

Studies in the nitrogen cycle of Surtsey in 1972

By

LARS ERIC HENRIKSSON

and

ELISABET HENRIKSSON

Institute of Physiological Botany of the University of Uppsala,
S-751 21 Uppsala, Sweden.

INTRODUCTION

Blue-green algae with ability to fix nitrogen seem to have good qualifications for growth on Surtsey, owing to the low content of bound nitrogen and organic substances in the lava and tephra sand of this island. Behre and Schwabe have confirmed in several investigations that blue-green algae are among the first pioneers (Behre and Schwabe 1970, Schwabe 1970 a, 1970 b, 1971, 1974, Schwabe and Behre 1972). Their results also support the opinion that most of the blue-green algae are cosmopolites and are easily dispersed by water, air, and animals (Fogg et al. 1973). Biological nitrogen fixation in soil samples from Surtsey has been demonstrated, and the algae involved were species of *Anabaena*, *Nodularia*, *Nostoc*, and *Tolypothrix* (Henriksson et al. 1972 b).

In order to determine the biological nitrogen fixation *in situ*, the authors visited Surtsey on July 5-10, 1972. At that time soil samples also were taken from the locations studied and from some other sites as well, for the purpose of investigation in the laboratory of other activities in the inorganic nitrogen cycle, specially microbial nitrification and denitrification. In addition, the amount of nitrogen available for other plants was analysed. Special interest was also paid to the occurrence of nitrogen fixing blue-green algae and *Azotobacter*. The locations mentioned in this paper are plotted in Figure 1, and the descriptions of them are found in Table 1. The same sites and soil samples were also used for studies of the terrestrial fungi (Henriksson and Henriksson 1974) and of the terrestrial microfauna (Holmberg and Pejler 1974).

In this paper, nitrogen fixation on Surtsey is compared with nitrogen fixation in some other Icelandic volcanic areas (Hekla), and in Swedish uncultivated and cultivated fields (Uppland). The chemical characteristics of the soil of Surtsey are also compared with those from Swedish wheat fields.

The microflora of Surtsey, including algae, fungi, and bacteria, has been studied also by Brock (1972, 1973) and Schwartz and Schwartz (1972). Some of their results are discussed in this paper.

MATERIAL AND METHODS

Samplings

The soil samples were aseptically deposited in small sterilized plastic capsules (Cerbo, Sweden, No. 18010) of 20 ml volumes with sample spoons attached inside the screwcaps. One spoonful of lava or tephra sand was found to be equivalent to about 0.5 g. Four spoon samples from 5 spots of the surface layer of each site (about 1 m²) were put in the plastic capsules and carefully mixed.

With respect to the very limited number of higher plants on the island, the rhizosphere of only one plant was examined (locality No. 13). The occurrence of the microorganisms studied, was also tested in the vicinity and on the surface of stranded wood in the lowland of Surtsey (localities No. 6, 8, and 11). In addition, samplings were made outside and inside two caves (localities No. 9, 10, 15, and 16). In the cave, "The Bell" (locality No. 16), thermophilic species of the microflora have been verified (Castenholtz 1972, Schwabe 1974).

The enrichment tests started in the laboratory one week after the samplings. In the meantime

