vent with high amount of steam.

3 Results

3.1 Bryophytes found in geothermal areas

In the following table all bryophyte species that were found in geothermal areas are listed according to their taxonomical relation.

The third column gives information about the general occurrence in Iceland according to the literature by Bergþór Jóhannsson.

Meaning of the abbreviations:

y	general habitat includes geothermal areas.
n	geothermal areas are not yet described as typical habitat of the concerning species.
rare	existing maps show a very limited distribution
n.d.	the species is listed as bryophyte in Iceland, but neither the typical habitat, nor the distribution in Iceland is described in the literature used

Table 3-1. Survey of the sampled species and their general occurrence in Icelandic geothermal areas

Taxon		in geoth. areas
Hepaticae		
<u>Marchantiopsida</u>		
Marchantiales	<i>Marchantia alpestris</i> (Nees) Burgeff	n. d.
	<i>Preissia quadrata</i> (Scop.) Nees	y
	<i>Riccia beyrichiana</i> Hampe ex Lehm	y
	<i>Riccia sorocarpa</i> Bisch.	y
<u>Jungermanniopsida</u>		
Metzgeriales	<i>Moerckia blytii</i> (Moerch)	n (rare)
	<i>Riccardia chamaedrifolia</i> (With.) Grolle	n
Jungermanniales	<i>Calypogeia muelleriana</i> (Schiffn.) Müll.Frib.	y
	<i>Cephaloziella rubella</i> (Nees)	n
	<i>Gymnocolea inflata</i> (Huds.) Dum.	y
	<i>Jungermannia polaris</i> Lindb.	n
	<i>Lophozia sudetica</i> (Nees)	n
	<i>Nardia scalaris</i> S.Gray	y
	<i>Scapania irrigua</i> (Nees)	y
<u>Blasiopsida</u>	<i>Blasia pusilla</i> L.	y
<u>Fossombroniopsida</u>		
	<i>Fossombronia foveolata</i> Lindb.	y
	<i>Fossombronia wondraczekii</i> (Corda) Lindb.	y
Bryophytina		
<u>Sphagnopsida</u>		
Sphagnales	<i>Sphagnum palustre</i> L.	y (rare)
<u>Bryopsida</u>		
Polytrichidae		
Polytrichales	<i>Atrichum angustatum</i> (Brid.) B.&S.	y (rare)
	<i>Polytrichum alpinum</i> Hedw.	n

	<i>Polytrichum commune</i> Hedw.	y
	<i>Polytrichum piliferum</i> Hedw.	n
	<i>Polytrichum sexangulare</i> Brid.	n
Bryidae		
Archidiales	<i>Archidium alternifolium</i> (Hedw.) Schimp.	y
Dicranales	<i>Campylopus introflexus</i> (Hedw.) Brid.	y (rare)
	<i>Campylopus shimperii</i> Milde	n
	<i>Campylopus subulatus</i> Schimp.	y
	<i>Ceratodon purpureus</i> (Hedw.)	y
	<i>Dicranum bonjeanii</i> DeNot.	y
	<i>Ditrichum cylindricum</i> (Hedw.)	y
	<i>Ditrichum heteromallum</i> (Hedw.)	y
	<i>Ditrichum lineare</i> (Sw.) Lindb.	y
	<i>Ditrichum plumbicula</i> Crundw.	
	<i>Ditrichum pusillum</i> (Hedw.)	y (rare)
Fissidentales	<i>Fissidens osmundoides</i> Hedw.	y
Grimmiales	<i>Racomitrium canescens</i> (Hedw.) Brid.	y
	<i>Racomitrium elongatum</i> (Ehrh.) Frisvoll	y
	<i>Racomitrium ericoides</i> (Brid.) Brid	n
	<i>Racomitrium lanuginosum</i> (Hedw.) Brid.	n
Bryales	<i>Bryum bryoides</i> (R.Brown) Angstr.	n (rare)
Hypnales	<i>Brachytecium salebrosum</i> (Web.&Mohr) B.,S.&G.	
	<i>Calliergonella lindbergii</i> (Mitt.) Heden.	n
	<i>Calliergon stramineum</i> (Brid.) Kindb.	n.d.
	<i>Campylium elodes</i> (Lindb.) Kindb.	
	<i>Drepanocladus aduncus</i> (Hedw.) Warnst.	n
	<i>Hylocomium pyrenaicum</i> (Spruce) Lindb.	n (rare)
	<i>Hylocomium splendens</i> (Hedw.) B.,S.&G.	n
	<i>Hypnum callichroum</i> Brid.	n
	<i>Hypnum cupressiforme</i> Hedw.	n
	<i>Hypnum hamulosum</i> B.,S.&G.	n
	<i>Hypnum lindbergii</i> Mitt.	n
	<i>Pleurozium shreberi</i> (Brid.) Mitt.	n
	<i>Rhytidiadelphus squarrosus</i> (Hedw.) Warnst.	n
	<i>Rhytidium rugosum</i> (Hedw.) Kindb.	n.d.
Bartramiales	<i>Aulacomnium palustre</i> (Hedw.) Schwaegr	n
	<i>Philonotis fontana</i> (Hedw.) Brid.	n
	<i>Philonotis tomentella</i> Mol.	y

A total of 56 bryophyte species was sampled, including 40 mosses and 16 hepatics.

Remarkable is a ratio of nearly 1:1 concerning the typical occurrence of the species in geothermal areas- typical for this habitat are 26 species in contrast to 30 that do usually not grow on warm soil or near steam vents or hot springs, respectively. Rare plants concerning their distribution in Iceland are *Moerckia blytii*, *Sphagnum palustre*, *Atrichum angustatum*, *Campylopus introflexus*, *Ditrichum pusillum*, *Bryum bryoides* and *Hylocomium pyrenaicum*.

Although some species have not been described in the used literature from Bergþór Jóhannson, in his list of Icelandic bryophyte species from 1983 all sampled bryophytes do occur.

Further it's remarkable, that contrary to what one would expect under such severe conditions, the vast majority of bryophytes seemed very vital. At least no reduced growth or decreased contents of chlorophyll were obvious on first sight.

Although no impact on the gametophyte was noticeable, nearly no bryophytes that produced capsules could be observed. Only *Polytrichum commune* on a plot near Hveragerð had sporophytes

3.2 Description of the bryophyte vegetation in the regions

3.2.1 Mývatn



Figure 3-1. Vegetation next to a steam vent in the Mývatn area (Plot 3)

Altogether 16 bryophyte species were found in three different plots, including eleven mosses and five hepatics. Four different units can be distinguished. In all of them there is found a cluster of species that are common in many geothermal areas in Iceland: *Racomitrium lanuginosum* with constantly high occurrence and *Campylopus introflexus* with lower cover values.

Besides these the first unit, characterized by a slightly acidic soil pH around 6, medium heat (46°C) and high amounts of steam, comprises higher cover values of *Campylopus introflexus* than the other units. A low share of *Riccia beyrichiana*, especially in relevés with higher temperature and higher pH is also distinct. *Gymnocolea inflata*, *Ditrichum plumbicula*, *Polytrichum alpinum*, *Riccia sorocarpa* as well as *Ceratodon purpureus* can be classified as companions.

The species composition of unit two is similar to the first one, but in contrast to this with a stable occurrence of *Fossombronia wondraczekii*. *Ditrichum lineare* and lower values of *Polytrichum piliferum* occur, but only in relevés with less heat (max. 30°C) and a pH beneath 5,11.

The physical conditions in unit three show only small differences like a nearly neutral soil pH and the lack of temperature peaks, still there are some differences concerning the occurring species. The species with an overall high constancy (*Racomitrium lanuginosum*, *Campylopus introflexus*, *Fossombronia wondraczekii*) have noticeable low cover values. Instead *Archidium alternifolium* and *Campylopus subulatus* are common and *Polytrichum sexangulare* as well as *Preissia quadrata* occur as companions.

Minima concerning pH (5,94) and temperature (24°C) for the Mývatn area distinguish the fourth unit. Only four species were found in the examined relevés, *Racomitrium ericoides* with the highest cover values, followed by *Racomitrium lanuginosum* and *Gymnocolea inflata*. Few plants of *Polytrichum sexangulare* were growing in between the dense cushions, built by the other bryophytes.

Community	Racomitrium lanuginosum group				Constancy class
	Campylopus introflexus	Camp. int.-Foss. won.	Fossombronia wondraczekii-Archidium alternifolium	Racomitrium ericoides-Polytrichum sexangulare-Gymnocolea inflata	
	Unit number	1	2	3	4
	Number of relevés	6	5	6	6
	Plot number	7,2	2,7	3	3,2
	Humidity	s2	s0, s2	s2	s2, s1
	pH (range)	5,01-6,92	4,98-7,36	6,39-6,80	5,31-5,74
	pH (mean)	6,03	5,90	6,60	5,49
	Temperature (range)	33-59°C	24-48°C	31-37°C	22-30°C
	Temperature (mean)	46°C	34°C	35,67°C	23,83°C
<i>Racomitrium lanuginosum</i>	III (1-5)	I (1-3)	I (+2)	II (1-4)	V
<i>Campylopus introflexus</i>	III (1-4)	II (+3)	+ (+1)	I (3)	IV
<i>Fossombronia wondraczekii</i>	.	II (1-2)	I	.	III
<i>Racomitrium ericoides</i>	.	.	.	III (1-5)	II
<i>Archidium alternifolium</i>	.	.	II (+4)	.	II
<i>Polytrichum sexangulare</i>	.	.	+ (+1)	+	II
<i>Gymnocolea inflata</i>	+ (2)	.	.	I (+3)	II
<i>Ditrichum plumbicula</i>	+ (+1)	+ (1)	.	.	II
<i>Polytrichum alpinum</i>	+ (+1)	+	.	.	I
<i>Riccia sorocarpa</i>	+	I (+2)	.	.	I
<i>Preissia quadrata</i>	.	.	+ (+1)	.	I
<i>Campylopus subulatus</i>	.	.	I (+2)	.	I
<i>Riccia beyrichiana</i>	I (1-3)	I (1-3)	.	.	I
<i>Ditrichum lineare</i>	.	II (3-4)	.	.	I
<i>Polytrichum piliferum</i>	.	I	.	.	I
<i>Ceratodon purpureus</i>	+ (1)	.	.	.	+

Table 3-2. Vegetation at Mývatn

3.2.2 Leirhnúkur



Figure 3-2. Sparse vegetation at Leirhnúkur

With a pH around 6, medium amounts of steam and temperatures up to 60°C, the Leirhnúkur area was one of the more extreme habitats for bryophytes. Still a total of 12 bryophyte species (nine mosses and three hepatics) were found.

Three units of slightly different bryophyte vegetation can be distinguished with *Philonotis fontana* occurring in all examined relevés.

Aulacomnium palustre is a frequent species in vegetation unit number five, especially in relevés with temperature maxima. *Racomitrium canescens* and *Preissia quadrata* have only low cover values as well as certain companions, like *Dicranum bonjeanii*, *Hylocomium pyrenaicum* and *Racomitrium ericoides*.

Unit six is characterized by a pH slightly below seven and the lowest temperatures in the area with only an average of 48°C. Gappy *Ceratodon purpureus* and *Philonotis Fontana* turfs with only few intermittent other bryophytes were typical for these relevés. *Drepanocladus aduncus* and *Racomitrium elongatum* are species that concerning the Leirhnúkur area occur only in unit six.

The physical conditions of unit number seven are similar to unit five. However *Aulacomnium palustre* is not found in the relevés, instead *Ceratodon purpureus* and *Riccia sorocarpa* do occur. So, referring to the composition of species, unit seven can be seen as intermittent between unit five and six.

Table 3-3. Vegetation at Leirhnúkur

Community	Philonotis fontana group			Constancy class
	Aula.pal.-Raco can. turf	Cera.pur.- Ric.sor.	Cera.pur.- Raco.can.- Ric.sor.	
Unit number	5	6	7	
Number of relevés	5	2	4	
Plot number	5	5	5	
Humidity	s1	s1	s1	
pH (range)	5,47-5,63	5,31-7,84	5,28-6,12	
pH (mean)	5,57	6,58	5,79	
Temperature (range)	46-60°C	46-50°C	44-59°C	
Temperature (mean))	54,4°C	48°C	54,25°C	
<i>Philonotis fontana</i>	IV (3-5)	III (1-4)	III (1-5)	V
<i>Aulacomnium palustre</i>	II (1-4)	I	.	IV
<i>Racomitrium canescens</i>	I (1-3)	I	I (+-1)	IV
<i>Ceratodon purpureus</i>	.	III (2-4)	III (2-4)	III
<i>Riccia sorocarpa</i>	.	I	I (+-1)	III
<i>Preissia quadrata</i>	I (1-2)	.	+ (1)	II
<i>Fossombronia wondraczekii</i>		I(+1)	+	II
<i>Dicranum bonjeanii</i>	+ (+-1)	.	+	II
<i>Hylocomium pyrenaicum</i>	+	I		
<i>Racomitrium ericoides</i>	+ (2)	.	I (3)	I
<i>Drepanocladus aduncus</i>	.	I	.	+
<i>Racomitrium elongatum</i>	.	I	.	+

3.2.3 Landmannalaugar

In Landmannalaugar a variety of different plots with great differences in humidity and vegetation was examined. Similarities are an acidic soil, as well as moderate temperatures around 40 °C. In total 15 bryophytes were recorded for the examined sites, including ten mosses and five hepatics. Five units with more or less different species can be distinguished, with *Atrichum angustatum* occurring in all units.

Dense *Racomitrium ericoides* cushions are typical for unit eight, which includes relevés that are influenced by huge amounts of warm steam, but only low soil temperatures (mean of 31°C). *Polytrichum commune* was present with very low cover values and *Atrichum angustatum*, *Racomitrium lanuginosum*, and *Lophozia sudetica* occur as companions in relevés with temperature minima and steam maxima.



Figure 3-3. Steam vents in Laugahraun, Landmannalaugar

Contrary to the preceding unit, unit number nine, is not influenced by steam and has higher soil temperatures up to 53°C. *Racomitrium lanuginosum* and *Archidium alternifolium* show the highest cover values, *Racomitrium ericoides* is less important. New companions do occur: *Campylopus subulatus*, *Fossombronia foveolata*, *Riccia beyrichiana*.

Unit ten is composed of nine relevés in which *Racomitrium ericoides* and *Fossombronia wondraczekii* are predominating. With a total of ten species the relevés have a great variety of different bryophytes with low covering.

Unit eleven is very similar to unit ten, but lacks a range of companions like *Riccia beyrichiana* and *Lophozia sudetica*. Remarkable is the absence of *Racomitrium ericoides*.

Racomitrium elongatum and *Lophozia sudetica* are two species that occur only in unit 12 which is characterized by little steam, moderate soil temperatures around 40°C and an average soil pH of 5,6. In the relevés of this unit, *Racomitrium ericoides* has the highest cover values compared to other units in Landmannalaugar. *Campylopus subulatus*, *Fossombronia foveolata* and *Calliergon stramineum* have only minor cover values; *Archidium alternifolium* and *Polytrichum piliferum* cover less than one percent in the concerning relevés.

Table 3-4. Vegetation at Landmannalaugar

	Atrichum angustatum group					Constancy class
	cooler & more humid than ->	Racomitrium lanuginosum-Archidium alternifolium-turf	Racomitrium ericoides turf	Raco eric.-Raco lanu. turf with Calliergon	Fossombronia w.-Calliergon str. turf	Calliergon str.-Fossombronia fov.
Community						
Uni number	8	9	10	11	12	
Number of relevés	5	9	9	8	7	
Plot numbers	9, 10	8	9	9	11	
Humidity	s2-s3	n.s.	s3	s3	s1	
pH (range)	5,48-6,33	5,34-5,91	4,49-6,81	5,65-6,81	5,45-5,87	
pH (mean)	5,79	5,68	5,77	6,23	5,60	
Temperature (range)	28-34°C	40-53°C	21-51°C	35-56°C	36-46°C	
Temperature (mean)	31°C	47,44°C	36,22°C	45°C	40,29°C	
<i>Atrichum angustatum</i>	+	I (+-2)	I (+-2)	II (1-3)	III (1-5)	V
<i>Racomitrium ericoides</i>	V (4-5)	II (1-4)	II (1-3)	.	.	III
<i>Racomitrium lanuginosum</i>	++ (+1)	III (2-4)	I (1-3)	I (+-3)	.	III
<i>Calliergon stramineum</i>	.	.	I (+-3)	I (+-3)	I	III
<i>Archidium alternifolium</i>	.	III (1-4)	++ (1)	++ (1)	++ (1)	III
<i>Fossombronia wondraczekii</i>	.	.	II (1-4)	III (2-5)	.	III
<i>Campylopus subulatus</i>	.	++ (+-1)	.	+	I (+-2)	II
<i>Fossombronia foveolata</i>	.	+	.	.	I (1-2)	II
<i>Racomitrium elongatum</i>	II (1-3)	I
<i>Riccia beyrichiana</i>	.	+	++ (+-1)	.	.	I
<i>Lophozia sudetica</i>	++ (1)	.	++ (+-1)	.	.	I
<i>Polytrichum commune</i>	I (1-2)	.	I (1-3)	+	.	I
<i>Polytrichum piliferum</i>	I	.	.	.	++ (+-1)	I
<i>Scapania irrigua</i>	I (1-3)	I
<i>Conostomum tetragonum</i>	.	.	++ (+-1)	+	.	I

3.2.4 Hveragerði



Figure 3-4. Dry geothermal ground near Hveragerði

Extreme conditions for plants characterize the examined sites near Hveragerði: temperatures up to 81°C, a soil pH around 4,5 (minima of 3,1) and often dryness. Yet, there is a total of 13 bryophytes (no hepatics); around four per vegetation unit. From the five distinct units, nearly all had medium cover values of *Racomitrium elongatum* and *Rhytidiadelphus squarrosus*.

Unit 13, which has the lowest pH in the area (mean: 4,18) is predominated by *Polytrichum commune* and *Hypnum lindbergii*.

The most prominent feature of unit 14 are the high temperatures: an average of 63,76°C and peaks up to 81°C. Concerning the Hveragerði area, *Dicranum bonjeanii* and *Archidium alternifolium* are unique in this unit.

A slightly higher pH (mean: 5,42) and lower temperatures around 57°C are typical for unit 15. *Racomitrium ericoides* has a cover value of more than 50 percent, followed by *Hypnum hamulosum* and *Racomitrium elongatum*. In between this turf isolated plants of *Hylocomium splendens* were growing.

The conditions in the relevés of unit 16 are very similar to the ones in the preceding unit; still there are remarkable differences in the vegetation. *Hylocomium splendens*, *Racomitrium ericoides* and *Rhytidiadelphus squarrosus* nearly covered 100 percent

of the relevés. Single plants of *Ceratodon purpureus* were growing in this dense cover.

Unit 17 contains relevés that are in contrast to all other examined sites in this area, influenced by moderate amounts of steam from a neighbouring stream with warm water. The temperatures are relatively low (around 35°C) and the soil is acid (mean: 4,27). *Polytrichum commune*, *Hypnum lindbergii* and *Calliergonella lindbergii* built a dense turf. Few plants of *Racomitrium elongatum* and *Rhytidiadelphus squarrosus* were growing in the examined relevés.

Community	Racomitrium elongatum group			Rhytidiadelphus squarrosus group		Constancy class
	Hypnum lindbergii turf	Hypnum lindbergii-Dicranum bonjeanii turf	Raco.eric. - Hyp.hamu.-Hyl.spl. turf	Raco.eri.-Hylo.spl.-Call.lind. turf	Poly.com.-Hyp.call. turf	
Unit number	13	14	15	16	17	
Number of relevés	4	17	6	11	7	
Average number of species	3,5	4,23	4,83	4,27	3,29	
Humidity	n.s	n.s	n.s.	n.s.	s1	
pH (range)	4,0- 4,27	3,1-6,9	5,3-5,7	5,2-5,8	3,9-5,0	
pH (mean)	4,18	4,97	5,42	5,55	4,27	
Temperature d. (range)	36-68°C	54-81°C	51-62°C	54-67°C	35-37°C	
Temperature d. (mean)	57,25°C	63,76°C	57,33°C	56,72°C	35,71°C	
<i>Racomitrium elongatum</i>	II (1-3)	III (1-5)	III (1-4)	.	I (1-3)	IV
<i>Rhytidiadelphus squarrosus</i>	II (1-4)	I (+5)	.	II (+4)	I (1-2)	IV
<i>Hypnum lindbergii</i>	IV (2-4)	II (+-4)	.	.	.	III
<i>Dicranum bonjeanii</i>	.	I (+2)	.	.	.	II
<i>Hylocomium splendens</i>	.	.	I	III (1-5)	.	II
<i>Racomitrium ericoides</i>	.	.	V (4-5)	III (+5)	.	II
<i>Hypnum hamulosum</i>	.	+ (+-2)	II (1-2)	.	.	II
<i>Calliergonella lindbergii</i>	II (1-3)	II
<i>Hypnum callichroum</i>	I	.	.	.	II (1-3)	I
<i>Polytrichum commune</i>	V	.	.	.	III (1-5)	I
<i>Racomitrium lanuginosum</i>	.	.	I	.	.	I
<i>Archidium alternifolium</i>	.	+ (+-1)	.	.	.	I
<i>Ceratodon purpureus</i>	.	.	.	+ (+-1)	.	+

3.2.5 Reykjanes

All relevés in the Reykjanes area were influenced by steam and extraordinary high soil temperatures. Two community clusters with a total of nine mosses could be identified. Six relevés with a mean temperature of 60,5°C and mean pH of 5,4 were dominated by *Hypnum hamulosum*. *Racomitrium ericoides* and *Brachytecium salebrosum* also occurred with high cover values *Ceratodon purpureus* and *Polytrichum piliferum* were present in all relevés but only with low covering. A transition community in the same plot but with increased temperature and pH also had high cover values of *Hypnum hamulosum* and *Racomitrium ericoides*, but was lacking of the other species described above.

Five relevés in the neighbouring plot (unit 20) were less influenced by steam but had a slightly lower pH and an average temperature of even 70,8°C. Despite the heat the bryophyte cover was still nearly 100% with *Rhytidiadelphus squarrosus* as predominant species and lower cover values of *Brachytecium salebrosum*.

Table 3-6. Vegetation at Reykjanes

Community	Transition community				Hyp.ham.- Raco.eri.- Bra.sal.- poly.pili. turf	Rhytidiadelphus squarrosus- Hypnum lindbergii turf	Constancy class
Unit number	18				19	20	
Number of relevés	4				6	5	
Plot number	20				20	23	
Humidity	s2				s2	s1	
pH (range)	5,55	5,75	5,75	5,42	5,03-5,65	4,91-5,42	
pH (mean)	5,62				5,40	5,15	
Temperature (range)	62	68	68	58	54-66°C	69-76°C	
Temperature (mean)	64°C				60,5°C	70,8°C	
<i>Hypnum hamulosum</i>	V	V	V	IV	V (4-5)	.	IV
<i>Racomitrium ericoides</i>	II	II	III	IV	III (2-4)	.	IV
<i>Ceratodon purpureus</i>	.	.	+	.	I	.	III
<i>Polytrichum piliferum</i>	.	.	.	I	I (+-1)	.	III
<i>Brachytecium salebrosum</i>	II (1-3)	.	II
<i>Hypnum lindbergii</i>	II (1-3)	II
<i>Rhytidiadelphus squarrosus</i>	V	II
<i>Hylocomium splendens</i>	I	+
<i>Racomitrium lanuginosum</i>	.	.	I	.	.	.	+

3.2.6 Askja

The examined plots with their dry and medium warm conditions had a total of only three mosses with *Racomitrium ericoides* as the dominating species. Concerning the other species found in this area a change of the species composition dependent on the temperature is noticeable. In relevés with a mean temperature of 18°C also *Polytrichum alpinum*, a species which is usually not found in geothermal areas but for example in snow valleys, was present.

With increasing temperature *Polytrichum alpinum* became less and *Polytrichum piliferum* more important.

Table 3-7. Vegetation at Askja

Community	Racomitrium ericoides group			Constancy class
	Polytrichum alpinum	Polytrichum alpinum- Polytrichum piliferum	Polytrichum piliferum	
Unit number	21	22	23	
Number of relevés	2	3	3	
Plot number	25	25	26	
Humidity	n.s.	n.s.	n.s.	
Temperature (range)	18	17-20°C	28-48°C	
Temperature (mean)	18	18,33°C	37	
<i>Racomitrium ericoides</i>	IV (3-4)	IV (2-5)	V	V
<i>Polytrichum alpinum</i>	II (1-2)	I	+	V
<i>Polytrichum piliferum</i>	.	II (1-2)	I (1-2)	IV

3.2.7 Geysir

The examined area around Geysir had a total of six bryophyte species, all of them mosses. The growth conditions are nearly the same in the two distinguished units: temperatures around 40°C, the soil has a pH of approximately 5,5 and there is no humidity from neighbouring steam vents or only small amounts of steam, respectively.

The differences between the units are not the general occurrence of certain species (except *Aulacomnium palustre*), but the cover values of the single bryophytes.

In unit 24, which is slightly dryer than the relevés of the following unit, *Racomitrium ericoides* is the species with the highest cover values. In this turf also grows

Hylocomium splendens, *Rhytidiadelphus squarrosus*, *Racomitrium canescens* and only few plants of *Hypnum cupressiforme*.

In unit 25 the cover values of the single plants are contrary to ones in the preceeding unit. *Racomitrium canescens* is the predominant species; *Rhytidiadelphus squarrosus*, *Hypnum cupressiforme* and *Racomitrium ericoides* have medium cover values. *Hylocomium splendens* occurs only in the form of single plants in between the turf.

Table 3-8. Vegetation at Geysir

Community	Rac.eri.-Hylo.spl.-Rhy.sq. Group		Constancy class
	Rhytidiadelphus squarrosus turf	Racomitrium canescens- Rhytidiadelphus squarrosus-Hypnum cupressiforme- Aulacomnium palustre turf	
Unit number	24	25	
Number of relevés	7	5	
Humidity	n.s. (-s1)	s1	
pH (range)	5,60-6,11	4,72-5,65	
pH (mean)	5,88	5,40	
Temperature d (range)	34-44°C	38-43°C	
Temperature d (mean)	38,71°C	40,80°C	
<i>Hylocomium splendens</i>	II (1-2)	I (1-2)	V
<i>Racomitrium ericoides</i>	IV (2-5)	II (1-4)	V
<i>Rhytidiadelphus squarrosus</i>	I (+-4)	III (+-4)	V
<i>Racomitrium canescens</i>	I (3-4)	IV (3-4)	III
<i>Hypnum cupressiforme</i>	+ (2)	III (2-4)	III
<i>Aulacomnium palustre</i>	.	I (+-1)	III

3.2.8 Hveravellir



Figure 3-5. Bryophytes on the geothermal ground in Hveravellir

In total 12 bryophytes were recorded for the area, including nine mosses and three hepatics. The vegetation shows a basic species group, consisting of *Ditrichum lineare*, *Hylocomium pyrenaicum*, *Dicranum bonjeanii* and *Campylopus shimperii* occurring in both of the two distinct units.