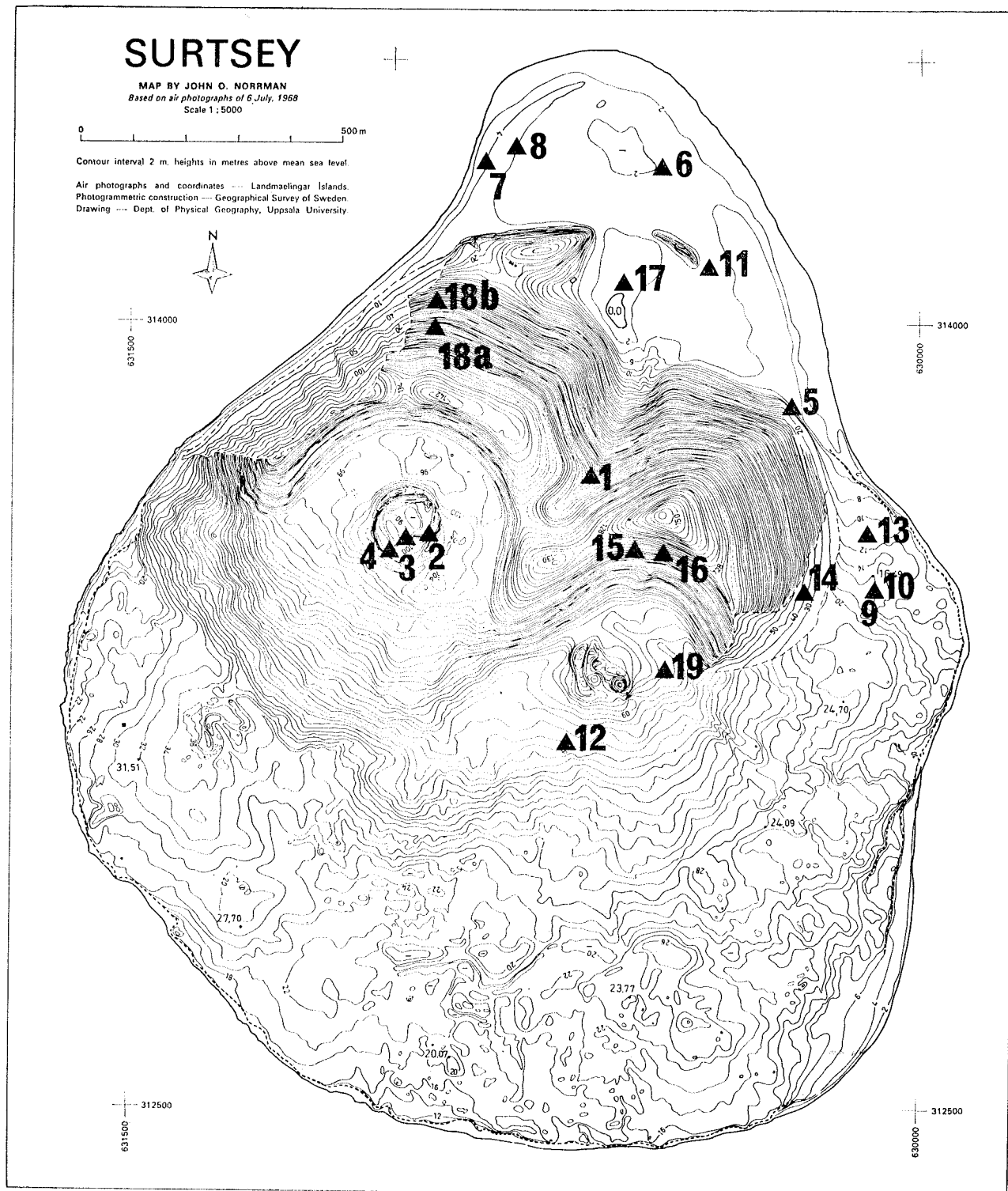


Figure 1. The symbols show the locations for the samplings and the nitrogen fixing experiments *in situ*, July 1972. — Map of Surtsey by John O. Norrman, Uppsala.