The first unit comprises seven relevés with a low soil pH around 5,44 and a mean temperature of 39,43°C, all in a great distance to the next steam vent. In this unit the basic species group is predominated by *Ditrichum lineare* and *Campylopus shimperii*. Additionally there are lower cover values of *Racomitrium ericoides* and *Fossombronia wondraczekii*. In contrast to this unit, a second one with a nearly neutral soil pH and an increased soil temperature with around 63,5°C could be distinguished. Under these circumstances *Campylopus shimperii* lost cover values, whereas *Dicranum bonjeanii* got more important. *Campylium elodes* as well as *Philonotis fontana* occurred as well as a variety of companions, for example in the form of intermittent *Fossombronia wondraczekii* and *Riccardia chamaedrifolia* plants.

Table 3-9. Vegetation at Hveravellir

Community	Ditrichum lineare-group		Constancy class
	Racomitrium ericoides turf	Ph.fon.- Camp.elo.Foss.won.Ric.cha.	
Unit number	26	27	
Number of relevés	7	2	
Plot number	30	31	
Humidity	n.s. (s0)	s0	
pH (range)	4,93-5,95	7,07-7,17	
pH (mean)	5,44	7,12	
Temperature (range)	36-46°C	57-70°C	
Temperature (mean)	39,43°C	63,5	
<i>Ditrichum lineare</i>	IV (4-5)	III (2-4)	V
<i>Campylopus shimperii</i>	III (3-4)	+	V
<i>Hylocomium pyrenaicum</i>	I (+-1)	I (+-2)	V
<i>Dicranum bonjeanii</i>	I (+-1)	IV (3-4)	V
<i>Racomitrium ericoides</i>	II (1-5)	.	IV
<i>Fossombronia wondraczekii</i>	+ (1)	I	II
<i>Campylium elodes</i>	.	II	II
<i>Riccardia chamaedrifolia</i>	.	I	II
<i>Philonotis fontana</i>	.	II (1-3)	II
<i>Bryum bryoides</i>	.	I	I
<i>Pleurozium shreberi</i>	.	+	I
<i>Scapania irrigua</i>	.	+	I

3.3 Correlation between the parameter

With help of Statistica the correlation between the parameter surface temperature and temperature in a depth of three cm as well as possible correlation between the depth temperature and the pH was tested.

The correlation coefficient for the second test (temperature/pH) was only 0,0590, so there seems to be no correlation between these parameters.

In contrast to this the coefficient for the correlation between the temperature on the bryophyte surface and the temperature of the soil in a depth of three cm is 0,46433, so it's nearly significant. Reasons for this relatively low correlation, which are already given in the methods chapter, are influence of the changing intensity of the sun, and varying amounts of warm steam leaving the vent as well as the air temperatures, that despite summertime had a range of about 25°C.

Another factor could be the different thickness of the bryophyte cushion and hence the different isolation of the geothermal heat.

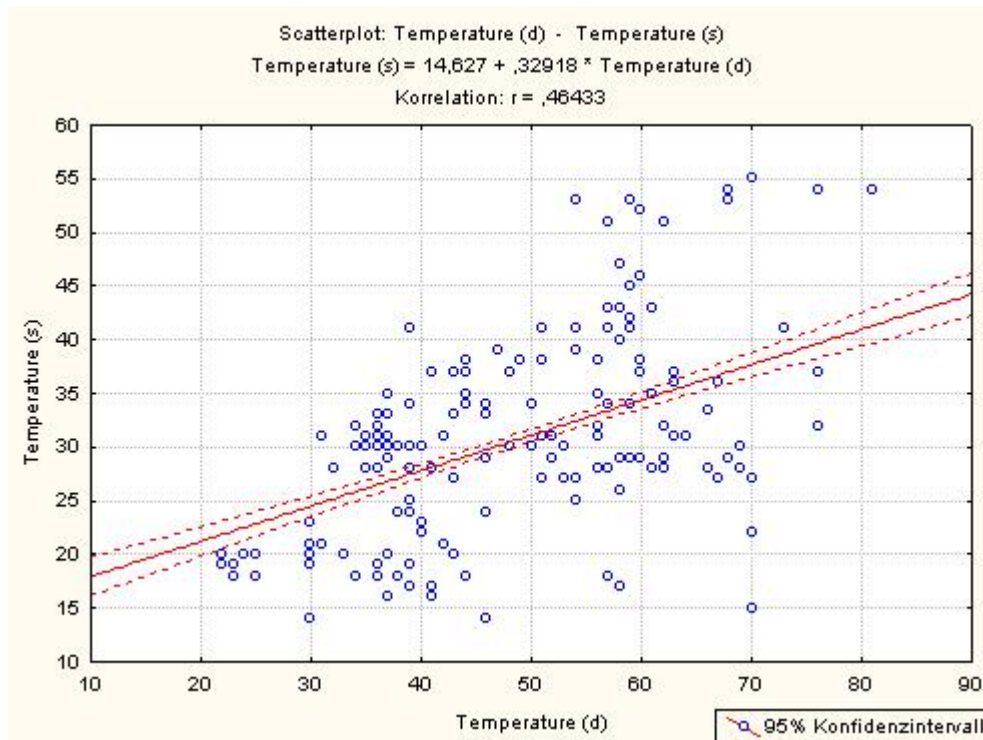


Figure 3-6. Relation between the surface temperature and the temperature in three cm depth

3.4 Relation between pH and species occurrence

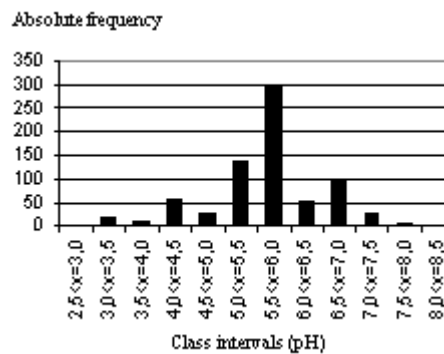


Figure 3-7. Absolute frequency of pH intervals

The soil pH in the examined areas with vegetation varies between a minimum of 3,14 for bryophytes like *Archidium alternifolium*, *Aulacomnium palustre* and some others and a maximum of 7,84 for example found on relevés with *Riccia beyrichiana* and *Preissia quadrata*. On average, *Racomitrium lanuginosum* with a mean of 4,23 was growing on the most acid relevés, whereas *Riccia sorrocarpa* is found in sites with the highest pH (mean of 6,32).

Figure 3-7. shows the absolute frequency of the different class intervals. In most cases the measured pH was slightly acid- most data is located in the range between 5,0 and 6,0.

Table 3-10. Minimum, maximum and mean of the pH, concerning the different species

	ph mean		ph min		ph max
<i>Racomitrium elongatum</i>	4,23	<i>Archidium alternifolium</i>	3,14	<i>Hypnum callichroum</i>	3,14
<i>Hypnum callichroum</i>	4,84	<i>Aulacomnium palustre</i>	3,14	<i>Polytrichum commune</i>	3,90
<i>Hypnum cupressiforme</i>	4,95	<i>Dicranum bonjeanii</i>	3,14	<i>Hypnum lindbergii</i>	5,56
<i>Brachytecium salebrosum</i>	5,10	<i>Fossombronia wondraczekii</i>	3,14	<i>Racomitrium elongatum</i>	5,65
<i>Conostomum tetragonum</i>	5,11	<i>Hypnum lindbergii</i>	3,14	<i>Racomitrium ericoides</i>	5,65
<i>Lophozia sudetica</i>	5,20	<i>Rhytidiadelphus squarrosus</i>	3,14	<i>Nardia scalaris</i>	5,65
<i>Nardia scalaris</i>	5,20	<i>Polytrichum commune</i>	3,90	<i>Rhytidiadelphus squarrosus</i>	5,65
<i>Polytrichum commune</i>	5,23	<i>Hypnum hamulosum</i>	4,27	<i>Dicranum bonjeanii</i>	5,65
<i>Calliergonella lindbergii</i>	5,28	<i>Atrichum angustatum</i>	4,49	<i>Lophozia sudetica</i>	5,82
<i>Fossombronia foveolata</i>	5,39	<i>Nardia scalaris</i>	4,49	<i>Brachytecium salebrosum</i>	5,87
<i>Racomitrium canescens</i>	5,44	<i>Racomitrium ericoides</i>	4,49	<i>Polytrichum piliferum</i>	6,12
<i>Gymnocolea inflata</i>	5,46	<i>Racomitrium lanuginosum</i>	4,58	<i>Hypnum cupressiforme</i>	6,13
<i>Hylocomium splendens</i>	5,54	<i>Racomitrium canescens</i>	4,72	<i>Hypnum hamulosum</i>	6,13
<i>Polytrichum piliferum</i>	5,56	<i>Ditrichum lineare</i>	4,93	<i>Racomitrium canescens</i>	6,33
<i>Polytrichum sexangulare</i>	5,57	<i>Campylopus introflexus</i>	4,98	<i>Fossombronia foveolata</i>	6,80
<i>Preissia quadrata</i>	5,60	<i>Polytrichum piliferum</i>	4,98	<i>Gymnocolea inflata</i>	6,80
<i>Atrichum angustatum</i>	5,60	<i>Hypnum callichroum</i>	4,99	<i>Philonotis fontana</i>	6,81
<i>Calliergon stramineum</i>	5,62	<i>Lophozia sudetica</i>	4,99	<i>Hylocomium splendens</i>	6,81
<i>Campylopus subulatus</i>	5,65	<i>Ditrichum plumbicula</i>	5,01	<i>Conostomum tetragonum</i>	6,81
<i>Racomitrium ericoides</i>	5,66	<i>Polytrichum alpinum</i>	5,01	<i>Aulacomnium palustre</i>	6,81
<i>Hypnum hamulosum</i>	5,71	<i>Brachytecium salebrosum</i>	5,03	<i>Archidium alternifolium</i>	6,84
<i>Archidium alternifolium</i>	5,72	<i>Ceratodon purpureus</i>	5,03	<i>Ceratodon purpureus</i>	6,86
<i>Hypnum lindbergii</i>	5,72	<i>Fossombronia foveolata</i>	5,05	<i>Ditrichum lineare</i>	6,86
<i>Rhytidiadelphus squarrosus</i>	5,76	<i>Riccia beyrichiana</i>	5,10	<i>Atrichum angustatum</i>	6,86
<i>Polytrichum alpinum</i>	5,79	<i>Calliergonella lindbergii</i>	5,22	<i>Riccia sorocarpa</i>	6,94
<i>Dicranum bonjeanii</i>	5,86	<i>Hylocomium splendens</i>	5,22	<i>Polytrichum alpinum</i>	7,17
<i>Ditrichum lineare</i>	5,88	<i>Philonotis fontana</i>	5,28	<i>Hylocomium pyrenaicum</i>	7,17
<i>Hylocomium pyrenaicum</i>	5,88	<i>Hylocomium pyrenaicum</i>	5,29	<i>Racomitrium lanuginosum</i>	7,17
<i>Scapania irrigua</i>	5,89	<i>Campylopus shimperii</i>	5,29	<i>Polytrichum sexangulare</i>	7,17
<i>Campylopus shimperii</i>	5,92	<i>Gymnocolea inflata</i>	5,31	<i>Campylopus shimperii</i>	7,17
<i>Campylopus introflexus</i>	5,99	<i>Polytrichum sexangulare</i>	5,31	<i>Campylopus introflexus</i>	7,36
<i>Ditrichum plumbicula</i>	5,99	<i>Hypnum cupressiforme</i>	5,40	<i>Fossombronia wondraczekii</i>	7,36
<i>Racomitrium lanuginosum</i>	6,00	<i>Campylopus subulatus</i>	5,45	<i>Calliergonella lindbergii</i>	7,36
<i>Riccia beyrichiana</i>	6,00	<i>Preissia quadrata</i>	5,47	<i>Calliergon stramineum</i>	7,36
<i>Aulacomnium palustre</i>	6,01	<i>Calliergon stramineum</i>	5,48	<i>Campylopus subulatus</i>	7,84
<i>Ceratodon purpureus</i>	6,05	<i>Scapania irrigua</i>	5,53	<i>Scapania irrigua</i>	7,84
<i>Fossombronia wondraczekii</i>	6,13	<i>Conostomum tetragonum</i>	5,65	<i>Ditrichum plumbicula</i>	7,84
<i>Philonotis fontana</i>	6,18	<i>Riccia sorocarpa</i>	5,98	<i>Preissia quadrata</i>	7,84
<i>Riccia sorocarpa</i>	6,32	<i>Racomitrium elongatum</i>	7,84	<i>Riccia beyrichiana</i>	7,84

3.5 Relation between temperature and species occurrence

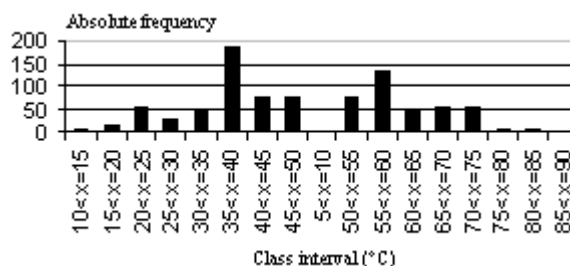


Figure 3-8. Absolute frequency of temperature intervals

The mean soil temperature in a depth of three cm varies between 27,17°C for *Gymnocolea inflata* and 64,96°C for *Hypnum lindbergii*. Despite a maximum temperature of 81°C, *Racomitrium elongatum* is still able to establish on the geothermal ground (Tab.3-11.). Like the absolute frequency of the different class intervals in Fig.3-8. shows that most bryophytes are found on soil with temperatures in between 35 and 40°C, another peak is reached for the interval 55-60°C. Only few plants are able to survive under conditions with temperatures above 75°C.

The low amount of plants growing on slightly warmer ground is influenced by the choice of habitats that were as extreme as possible, which changed the ratio of extraordinary warm to extraordinary moderate habitats examined.

Table 3-11. Mean and maxima of the soil temperature in a depth of three cm, concerning the different species.

	Temperature mean (°C)		Temperature max (°C)
<i>Gymnocolea inflata</i>	27,17	<i>Nardia scalaris</i>	34,00
<i>Polytrichum sexangulare</i>	27,33	<i>Hypnum callichroum</i>	37,00
<i>Nardia scalaris</i>	27,60	<i>Polytrichum sexangulare</i>	37,00
<i>Polytrichum alpinum</i>	30,38	<i>Lophozia sudetica</i>	39,00
<i>Lophozia sudetica</i>	30,67	<i>Polytrichum commune</i>	39,00
<i>Polytrichum commune</i>	35,07	<i>Hypnum cupressiforme</i>	43,00
<i>Hypnum callichroum</i>	35,75	<i>Conostomum tetragonum</i>	48,00
<i>Campylopus introflexus</i>	39,00	<i>Ditrichum plumbicula</i>	48,00
<i>Preissia quadrata</i>	39,50	<i>Gymnocolea inflata</i>	51,00
<i>Conostomum tetragonum</i>	40,00	<i>Polytrichum alpinum</i>	51,00
<i>Polytrichum piliferum</i>	40,14	<i>Preissia quadrata</i>	51,00
<i>Hypnum cupressiforme</i>	40,43	<i>Fossombronia foveolata</i>	53,00
<i>Fossombronia wondraczekii</i>	40,76	<i>Atrichum angustatum</i>	56,00
<i>Riccia sorocarpa</i>	40,89	<i>Calliergon stramineum</i>	56,00
<i>Atrichum angustatum</i>	41,00	<i>Campylopus subulatus</i>	56,00
<i>Racomitrium lanuginosum</i>	41,26	<i>Campylopus introflexus</i>	59,00

<i>Ditrichum plumbicula</i>	41,29	<i>Racomitrium canescens</i>	59,00
<i>Ditrichum lineare</i>	41,54	<i>Riccia beyrichiana</i>	59,00
<i>Calliergon stramineum</i>	42,00	<i>Riccia sorocarpa</i>	59,00
<i>Campylopus subulatus</i>	42,00	<i>Aulacomnium palustre</i>	60,00
<i>Fossombronia foveolata</i>	42,67	<i>Brachytecium salebrosum</i>	66,00
<i>Racomitrium ericoides</i>	43,62	<i>Polytrichum piliferum</i>	66,00
<i>Scapania irrigua</i>	45,29	<i>Calliergonella lindbergii</i>	67,00
<i>Aulacomnium palustre</i>	46,00	<i>Hylocomium splendens</i>	67,00
<i>Campylopus shimperii</i>	46,10	<i>Ceratodon purpureus</i>	68,00
<i>Archidium alternifolium</i>	46,22	<i>Hypnum hamulosum</i>	68,00
<i>Racomitrium canescens</i>	47,38	<i>Racomitrium ericoides</i>	68,00
<i>Hylocomium pyrenaicum</i>	48,00	<i>Racomitrium lanuginosum</i>	68,00
<i>Riccia beyrichiana</i>	48,10	<i>Ditrichum lineare</i>	70,00
<i>Hylocomium splendens</i>	50,06	<i>Fossombronia wondraczekii</i>	70,00
<i>Rhytidiadelphus squarrosus</i>	50,94	<i>Hylocomium pyrenaicum</i>	70,00
<i>Ceratodon purpureus</i>	52,01	<i>Philonotis fontana</i>	70,00
<i>Philonotis fontana</i>	53,64	<i>Scapania irrigua</i>	70,00
<i>Racomitrium elongatum</i>	55,77	<i>Campylopus shimperii</i>	70,00
<i>Calliergonella lindbergii</i>	57,00	<i>Rhytidiadelphus squarrosus</i>	76,00
<i>Dicranum bonjeanii</i>	57,94	<i>Archidium alternifolium</i>	81,00
<i>Brachytecium salebrosum</i>	59,00	<i>Dicranum bonjeanii</i>	81,00
<i>Hypnum hamulosum</i>	60,34	<i>Hypnum lindbergii</i>	81,00
<i>Hypnum lindbergii</i>	64,96	<i>Racomitrium elongatum</i>	81,00

3.6 Relation between humidity and species occurrence

Much of the examined geothermal vegetation was located near a steam vent. Hence not only temperature but the mutual effects of humidity and heat are important. The table below shows how numerous different species were in the respective humidity class. Like explained above the amount of steam is increasing from no steam (n.s.), over to places where obviously had been steam, that vanished because of changes in the geological activity (s0), to places near steam vents with different amounts of steam coming out of the vent (s1, s2, s3).

The species are listed according their occurrence in the different classes. On the top there are bryophytes which often occurred in areas with no steam. In contrast to this, the species listed at the bottom were usually found in relevés near to a steam vent with high amounts of water vapour.

Table 3-12. Frequency of the occurrence of species in the different humidity classes

Species	H.	n.s	s0	s1	s2	s3
<i>Calliergonella lindbergii</i>	?	11	0	0	0	0
<i>Dicranum bonjeanii</i>	w/m	25	4	3	0	0
<i>Campylopus shimperii</i>	d	6	4	0	0	0
<i>Hypnum lindbergii</i>	w/m	20	0	6	0	0
<i>Hylocomium splendens</i>	m/d	26	0	7	1	0
<i>Ditrichum lineare</i>	m	6	7	0	0	0

<i>Racomitrium elongatum</i>	?	31	0	11	0	0
<i>Hylocomium pyrenaicum</i>	d	5	4	2	0	0
<i>Rhytidiadelphus squarrosus</i>	m	29	0	20	0	0
<i>Campylium elodes</i>	w/m	0	3	0	0	0
<i>Pleurozium shreberi</i>	m/d	0	2	0	0	0
<i>Riccardia chamaedrifolia</i>	w/m	0	3	0	0	0
<i>Polytrichum alpinum</i>	d	7	0	1	4	0
<i>Hypnum hamulosum</i>	m	12	0	0	10	0
<i>Racomitrium ericoides</i>	d/m	48	1	11	18	12
<i>Campylopus introflexus</i>	d	0	6	3	1	0
<i>Archidium alternifolium</i>	w/m	15	0	2	7	6
<i>Scapania irrigua</i>	w/m	0	2	6	0	0
<i>Riccia sorocarpa</i>	m/d	0	3	5	1	0
<i>Fossombronina foveolata</i>	w/m	2	0	6	0	1
<i>Polytrichum piliferum</i>	d	6	3	3	10	0
<i>Philonotis fontana</i>	w	0	2	11	0	0
<i>Aulacomnium palustre</i>	w/m	0	0	12	0	0
<i>Drepanocladus aduncus</i>	w/m	0	0	1	0	0
<i>Hypnum callichroum</i>	m	0	0	8	0	0
<i>Hypnum cupressiforme</i>	m/d	0	0	6	0	0
<i>Racomitrium canescens</i>	m	0	0	14	0	0
<i>Ceratodon purpureus</i>	m/d	4	0	6	8	0
<i>Campylopus subulatus</i>	m/d	4	0	3	4	2
<i>Racomitrium lanuginosum</i>	m/d	16	2	3	19	12
<i>Riccia beyrichiana</i>	w/m	3	0	0	4	3
<i>Brachytecium salebrosum</i>	d	0	2	0	6	0
<i>Preissia quadrata</i>	m	0	0	4	4	0
<i>Ditrichum plumbicula</i>	m	0	0	1	5	0
<i>Polytrichum commune</i>	m	0	0	8	0	6
<i>Gymnocolea inflata</i>	m	0	0	0	6	0
<i>Polytrichum sexangulare</i>	w	0	0	0	6	0
<i>Fossombronina wondraczekii</i>	m/d	0	6	3	8	17
<i>Atrichum angustatum</i>	m	0	0	8	9	19
<i>Calliergon stramineum</i>	w/m	0	0	6	0	14
<i>Conostomum tetragonum</i>	?	0	0	0	0	6
<i>Lophozia sudetica</i>	m	0	0	0	0	6

According to the table there are species like e.g. *Calliergonella lindbergii*, *Dicranum bonjeanii* or *Hypnum lindbergii* that seem to be restricted to areas with no/not much steam. Some others occur in all classes, like *Racomitrium ericoides* and *Archidium alternifolium*, but do have their main habitat in dry areas. Species that seem to prefer a moderate amount of humidity in between the extremes of constant hot vapour and dryness are located in the middle and slightly below the middle of the table. Examples are *Aulacomnium palustre*, *Hypnum callichroum* or *Racomitrium canescens*. Some other species never were sampled in dry relevés, but seemingly preferred habitats near a vent (*Atrichum angustatum*, *Calliergon stramineum*, *Lophozia sudetica*). I

Additionally, the second column (H.) gives information about the conditions which are typical for the habitat of the certain species (Frahm 2004, Nyholm 1954): dry (**d**), moist (**m**) and wet (**w**).

In most cases the typical and observed conditions are congruent. *Calliergon stramineum* for example is supposed to grow in a moist or even wet surrounding. All 20 relevés in which it was growing were near a steam vent, most of them (14) even near a vent with high amounts of steam.

Species that grew under different conditions as expected are written in bold letters. *Dicranum bonjeanii* is usually found in wet or moist habitats, but the majority of geothermal areas where it was sampled were without neighbouring steam vent and hence rather dry. Another example is *Racomitrium lanuginosum*. Thick layers of this moss cover the lava fields in the south of Iceland where moderate rain is the only source of water, which seeps fast into the porous lava. In contrast to this, most relevés with *Racomitrium lanuginosum* were near very active steam vents.

3.7 Bryophytes along a warm stream in Reykjadalur



Figure 3-9. vegetation at the bank of a warm stream in Reykjadalur

Reykjadalur is located north of Hveragerði and hosts an approximately 40°C warm stream. The bank of this stream is very steep and strongly influenced by uprising water vapour. Because it was not possible to assess the vegetation properly, samples of bryophytes growing on the loamy slope were taken, in order to get an overview of

the species living in this habitat. Species found in this habitat were dense turfs of *Archidium alternifolium* as well as *Blasia pusilla* and *Marchantia alpestris* near the water line. Besides *Drepanocladus aduncus*, *Calypogeia muelleriana*, *Atrichum angustatum*, *Philonotis fontana*, *Philonotis tomentella*, *Fossombronia wondraczekii* and *Fossombronia foveolata* were sampled.

Remarkably many of these species occurred only in this extraordinary humid habitat and were not sampled in other plots. This is the case for *Blasia pusilla*, *Marchantia alpestris*, *Calypogeia muelleriana* and *Philonotis tomentella*.

3.8 *Non-bryophytes on the examined areas*

Although in many geothermal areas the majority of plants growing on the warm ground were bryophytes, often a few tracheophytes were able to survive in between the mosses. Very common on geothermal ground was *Thymus praecox ssp. arcticus*, a plant that is often found on sandy ground, heathland, dry meadows and on debris and walls of rock in Iceland (Kristinsson 1986). It often grew on around 5-10 % of the examined area, usually with blossoms.

Another plant, that was found on hot ground, especially on areas near Lake Mývatn was *Euphrasia frigida* that is also common on dry meadows on the whole Island and in most cases was blossoming, too.

Sagina procumbens was also quite common. It is usually found in riverbeds, on rocks and steep coast near the sea, as well as on humid soil near, for example nearby a spring (Kristinsson 1986).

Prunella vulgaris and *Saxifraga stellaris* occurred very seldom in some areas.

Interesting to observe was, that most tracheophytes on geothermal ground were growing in relatively moist areas near steam vents and not isolated, but in between the bryophytes.

Around the opening of the steam vent, where there is the permanent influence of hot water vapour, often thick layers of Cyanobacteria grew.

It was very remarkable, that lichens were never growing in the same area like bryophytes.

3.9 *Areas without vegetation*

Often there were areas with bare and strongly altered ground in the vicinity of bryophyte covered geothermal ground. In order to estimate the limitations of bryophyte growth, I measured temperature and pH in some of these areas.



Figure 3-10. Geothermal spot without vegetation near Hveragerði

Table 3-1. Parameter on vegetationless geothermal ground

	Range:	Mean:
Temperature (surface)	43-78°C	57,6°C
Temperature (deep)	39-113°C	78,2°C
pH	1,04-7,0	3,49

4 Discussion

4.1 General discussion of the species found

A wide range of different bryophyte taxa was among the sampled 56 species, growing on the examined areas; different concerning their general ecological demands, as well as their distribution.

Some species that occurred are typical generalists, like *Ceratodon purpureus*, others are- in Iceland limited to geothermal areas, which is the case for *Sphagnum palustre*. Like mentioned above, only 26 of the 56 examined taxa were so far described for geothermal habitats in contrast to some taxa like *Moerckia blytii*, which is exclusively found in snowvalleys. Many are typical pioneers on open ground (e.g. *Archidium alternifolium*), or usually grow in damp graslands, in swamps and bogs.

But remarkably all (except *Polytrichum commune*) were lacking sporophytes.

Additionally some taxa were found in areas for which they are not yet described.