TABLE 1

Sample location No.	ng N ₂ fixed cm ⁻² h ⁻¹ Mean of 9 samples	Occurrence of				Description of the locations and temperature and light conditions at time of sampling and during the <i>in situ</i> experiments
		nitrogen fixing blue-green algae	<i>Azoto-bacter</i>	nitrifying organisms	denitrifying organisms	
1	2.1 ± 0.2	—	—	+	+	Light-colored tephra, green-colored surface (olivine). Moist. Soil temp. 42°C, 24500 Lux.
2	5.5 ± 0.3	<i>N. musc.</i>	—	+	+	Crater border. Sparsely moss-covered. Black soil. Rather moist. Soil temp. 42°C, 26000 Lux.
3	2.0 ± 1.2	<i>N. musc.</i>	—	+	+	Crater border. Sparsely moss-covered. Salt crystals. Rather moist. Soil temp. 42°C, 28000 Lux.
4	11.7 ± 2.9	<i>N. musc.</i>	—	+	+	Crater border. Sparsely moss-covered. Black soil. Steam. Rather moist. Soil temp. 28°C, 34000 Lux.
5	0.2 ± 0.0	—	—	—	+	Rock-wall. Light colored lava. Soil temp. 21°C, 38000 Lux.
6 A			—	+	+	Lava-sand, sampled near a piece of drifted wood. Soil temp. 14°C.
6 B			—	—	+	Lava-sand, sampled under the same piece of wood. Soil temp. 14°C.
7	0.3 ± 0.1	—	—	+	+	Tephra. Traces of bird excrements. Soil temp. 14°C, 31000 Lux.
8			—	+	+	Tephra. Near an old piece of air-exposed, drifted plywood. Soil temp. 14°C.
9	62.0 ± 23.7	<i>An. var.</i>	—	—	+	Cave ceiling. Rather moist. Soil temp. 11°C, 13100 Lux.
10	4.0 ± 1.9	<i>An. var.</i>	—	+	+	Bottom of the same cave. Soil temp. 12°C, 8000 Lux.
11			—	—	+	Driftwood (unplaned pine wood) with myceliumspots of <i>Trichoderma viride</i> Pers. ex. S. F. Gray.
12 A	64.5 ± 12.5	<i>An. var.</i>	—	+	+	Moss-covered gray lava-stones. Ground temp. 21°C, 44000 Lux.
12 B	26.0 ± 11.5	—	—	—	+	Moss-covered red lava-stones. Ground temp. 24°C, 44000 Lux.
12 C	0.3 ± 0.1	<i>An. var.</i>	—	+	+	Rather moist soil without mosses. Soil temp. 18°C, 64000 Lux.
13			—	+	+	Rhizosphere of <i>Honkenya peploides</i> (L.) Ehrh. ssp. <i>diffusa</i> (Hornem.) A. Löve.
14 A			—	+	+	Lava-sand. From the surface.
14 B			—	+	+	Lava-sand. From 10–15 cm deep layer.
14 C			—	—	+	Lava-sand. From 20–25 cm deep layer.
15			—	+	+	At the entrance of the cave "The Bell" (according to G. H. Schwabe). Moss-covered. Moist. Soil temp. 22°C, steam temp. 54°C. Moss-covered.
16			—	+	+	On the wall, inside the same cave. Temp. 15°C. Moist. Moss-covered.
17	0.3 ± 0.1	—	—	+	+	Former old lagoon. Moist fine lava-sand 105 cm above sea-water-table. Soil temp. 17°C, 34000 Lux.
18 A	0.4 ± 0.2	—	—	+	+	Tephra. Surface layer. Soil temp. 17°C, 28000 Lux.
18 B			—	—	+	Tephra. From 15–20 cm deep layer. Soil temp. 22°C.
19 A			—	+	+	Just near a steam-hole. Light colored lava. Soil temp. 45°C.
19 B			—	+	+	30 cm from the same steam-hole. Light colored lava. Soil temp. 28°C.
19 C			—	+	+	60 cm from the same steam-hole. Light colored lava. Soil temp. 22°C.

Table 1. The occurrence of some different types of microorganisms involved in the nitrogen cycle of Surtsey, the results of the nitrogen fixing experiments *in situ*, and a description of the locations studied. Location numbers refer to Fig. 1. Organisms present +, absent —.

the samples were stored at low temperatures.