4.1.1 Distribution

In comparison to the distribution maps of Bergþór Jóhannsson some bryophyte species seem to have established in new areas. The following list contains the spots that may be added to the already existing maps. The names of the place are according to the names of the examined areas, and represent only this small part and not the whole area the name generally stands for.

Species:	New area:
<i>Brachytecium salebrosum</i>	Reykjanes
<i>Campylopus shimperi</i>	Hveravellir
<i>Dicranum bonjeanii</i>	Leirhnúkur, Hveravellir, Hveragerði (Reykjadalur)
<i>Fossombronia wondraczekii</i>	Landmannalaugar
<i>Gymnocolea inflata</i>	Myvatn
<i>Hylocomium pyrenaicum</i>	Leirhnúkur, Hveravellir
<i>Hypnum hamulosum</i>	Reykjanes
<i>Pleurozium shreberi</i>	Hveravellir
<i>Racomitrium elongatum</i>	Leirhnúkur, Hveragerði (Reykjadalur)
<i>Riccia sorocarpa</i>	Mývatn, Leirhnúkur

Campylopus introflexus is a neophyte that was brought into England 1941; originally its distribution was limited to the southern hemisphere (Frahm 2004). Today *Campylopus introflexus* is especially found on open, sandy ground, peat and rotten wood in the oceanic part of Western Europe. To the east and higher up it occurs rather seldom (Frey 1995).

Bergþór Jóhannsson (1991) mentions that it was collected on warm soil at Mývatn by Hermann Muhle in the year 1983.

During my fieldwork plants of *Campylopus introflexus* were found as well on warm soil east of lake Mývatn and in no other geothermal area. At least concerning the areas that were examined the species doesn't seem to have spread much in the last twenty years

4.1.2 Relation between cold hardiness and thermostability

Looking at the extreme temperatures in the examined geothermal areas, one would rather expect to find taxa that usually occur more southward in warmer habitats and which are enabled to grow north of their general distribution because of the unique circumstances geothermal phenomena create. Instead many taxa are also found near glaciers in alpine regions, snowvalleys and other habitats that are characterized by extraordinary low temperatures.

First of all there seems to be no difference of hot desert (Volk 1959 unpublished), tropical (Biebl 1964), temperate (Clausen 1965, Diercksen 1964) and arctic species (Biebl 1968) concerning their heat-tolerance limits. Besides no differences of upper heat limits could be stated between hepatics and mosses, yet (Kappen 1983).

Glime (2007) mentions that for bryophytes (like it's the case for tracheophytes), there seems to be a relation between cold hardiness and thermostability. Precisely an increase in cold hardiness seems to be coupled with an increase in thermostability at temperatures above the optimum.

This may be an explanation for the simultaneous occurrence of taxa in very cold and very hot habitats, like it's the case for e.g. *Preissia quadrata*, *Lophozia sudetica*, *Cephalozia rubella* or *Racomitrium ericoides*.

4.1.3 Lack of sporophytes

Beside the influences of heat on the survival of the bryophytes in geothermal areas, the extraordinary temperatures seemed to influence the life cycle of the mosses as

well. Except *Polytrichum commune* on a moist and moderate warm plot near Hveragerði, all bryophytes in the examined geothermal areas were lacking sporophytes.

The fact that only few bryophytes on geothermal ground produce capsules was already stated by Glime (2007) and Skotnicki et al. (2002). The latter examined bryophytes in geothermal areas in the Antarctic and found out that vegetative growth and dispersal were typical mechanisms in contrast to sexual propagation.

Dietert (1980) discovered that for the development of gametangia a cooler temperature is required than it's the case for germination. Additionally Monroe (1965) found out that the production of sex organs is enhanced by low temperatures around 10°C.

So, if the heat on geothermal ground prevents the bryophytes from getting gametangia, consequently no sporophytes can be developed. But besides this, after a successful fertilization of gametangia, the sporophyte itself has certain requirements (Glime 2007). In experiments with *Physcomitrella*, Hohe et. al. (2002) found out, that the number of sporophytes correlates with temperature. Although 25°C were the optimum for vegetative growth, the highest number of sporophytes occurred when the temperature was only 15°C. Glime (2007) suggests that the lack of sporophytes under warm conditions is a mechanism to separate the several energy-requiring activities like growth or reproduction and thus make survivorship of the certain bryophytes possible.

4.2 Discussion of the vegetation patterns

Having an overall look at the vegetation in the different relevés, three different patterns according to height and share of mosses and liverworts with eleven subdivisions can roughly be distinguished. All relevés united in no. one are characterized by a very dense vegetation of relatively high bryophytes; the vast majority of them mosses. In the relevés summarized in no. two, the vegetation consists of medium high turfs with mosses and hepatics near steam vents. Mosses as well as hepatics also occurred in the relevés of no. three, but the vegetation was not arranged in certain belts around a steam vent like in no. two. Here rather homogenous vegetation was growing on dry and hot ground.

The numbers put in parenthesis are the group numbers that also occur in the vegetation tables above.

1. High turfs; mosses

1.1. Rhytidiadelphus-Hypnum group (20)

1.2. Racomitrium group

1.2.1 Racomitrium ericoides-Hylocomium splendens-Hypnum group (15, 16, 24, 25)

1.3. Racomitrium-Polytrichum group

1.3.1 Polytrichum-Hypnum group (13, 17, 19)

1.3.2. Racomitrium-Polytrichum group (21, 22, 23)

1.3.3. Polytrichum-Racomitrium-Campylopus group (3, 4)

2. Mixed turfs around steam vents, hepatics and mosses

2.1. Racomitrium-Archidum-Atrichum group (9, 10, 11, 12)

2.2. Racomitrium-Campylopus-Riccia group (1)

3. Low turfs near/without steam vents, hepatics and mosses

3.1. Ditrichum lineare group (2, 26, 27)

3.2. Philonotis fontana group

3.2.1. Philonotis-Ceratodon group (6, 7)

3.3.2. Philonotis-Aulacomnium group (5)

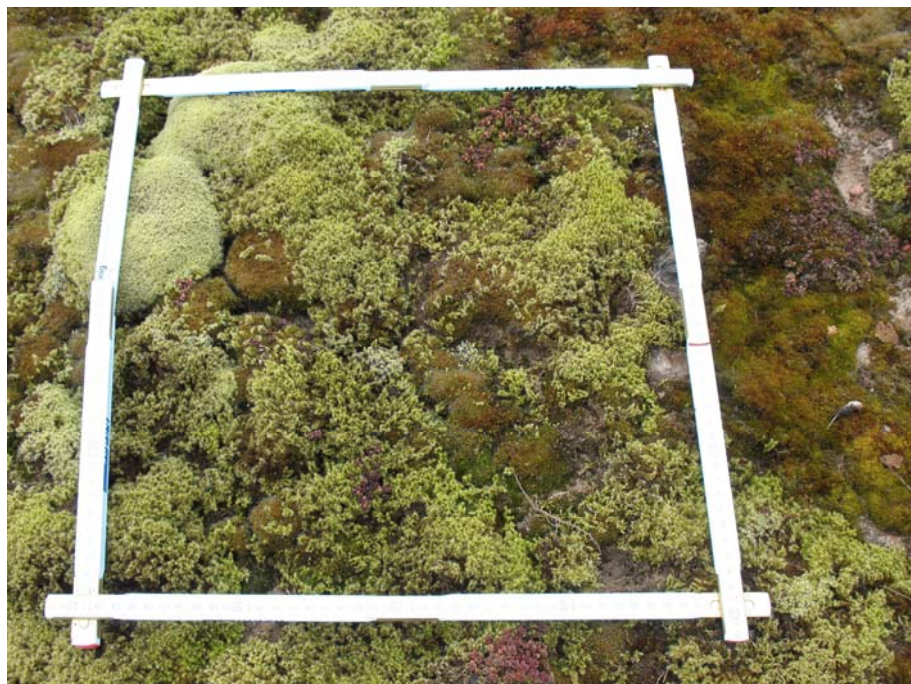


Figure 4-1. Relevé with high cover values of *Racomitrium* near Mývatn

4.2.1 Relation between vegetation patterns and parameters

Like seen above, concerning the bryophyte vegetation there was a distinct difference between three groups of geothermal bryophyte vegetation. First there is no. one with high turfs of mosses growing on rather dry ground. In these areas more or less homogenous vegetation with *Racomitrium*, *Polytrichum*, but also *Hypnum*, *Rhytidiadelphus* and *Hylocomium* was common. The high moss turfs were usually found in between meadows with rather dense vegetation. Although there was no visible difference between the conditions, in most cases some kind of a borderline around the bryophyte vegetation was distinct. Only sometimes transition communities of grass and bryophytes did exist. It made the impression that the heat in the soil beneath changed on such short distances, that the conditions were altered in a way that enabled bryophytes to compete with the usual vegetation. Enhanced dryness through increased temperatures together with the ability of the mosses to stand the dry conditions may be an explanation

In contrast to this, the groups belonging to no. two mostly unite relevés near a steam vent and show a diversity of mosses as well as hepatics. One thing has to be remarked concerning these relevés next to a vent: because of the shape and size of the relevé they usually contained more communities. This is caused by the nearness of different chemical and humidity conditions and hence the succeeding of different communities on small space, near a steam vent. Usually, next to the opening of a steam vent a layer of cyanobacteria was found, more distant, but still much influenced by heat and humidity, the first bryophytes, which often were *Fossombronia*, *Archidium* and *Riccia*, occurred. Often at distances of some ten cm *Campylopus*, *Atrichum* or *Polytrichum* were growing in between the smaller bryophytes mentioned above. Farthest away from the vent often a dense vegetation of *Polytrichum* and/or *Racomitrium* was examined. This observation is similar to the situation Glime (2008) outlines: Cyanobacteria grow in hot (and acidic) areas right next to the vent, followed by hepatics. According to her, mosses, sometimes together with shallow rooted grasses are common in the next zone. This outer zone of the vegetation around a steam vent is very similar to the one on dry geothermal ground, not influenced by steam. The low turfs around steam vents were often embedded in a landscape with very sparse, sometimes nearly no vegetation. Here, it seemed as if the steam is an advantage for the growth of plants because of the constant humidity in an otherwise very dry habitat.



Figure 4-2. Steam vent with *Fossombronia* and Cyanobacteria next to the opening of the vent and whitish cushions of *Racomitrium lanuginosum*

Another different type of vegetation is described in the groups of no. three. There the turfs were also very low and gappy, but in contrast to the bryophytes next to a steam vent, the vegetation was homogeneous and the ratio of mosses and hepatics was slightly different and more on the side of the mosses. Additionally to *Racomitrium*, *Riccia* and *Fossombronia*, taxa like *Philonotis*, *Ceratodon*, *Dicranum* and *Aulacomnium* occurred. The areas in which in this vegetation type was found, may best be characterized as some kind of volcanic deserts with generally only a few small plants growing on the bald ashes and clay. Although there were no visible steam vents, the bryophytes were clustered to several patches of vegetation. On the first sight differences concerning humidity, heat or sulphur content were not visible at these patches in contrast to the surrounding area.

So, it seems as if on the one hand the size of the bryophytes is somewhat important for their ability to withstand the extreme conditions on geothermal soil. On the other hand a different suitability for this habitat seems to exist in hepatics in contrast to mosses.

But do the conditions in the relevés of the different groups differ? In the table below, the average temperature and pH, as well as the distribution of the different humidity classes is given for the relevés of the three groups.

Table 4-1 Parameter in the different groups

	Low turfs	Mixed turfs	High turfs
No. of units	6	5	14
No. of relevés	25	39	88
Parameter:			
Mean Temperature	46,32°C	42,85	48,66
Mean pH	5,84	5,96	4,98
Humidity:			
n.s.	6	9	53
s0	7		
s1	11	7	18
s2	1	6	17
s3		17	

Concerning the temperature there are no great differences. The ground beneath mixed turfs was the coldest, slightly higher temperatures around 46°C were measured in relevés with low turfs. The dry geothermal areas with high moss turfs showed the highest temperatures.

The pH differs more significantly: the soil beneath the high turfs was by far the most acidic one, having an average pH of 4,98 in contrast to 5,96 for mixed and 5,84 for low turfs.

Another tendency can be assumed: low turfs are found on dry to slightly humid ground, whereas mixed turfs mostly grow next to active steam vents. Concerning the high turfs, most relevés had dry conditions. But the number of examined relevés is by far not sufficient to derive correlations that are universally valid.

4.2.2 Description of the groups

The differences concerning the species composition and parameters in the relevés of the proposed groups are described below. Additionally a short description of the general ecological demands and distribution of the taxa is added for every species, that hasn't already occurred in a group before. The information needed for this was taken from the descriptions of Frahm (2004), Jóhannsson (1989-2003) or Nyholm (1954).

1.1 Rhytidiadelphus-Hypnum group (20)

This vegetation with a dense turf, consisting only of *Rhytidiadelphus squarrosus* and *Hypnum lindbergii* was found in the Reykjanes area on extraordinary warm ground (mean of 63,76°C), an acidic pH around 5,15 and medium humidity (s1). *Hypnum lindbergii* is not very common in Iceland and typical for humid habitats along

streams, ponds and lakes or on moist meadows with slightly acidic soil. It occurs scattered in Eurasia and North-America.



Figure 4-3. *Rhytidiadelphus squarrosus*

Rhytidiadelphus squarrosus, a very common species in most parts of the northern hemisphere, also prefers humid grassy habitats. So the given circumstances at Reykjanes fit to their demands

Besides the examined sites at Askja, these relevés at Reykjanes had the lowest species diversity. This may be caused by the low diversity of microclimatic conditions: the ground was flat and without rocks, steam vents were only influencing the area from a distance.

1.2.1. *Racomitrium ericoides*-*Hylocomium splendens*-*Hypnum* group (15, 16, 24, 25)

In the geothermal area of Hveragerði as well as near Geysir very similar vegetation was found. Although the temperature in these relevés differs very much (34-67°C), all are rather dry and have a pH around 5,5. The most important species are *Racomitrium ericoides*, *Racomitrium canescens*, *Hylocomium splendens*, *Hypnum cupressiforme*, *Hypnum hamulosum* and *Rhytidiadelphus squarrosus*, with *Racomitrium* being the species, having the highest cover values.

Racomitrium ericoides is the most common species of the *Racomitrium* group in Iceland. It grows on rocks, lava, and lime free sand, near glaciers and in snowvalleys. In contrast to this, *Racomitrium canescens* is also found in geothermal areas next to steam vents and hot springs and is not as common as *R. ericoides*. *Racomitrium* (as

well as *Ceratodon purpureus*) seem to benefit from the open ground, created by disturbance in the thermal fields (Glime 2007). *Hylocomium splendens* is very common in Iceland and typical for grassland, forests, shrubs, rocks and lava. The distribution of the cosmopolitan *Hypnum cupressiforme* is limited to the oceanic areas. Typical habitats are rocks, lava, and sand. This is also the case for *Hypnum hamulosum*, a North-American/ Eurasian taxon, that's also found near the sea but not in the interior highlands of Iceland. Summarized more or less all species are common for dry grasslands like found in the examined areas.



Figure 4-4. Bryophyte community on dry geothermal ground near Hveragerði

1.3.1 Polytrichum-Hypnum group (13,17,19)

Besides *Rhytidiadelphus squarrosus* and *Racomitrium*, which seemed to be omnipresent in most examined geothermal areas; *Polytrichum* and *Hypnum* were found with high cover values in many relevés near Hveragerði and at Reykjanes. The pH on the relevés ranges from 3,9-5,65, the temperature from 35 up to 68°C. Additionally the humidity is not constant- some relevés of this group were influenced by much steam; some were dry with no neighbouring steam vent. Although the conditions differed so much, the vegetation was very similar. In unit 13 and 17 *Polytrichum commune* and *Hypnum lindbergii*/*Hypnum callichroum* have the highest cover values. Intermittent plants of *Rhytidiadelphus squarrosus* and *Racomitrium elongatum* occurred. In unit 19 the bryophyte composition was the same concerning

the genus, but the species differed: *Hypnum hamulosum*, *Racomitrium ericoides*, *Brachytecium salebrosum* and *Polytrichum piliferum* occurred. Additionally there were few plants of *Ceratodon purpureus*.

Concerning the general demands of the bryophytes which are not described so far: *Polytrichum commune*, an almost cosmopolitan species, is typical for humid sites, like swamps, bogs, and moist grasslands and also common near warm and hot springs. It's usually found in the more oceanic parts of Iceland and additionally in some clusters in the interior highlands. The cosmopolitan *Polytrichum piliferum* has a similar distribution on the island, but it's more common as a pioneer on sandy, dry and slightly acidic ground. *Hypnum callichroum* grows under more or less acidic and humid conditions on rocks and sand. In Iceland it's distributed only at a few spots, mainly near the coast in the western part of the island. *Racomitrium elongatum* prefers lime-free underground, especially clay, rocks, lava and is also found in grasslands and is rather sparse distributed in Iceland. *Brachytecium salebrosum* which grows on wood, soil and rather acidic rocks, especially in the northern hemisphere, is sparsely distributed all over Iceland. More common is *Ceratodon purpureus*, a cosmopolitan that's usually found on wood, soil and rock, among other habitats also on geothermal ground.

Keeping these general demands of the species in mind, it's interesting, that *Polytrichum commune* occurred in the dry relevés in contrast to *Polytrichum piliferum* that was found near an active steam vent; so contrary to their usual distribution. Concerning *Polytrichum commune* Glime (2007) had already stated that this species seems to prefer dryer habitats, when looking at geothermal areas, right in contrast to the general demands.

1.3.2. Racomitrium-Polytrichum group (21,22,23)

This group contains all units from the Askja area, all only with at most three species: *Racomitrium ericoides*, *Polytrichum alpinum* and *Polytrichum piliferum*. These bryophytes built a gappy patch of vegetation on the loose volcanic material in a nearly vegetationless and rather dry area. The relevés of the three units were all uninfluenced by steam, but slightly differed concerning their temperature. In unit 21, with a low soil temperature of 18°C, *Racomitrium ericoides* was predominant with intermittent plants of *Polytrichum alpinum*. Additionally *Polytrichum piliferum* grew on the relevés of unit 22 (18,3°C). In the last unit 23 *Racomitrium ericoides* and *Polytrichum piliferum* had the by far highest cover values and only a few single

plants of *Polytrichum alpinum* were found. But the correlation between the occurrence of *Polytrichum alpinum* and a lower soil temperature may be only coincidence, because this taxon was also found on warmer ground near Mývatn (unit 1).

In contrast to the *Polytrichum* species described yet, *Polytrichum alpinum* is a boreoalpine species widely distributed in Iceland. As this species is more typical for colder habitats like snowvalleys it's remarkable that it was growing on geothermal ground.

1.3.3. *Polytrichum-Racomitrium-Campylopus* group (3, 4)

On several relevés with a rather low temperature around 30°C, a slightly acidic soil and influenced by high amounts of steam a similar set of bryophytes was found. *Polytrichum sexangulare*, *Racomitrium lanuginosum* and *Campylopus introflexus* occurred in both units. In some relevés additionally *Racomitrium ericoides*, *Campylopus subulatus*, *Preissia quadrata* as well as *Gymnocola inflata* were growing. Like the in the group before, this vegetation was growing in a dry, sparsely vegetated area with loose volcanic ashes covering the ground. But in this case the vegetation was found along a cleft with huge amounts of escaping steam, so constant humidity could explain the occurrence of vegetation in an otherwise rather vegetationless site.

Concerning the general demands the arctic-alpine *Polytrichum sexangulare* is like *Polytrichum alpinum* a species that's typical for cooler areas where snow stays far into spring. The neophyte *Campylopus introflexus* and *Campylopus subulatus* are both rare in Iceland, the first occurring only near Lake Mývatn. Additionally both species are common on slightly acidic open soil and are already described for geothermal areas.

Unlike many other areas with high turfs, few hepatics grew in between the mosses in the relevés, belonging to this group. The Marchantiaceae *Preissia quadrata* is usually growing on loamy soil near lakes and warm springs and on wet rock in rather few places in Iceland. Glime and Iwatsuki (Glime 2007) examined this species in Iceland before and found a heat resistance of this species that is located between 41 and 48°C. Another species that's not very common and also found on clay near warm springs is *Gymnocola inflata*.

2.1. *Racomitrium-Archidum-Atrichum* group (9,10,11,12)

All relevés united in this group were examined in Landmannalaugar. Although the humidity ranges from no steam to very high amounts of steam, there are similarities: moderate temperatures around 45°C and a pH slightly below 6,0 (in unit 11 sometimes higher).

A high diversity of bryophytes is characteristic for the relevés belonging to this group. This may be caused by a great variety of available conditions near a steam vent and generally in this region: different surfaces from lava or clay to coarse grained soil many substrates are available. Furthermore different habitats concerning the humidity were close together, as well as a generally rather high amount of precipitation in this area.

The units ten and eleven were both next to a very active steam vent and their bryophyte vegetation are very similar. Unit twelve is near a less active vent, and the relevés of unit nine are not influenced by steam. But despite this difference, the species occurring in all four units are nearly the same, only the cover values of the different species vary. In the humid relevés hepatics are more dominant than they are in the dryer ones.

Bigger mosses, like *Racomitrium ericoides*, *R. elongatum*, *R. lanuginosum*, *Calliergon stramineum* and *Polytrichum commune* were growing farthest away from the opening of the steam vent. Next to the opening, where humidity and heat reach a maximum, especially hepatics like *Fossombronina foveolata*, *F. wondraczekii*, *Riccia beyrichiana*, *Lophozia sudetica* and *Scapania irrigua* were growing.



Figure 4-5. *Fossombronina* and *Riccia* near a steam vent

In between these zones, there is transition vegetation with intermittent plants of *Polytrichum piliferum*, *Atrichum angustatum*, *Archidium alternifolium*, *Campylopus subulatus*, *Conostomum tetragonum* and *Polytrichum piliferum* growing in the hepatics vegetation, mentioned before.

The Amblystegiaceae *Calliergon stramineum*, a species generally distributed in the northern hemisphere and South America, is found in Icelandic fens and swamps. *Fossombronia foveolata* is generally, found on acidic, muddy soil in Europe and North America and common in the surrounding vegetation of warm and hot springs in Iceland. The related *Fossombronia wondraczekii* is also found on moist geothermal ground near hot springs, but not as common as *F. foveolata*.

Riccia beyrichiana is a rare species, growing on wet and open ground, mostly in geothermal areas. Worldwide it's distributed in only in Europe and North America.

Another hepatic, *Lophozia sudetica* is a bryophyte that's widely distributed on lime free rocks lava and sand in Iceland and besides found in the northern hemisphere, especially in arctic-alpine areas. *Scapania irrigua*, found in boreal and arctic regions, is also growing in many areas in Iceland, especially those with moist clay, in swamps, fens and near hot springs. Concerning the general demands of the mosses, *Atrichum angustatum* prefers moist sand or loam. In Iceland, its distribution is limited on two geothermal areas in the interior highlands. Also found on geothermal ground is *Campylopus subulatus*. This species, generally distributed in Western Europe, Asia and North America is furthermore found in on loamy, lime free ground in few places in Iceland. *Conostomum tetragonum* is a north hemispherean species, found on damp soil and late snow patches and in alpine regions.

So, most of the taxa have general demands, that are congruent with the conditions in the examined areas, at least concerning the soil and humidity. But it's remarkable, that many bryophytes are typical for geothermal ground, but others are usually found in cold habitats, like late snow patches. It would be interesting to know, if humidity and open ground are perhaps more important for these species than cool temperatures in order to compete with other bryophytes.

3.1. *Ditrichum lineare* group (2, 26 ,27)

In this group three units from Hveravellir and the Mývatn area, respectively are combined. The parameter are ranging from slightly acidic to neutral concerning the pH and temperatures between 24 and 70°C were measured. Similar in all examined relevés is the dryness and a ceratain set of species occuring in all units. *Ditrichum*

lineare and *Fossombronia wondraczekii* as well as the genera *Campylopus* (*shimperii*/ *introflexus*) were found in all units. *Racomitrium* and *Dicranum bonjeanii* occur in two of the three units. Taxa occurring as companions in only some of the relevés are *Campylium elodes*, *Ditrichum plumbicola*, *Hylocomium pyrenaicum*, *Philonotis fontana*, *Pleurozium shreberi*, *Polytrichum piliferum*, *Polytrichum alpinum*, *Riccardia chamaedrifolia*, *Riccia beyrichiana*, *Riccia sorocarpa* and *Scapania irrigua*. So, this group is characterized by a high number of different taxa in one relevé, with some taxa occurring in most relevés, as well as typical dryness. Still the group is not as homogeneous as the others before.

Ditrichum lineare is a subarctic species in the northern hemisphere, that's growing in a few areas in Iceland, mainly on clay near hot and warm springs. The related *Ditrichum plumbicola* was first described on soil rich in heavy metals and is already listed for Iceland. *Dicranum bonjeanii*, distributed in humid habitats in the northern hemisphere, in Iceland is found in few places in wetlands and near hot springs. *Hylocomium pyrenaicum* distributed in alpine regions in the northern hemisphere is described for only two spots in North-Iceland, so far. In contrast to this *Philonotis fontana* is very common in Iceland, growing on damp soil near springs, rivers and lakes or on wet rock. Typical on acidic and damp to dry ground in woodland, grassland and on lava is *Pleurozium shreberi*. It's distributed in the northern hemisphere, especially in boreal woods, as well as in South America. In Iceland the majority of this bryophyte is growing in the west, north-west and east. *Campylium elodes* is a rare Eurasian species, growing on damp soil. Concerning the hepatics, *Riccardia chamaedrifolia*, a circumboreal species is found in few places in Iceland, usually submers or in fens. Also not very frequent in Iceland is the cosmopolitan *Riccia sorocarpa*, which is often found on sandy and loamy ground and also grows near hot springs.

Summarized the general demands of the species fit to the examined conditions. The occurrence of *Philonotis fontana* is remarkable, because this species was found on dry and extraordinary warm ground, although it usually grows near cold springs. Additionally *Riccardia chamaedrifolia* was growing under dry condition, in contrast to its usual needs of high humidity. Perhaps the microclimate inbetween the other bryophytes is more humid than the general one. An indication for a possibly higher content of heavy metals in the examined geothermal area near Lake Mývatn gives the occurrence of *Ditrichum plumbicola*.

3.2.1 Philonotis-Ceratodon group (6, 7)

The two units of this group both contain relevés from the Leirhnúkur area that are influenced by moderate amounts of steam (s1). The temperature ranges from 44 to 59°C and the pH from slightly acidic to neutral. In unit six and seven, the bryophytes were growing in depressions in an almost vegetationless hill with strongly altered soil, containing sulphur. With increasing cover values the following bryophytes are found in both units: *Philonotis fontana*, *Ceratodon purpureus*, *Racomitrium canescens*, *Riccia sorocarpa*, *Preissia quadrata*, *Fossombonia wondraczekii* and *Dicranum bonjeanii*. In unit seven additionally *Racomitrium ericoides* was found; in unit six *Aulacomnium palustre* had high cover values and *Drepanocladus aduncus* as well as *Racomitrium elongatum* occurred. The mosses built a low and gappy turf; the hepatics were growing in the gaps with bare soil.