The samples from the lava fields of Hekla were collected Oct. 15-16, 1972 by Á. H. Bjarnason in the same manner, and the results obtained will also be used by him in his plant ecological investigation of Iceland.

Determinations of nitrogen fixation in situ and under controlled conditions

The acetylene reduction technique, introduced by Stewart et al. (1967, 1971) and adapted for analyses *in situ* by Henriksson et al. (1972 a), was used for determinations of nitrogen fixation. The method as slightly modified is as follows: Soil samples were taken with a sterilised cork borer (1.6 cm² in area) from the surface layer 5-7 mm) and put aseptically in separate serum bottles of 7 ml volume. Each soil sample represented about 1 ml. The bottles were sealed with screw caps and suitable rubber discs, specially tested for this type of analysis (free from ethylene). To avoid leakage after injections the rubber discs were coated with small amounts of silicone grease (Dow Corning nontoxic stopcock grease). In each bottle 0.6 ml pure acetylene at normal pressure was injected by a hypodermic syringe and incubated *in situ* for 1 hour. Every analysed site is represented by nine separate samples evenly dispersed on an area of 1 m². The nitrogenase activity was then stopped and the samples preserved by adding 0.5 ml saturated water solution of ammonium sulphate to each bottle. In the laboratory the gas phases were analysed for ethylene by a gas chromatograph (Perkin-Elmer model 880) fitted with a 2.5 m long, 3.18 mm diameter column of Porapac T (50-80 M). The column had a temperature of 100°C and pure nitrogen gas served as carrier gas at a flow of 25 ml/min. The amount of ethylene per sample was quantitatively determined

by comparison with runs of ethylene of known concentrations. The ethylene content of the acetylene gas was measured in the same manner and applied as a correction factor to the experimental data. The calculations of nitrogen fixation were based on the theoretical value 3:1 as the molar ratios of ethylene produced and N₂ fixed (Stewart 1968).

The determinations of nitrogen fixing capacities of the soil samples from Hekla and Uppland, discussed in this paper, were performed exactly in the same way as the Surtsey samples of 1970 (Henriksson et al. 1972 b, 1972 c, 1975).

Enrichment cultures of blue-green algae and Azotobacter

The enrichment medium for nitrogen fixing blue-green algae was as follows (after Gorham et al. 1964, modified): K₂HPO₄ 17.4 mg, FeCl₃ 0.3 mg, E.D.T.A. 7.4 mg, MgCl₂·6H₂O 19.0 mg, MgSO₄·7H₂O 49.0 mg, CaCl₂·2H₂O 14.7 mg, NaCl 58.5 mg, and redist. water up to 1000 ml. In addition trace elements were added according to Glendenning et al. (1956). The cultures in duplicate were placed at 20°C and 3000 Lux (Philips TL/33). The identification of algae was made after Geitler (1932). About 2 g of soil were tested from each locality.

For *Azotobacter* the enrichment nutrient solution recommended by Gebhardt and Anderson (1958) was used. The composition was as follows: mannitol 10 g, K₂HPO₄ 0.5 g, MgSO₄·7H₂O 0.2 g, NaCl 0.2 g, FeCl₃ 5 mg, MnSO₄·4H₂O 5 mg, redist. water up to 1000 ml. In addition 50 g sterilized CaCO₃ was added after autoclaving. The cultures in triplicate were placed at 25°C in dark for 7 weeks and were visually observed at intervals. About 1.5 g of soil were tested from each locality.

TABLE 2

Locality	Soil dated year	Number of locations	ng N ₂ fixed g ⁻¹ h ⁻¹	References
Hekla, Iceland				
Katlar	1766	10	2.2 ± 1.0	
Krakatindshraun (Nýjahraun)	1878	10	1.4 ± 0.9	
Lambafitarhraun	1913	10	4.3 ± 2.4	
Surtsey, Iceland	*1963-67	9	16.0 ± 6.0	Henriksson et al. (1972 b)
Uppsala, Sweden, uncult. soils	—	8	(2.7 ± 0.1) · 10 ³	Henriksson et al. (1972 c)
Uppsala, Sweden, cult. soils	—	6	(2.1 ± 0.5) · 10 ³	Henriksson et al. (1975)

Table 2. The nitrogen fixing capacities under controlled conditions of volcanic soils from Hekla and Surtsey, Iceland and of precambrian sedimentary soils from Uppland, Sweden.