The general demands of *Aulacomnium palustre* do not completely fit to the examined conditions. Usually this moss is found in wetlands, swamps and bogs, so under more humid conditions than at Leirhnúkur. *Aulacomnium palustre* is distributed in boreal and temperate regions on the northern as well as on the southern hemisphere and quiet common in Iceland. Also common is *Drepanocladus aduncus*, which is distributed nearly worldwide in wetlands at the shore of lakes and riverbanks.

In this group *Philonotis fontana* occurs again, although the conditions seemed to be too dry compared with its general demands.



Figure 4-6. Depression with bryophytes at Leirhnúkur

3.2.3. *Philonotis-Aulacomnium* group (5)

In unit five, which also contains relevés from the same hill at the Leirhnúkur area, the missing of some taxa gave reason to build another group apart of unit six and seven. In the relevés of this group a moderate humidity, temperatures around 54°C and a pH slightly above 5,5 was examined. The highest cover values do have *Philonotis fontana*, *Aulacomnium palustre* and *Racomitrium canescens*. Additionally *Preissia quadrata*, *Racomitrium ericoides*, *Hylocomium pyrenaicum* and *Dicranum bonjeanii* occurred.

With *Aulacomnium palustre* and *Philonotis fontana* again two species occur, that usually are growing in more humid habitats.

4.3 Outlook

Although research on the topic of bryophytes in geothermal areas has been done in the past and the vegetation of these special habitats in Iceland is examined by Àsrun Elmarsdóttir et al. in a current project, still a lot of questions are not settled, yet.

The extraordinary heat presumably has effects on all stages of the life cycle. In contrast to full-grown bryophytes, the younger stages in development are not able to insulate themselves with dead, lower parts against the harmful heat. Additionally most mosses and hepatics lack sporophytes. Hence it would be interesting to know on the one hand, if the bryophyte populations on geothermal heated ground need to be renewed by vegetative parts of bryophytes in the surrounding vegetation and on the other hand how spores manage to germinate and how protonemata survive under these conditions. Perhaps the cool above ground air temperatures in Iceland as well as cooling in winter and during rainfalls help to alter the temperature in a way that enables these fragile stages to survive.

Besides it's remarkable that many bryophytes were found in areas with simultaneous influence of heat and humidity. Usually mosses and hepatics are much more heat tolerant in a desiccated state than in a moistened one (Frahm 2001). Since these conditions are more or less permanent, the plants have to survive and even grow despite these stresses. Perhaps the activity of the steam vents changes with time, but still the mechanisms used to survive the moist heat would be interesting to know.

Concerning the distribution of the different taxa, it could be worthwhile to make an overall examination of the geothermal areas in Iceland and other countries to improve the knowledge about worldwide similarities, growth conditions, the

occurrence of communities and other phenomena. Long time measurements of temperature, humidity as well as of the chemistry of soil and steam would help to find reliable correlations between the different parameter and the occurrence of certain taxa and communities, respectively.

4.4 Endangering of geothermal vegetation

Beside the fact that geological processes can change the conditions for plants in geothermal areas there is another potential source of harm for the vegetation: geothermal utilization.

Geothermal utilization: today geothermal energy provides Iceland with 53% of the total energy consumption of the country (Kristmannsdóttir 2003). The other half is divided between hydropower and fossil fuel. Large scale utilization of geothermal energy for space heating started in the nineteen forties. Industrial utilization on larger scales includes a factory that dries and cleans diatomaceous slurry as well as a factory that uses the energy in order to dry seaweed for alginate production. More obvious is the use for agriculture: vegetables and flowers are cultivated on nearly 140.000 m² of geothermal heated greenhouses. Besides geothermal water and steam is utilized for other purposes, like fish hatching and drying, wool washing (Fridleifsson 1979).

Geothermal energy is considered to be a clean and sustainable energy source, although it has some aspects with a negative impact on the environment. Surface disturbances can occur because of drilling, excavations, during the construction and as a result of new roads that are built. As physical effects, land subsidence and lowering of the groundwater can be caused by water withdrawal. The huge amounts of waste water can also cause problems. Chemical pollution can occur in different ways: by spray during the construction as well as by chemicals that are discharged to the atmosphere via steam. Additionally chemicals like heavy metals, hydrogen sulphide, arsenic, ammonia and aluminium may be dissolved in liquid fractions in harmful concentrations. All this factors may cause negative biological effects (Kristmannsdóttir 2003).



Figure 4-7. The geothermal plant near Krafla

Tourists. Often geothermal areas are of unique beauty or of historical interest and hence are tourist attractions. Although many areas are fenced off because of their sensitivity and the endangering of humans by chemicals, heat and thin soil, still a lot of people leave the marked paths and step on the thin plant cover and may harm it in this way.

5 Summary

Created by geological processes and occurring in many parts of the world, geothermal areas stand out as a very unusual habitat. Plants have to cope with extraordinary high temperatures, often combined with constant humidity from a steam vent nearby. Additionally, the chemical conditions are often characterized by high concentrations of sulphur and heavy metals as well as a pH that may range from very acid to alkaline. This variety of influences make geothermal areas to one of the few bryophyte-dominated habitats. The fact, that mosses and liverworts predominate these extreme areas, could be explained with their poikilohydric character, their ability to insulate themselves against the heat, higher temperature limits and the high regenerative capacity of bryophytes as well as some phenomena that are not yet solved.

With this diploma thesis the bryophyte diversity and possible correlations with temperature, pH and humidity in Icelandic geothermal areas were examined.

In a total of 177 relevés in eight different regions 56 different bryophyte species were sampled, including 40 mosses and 16 hepatics. Remarkable is that 26 of these taxa are more or less typical for geothermal areas in contrast to 30 that thrive in other habitats. Despite of the extreme conditions, the majority of bryophytes was very vital, but all (except *Polytrichum commune*) were lacking sporophytes.

Three different patterns with eleven subgroups are suggested. Number one is characterized by high and homogeneous turfs of mosses like *Racomitrium*, *Hypnum*, *Rhytidiadelphus*, *Polytrichum* and *Hylocomium*. The relevés united in this group were often very warm, dry and mostly not influenced by steam vents. In contrast to this, the vegetation of number two was usually located around or near steam vents. Cyanobacteria were growing in the hottest area next to the opening of the vent, followed by a gappy vegetation of small hepatics like *Fossombronia* and *Riccia* as well as intermittent mosses (e.g. *Campylopus*, *Archidium*, *Atrichum*, *Polytrichum*). Farthest away from the influences of the hot steam a dense turf of mosses similar to the number one was growing.

A medium high turf of mosses and hepatics with a remarkable diversity of species was growing on the relevés summarized in group number three. The characteristic taxa were *Ditrichum*, *Fossombronia*, *Campylopus* and *Dicranum*.

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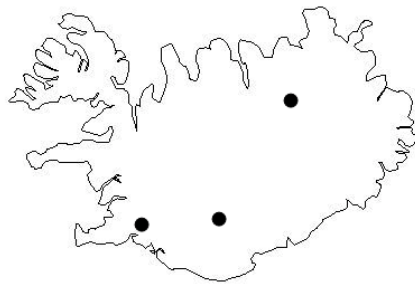
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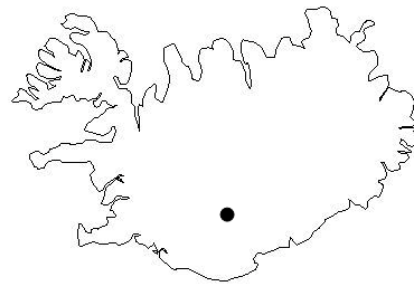
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8 Appendix

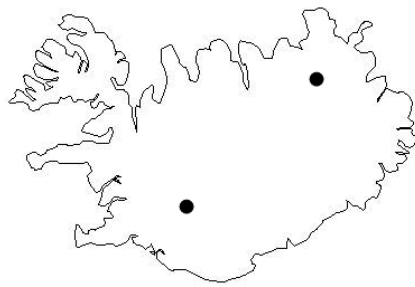
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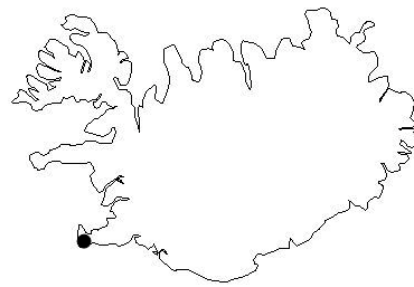
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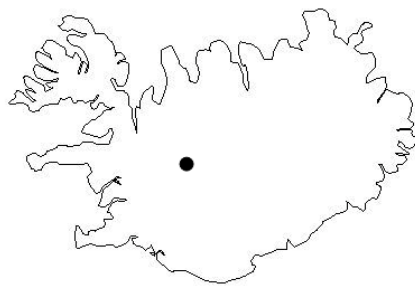
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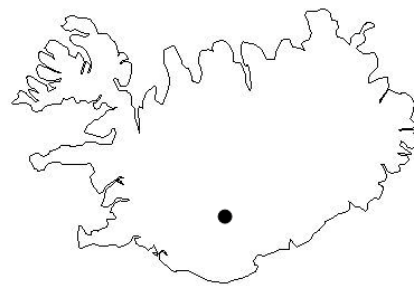
Aulacomnium palustre



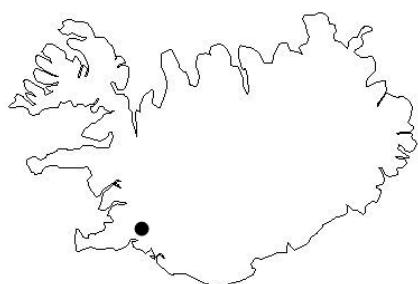
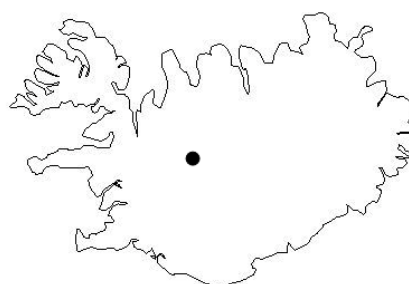
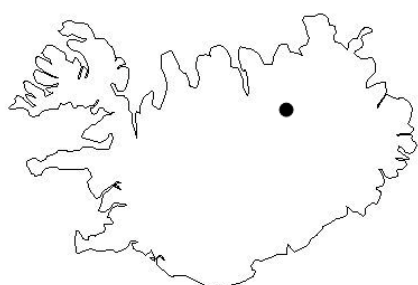
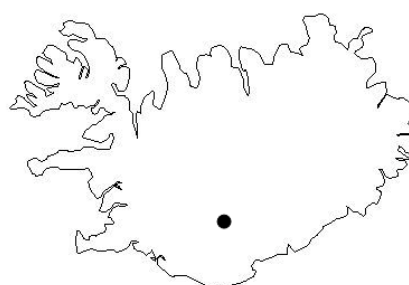
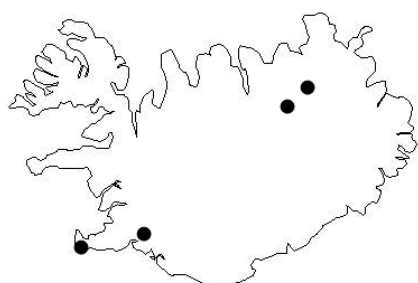
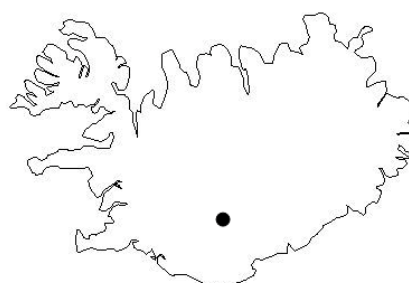
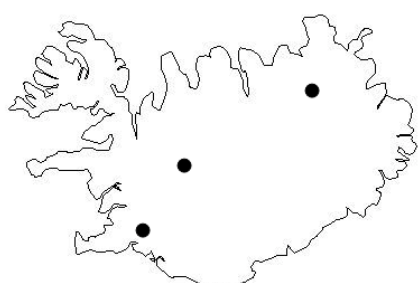
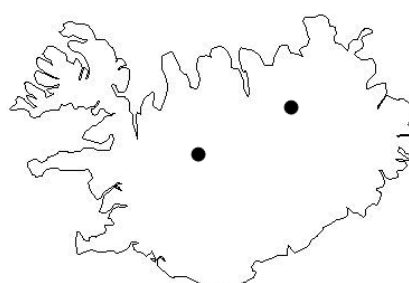
Brachytecium salebrosum

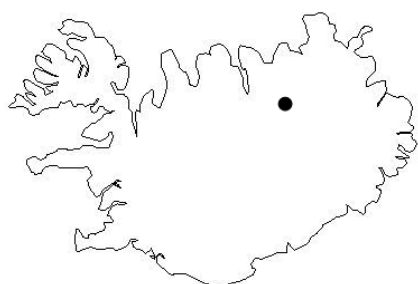


Bryum bryoides

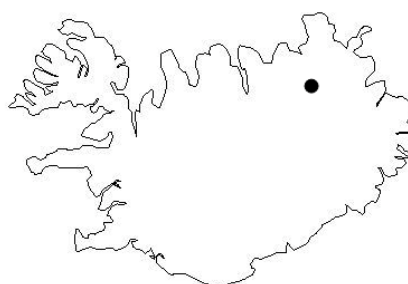


Calliergon stramineum

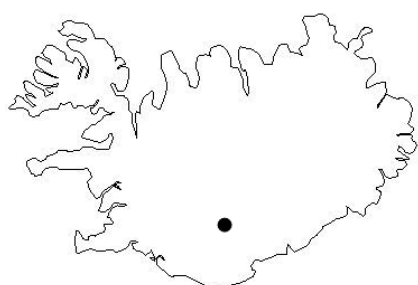
*Calliergonella lindbergii**Campylium elodes**Campylopus introflexus**Campylopus subulatus**Ceratodon purpureus**Conostomum tetragonum**Dicranum bonjeanii**Ditrichum lineare*



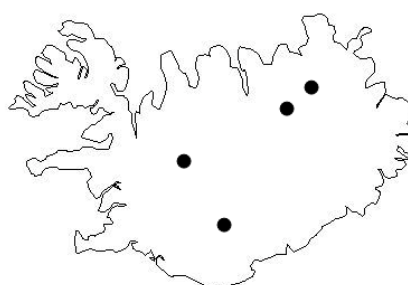
Ditrichum plumbicula



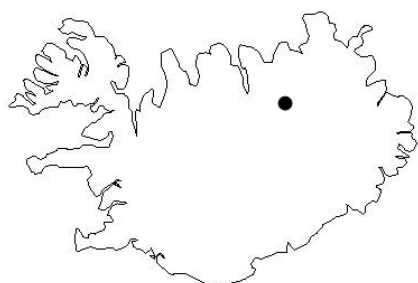
Drepanocladus aduncus



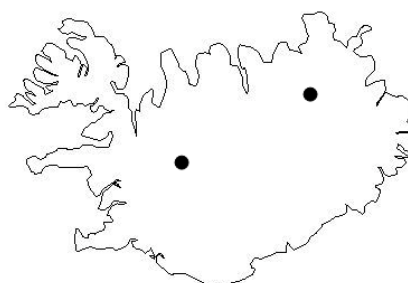
Fossombronia foveolata



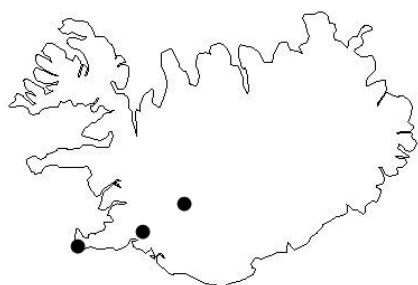
Fossombronia wondraczekii



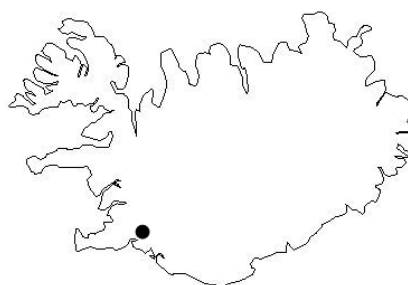
Gymnocolea inflata



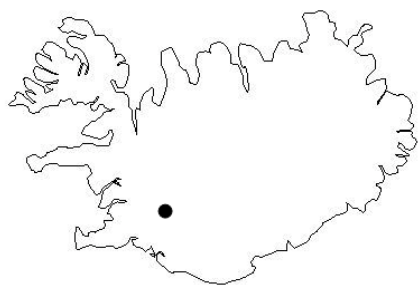
Hylocomium pyrenaicum



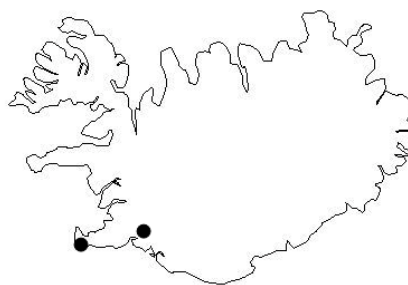
Hylocomium splendens



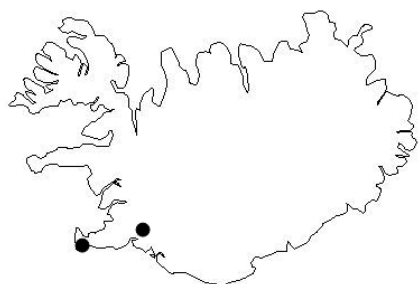
Hypnum callichroum



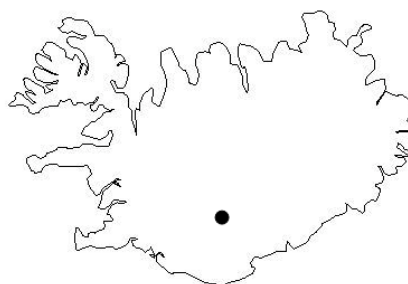
Hypnum cupressiforme



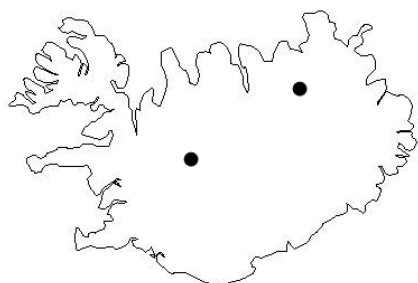
Hypnum hamulosum



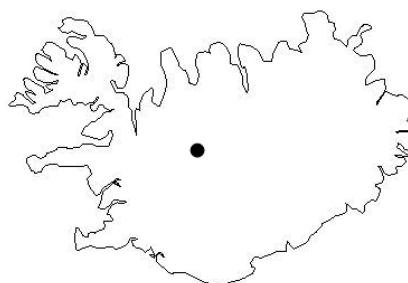
Hypnum lindbergii



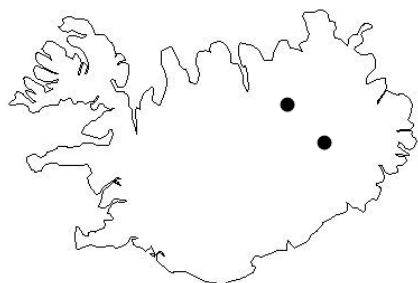
Lophozia sudetica



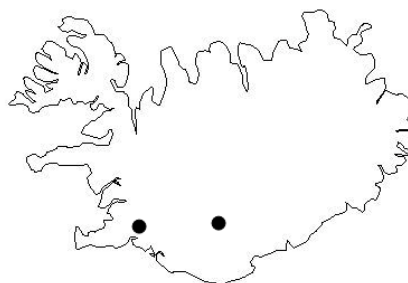
Philonotis fontana



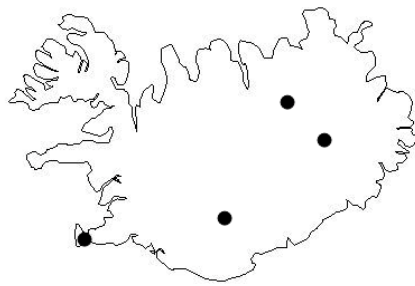
Pleurozium shreberi



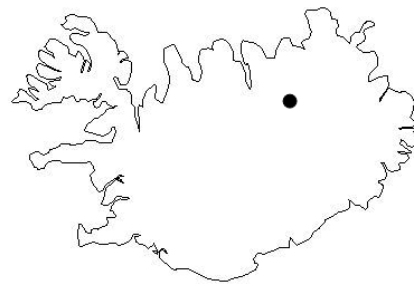
Polytrichum alpinum



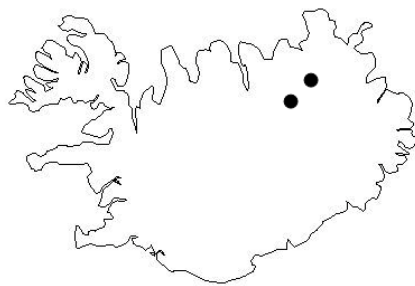
Polytrichum commune



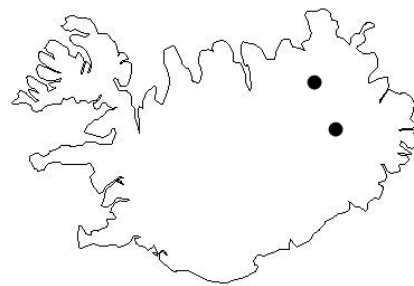
Polytrichum piliferum



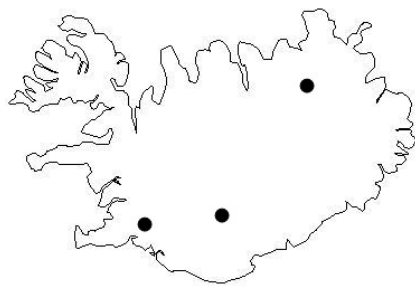
Polytrichum sexangulare



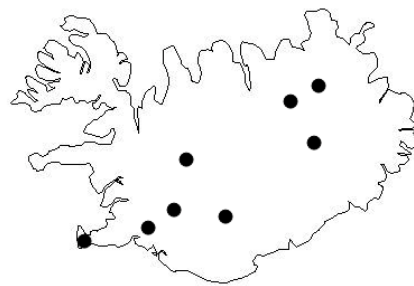
Preissia quadrata



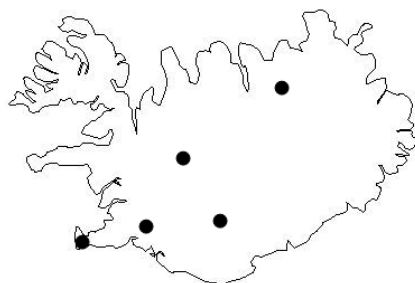
Racomitrium canescens



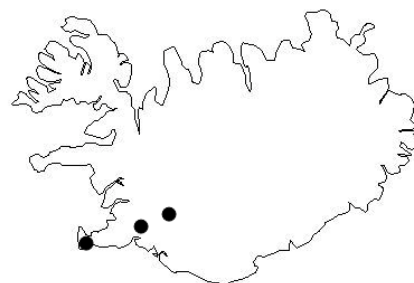
Racomitrium elongatum



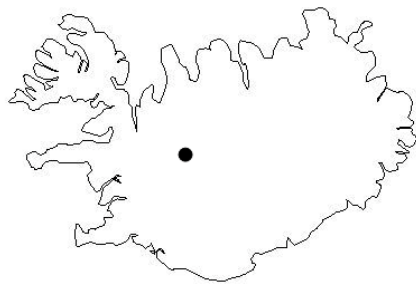
Racomitrium ericoides



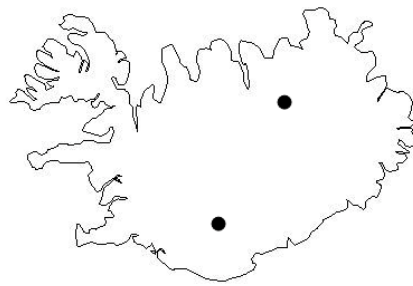
Racomitrium lanuginosum



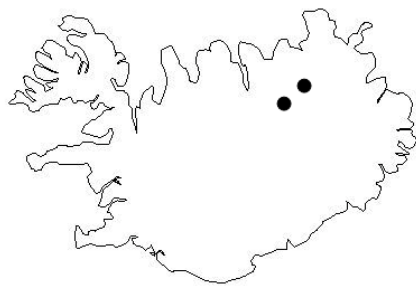
Rhytidiadelphus squarrosus



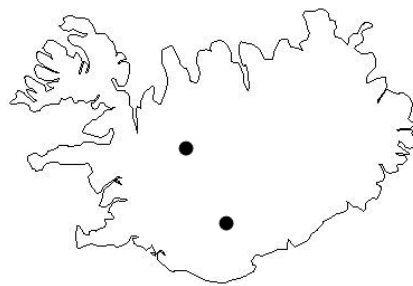
Riccardia chamaedrifolia



Riccia beyrichiana



Riccia sorocarpa



Scapania irrigua

Icelandic geothermal bryophyte species

In the following list all species that occur on geothermal heated ground as well as near hot springs and steam vents in Iceland are mentioned. Data is according to Bergþór Jóhannsson.

The species written in bold letters are bryophytes that were found during field work for the diploma thesis.

Archidium alternifolium

Blasia pusilla

Barbula fallax, B.icmadophila, B.unguiculata

Brachytecium mildeanum, B. turgidum

Bryum bicolor, B.klinggraffii, B.marratii, B.mikroerythrocarpum, B.pallens, B.sauteri, B.tenuisetum, B.violaceum

Calypogeia fissa, C.muelleriana

Campylopus introflexus, C.flexuosus, C.pyriformis

Cephalozia bicuspidate

Cephaloziella dentate

Ceratodon purpureus

Cladopodiella francisci

Dicranella heteromalla, D.rufescens, D.varia

Dicranum angustatum

Ditrichum lineare, D.cylindricum, D.heteromallum

Fissidens osmundoides, F.dubius, F.adianthoides

Fossombronia foveolata, **F.wondraczekii**

Funaria attenuate, F.obtusa

Gymnocolea inflata

Hypnum jutlandicum

Jungermannia caespiticia, J.gracilima, J.hyalina

Leicolea badensis

Leptobryum piriforme

Marchantia polymorpha

Marsupella funckii, M.spiniloba

Nardia scalaris

Odontoschisma elongatum

Pellia endiviifolia, P. neesiana

Phaeceros carolinianus

Philonotis tomentella, P. carspitosa, P. marchia

Pohlia annotina, P. bulbifera, P. nutans

Preissia quadrata

Racomitrium canescens, R. elongatum

Riccardia multifidae

Riccia beyrichiana, R. sorocarpa, R. cavernosa

Scapania irrigua, S. mucronata

Sphagnum palustre, S. angustifolium, S. capillifolium, S. compactum, S. contortum,
S. denticulatum, S. fimbriatum, S. girgensohnii, S. magellanicum, S. recurvum

Trichostomum brachydontium

Warnstorfia fluitane

Weissia controversa