TABLE 3

Constituents	mg / 100 g air dried soil		
	Surtsey sample 14/1972 Lava	Surtsey sample 18A/1972 Tephra	Means from 6 Swedish wheat fields
Phosphorus, P-AL	12.7	6.3	11.3
P-HCl	81.	77.	69.
Potassium, K-AL	13.3	15.5	27.6
K-HCl	370.	360.	388.
Magnesium, Mg-AL	56.0	61.0	29.6
Mg-HCl	3.550.	3.900.	950.
Calcium, Ca-AL	112.	122.	860.
Ca-HCl	3.200.	3.125.	1.060.
Sodium, Na-AL	60.	65.	10.6
Na-HCl	2.018.	2.190.	38.
Sulfur, S	20.	68.	52.
Nitrogen, NH ₄ -N	6.	7.	6.
NO ₃ -N	<1.	<1.	26.5
N-Kjeldahl	2.0	2.0	290.
Iron, Fe-AL	193.	200.	31.
Copper, Cu-HCl	40.4	43.7	3.2
Manganese, Mn	0.40	0.31	0.50
Boron, B	0.53	0.16	0.90
Spec. conductance, 20°C	90·10 ⁻⁶	100·10 ⁻⁶	50—190·10 ⁻⁶
pH	6.6	6.8	6.2—7.4

Table 3. Analyses of the virgin lava and tephra sand of Surtsey compared with cultivated soils from Uppland, Sweden. For the interpretation of the terms -AL and -HCl, see Material and Methods.

Qualitative analyses of nitrification and denitrification organisms

In order to find out if nitrification and denitrification processes are commonly present in the soil of Surtsey, enrichment cultures of nitrifying and denitrifying organisms were made from soil samples, and the presence of NO₃⁻, NO₂⁻, and NH₄⁺ ions in the culture media were analysed after 3, 6, and 8 weeks of incubation in the dark at 25°C.

The enrichment medium for the nitrite and nitrate forming bacteria of the genera *Nitrosomonas* and *Nitrobacter*, aerobic chemosynthetic autotrophs, was as follows (Aaronson 1970, slightly modified): (NH₄)₂SO₄ 0.66 g, NaCl 0.29 g, KH₂PO₄ 0.68 g, MgSO₄·7H₂O 0.25 g, CaCO₃ 10 g, FeCl₃ 5 mg, redist. water up to 1000 ml.

The enrichment medium for the denitrifying organisms, including several species, was as follows (slightly modified from Cunningham 1947, the nitrate addition according to Aaronson 1970): Oxoid bact. peptone 10 g, KH₂PO₄ 0.5 g, MgSO₄·7H₂O 0.5 g, NaNO₃ 1.0 g, FeCl₃ 5 mg, and redist. water up to 1000 ml.

To 15 ml of the autoclaved media 0.5 g soil was added aseptically. All the series were made

in triplicates. Uninoculated controls were incubated and treated in the same way as the soil cultures.

The analyses of NO₃⁻, NO₂⁻, and NH₄⁺ ions were made after detailed instructions and reagent descriptions made by Aaronson (1970). However, the test volumes used were half those recommended by Aaronson.

Soil analyses

The soil analyses recorded (Table 3) were carried out by the National (Swedish) Laboratory of Agricultural Chemistry, Uppsala. The analytical standard methods used are confirmed by Royal Proclamation of the National (Swedish) Board of Agriculture (1965).

The easily soluble constituents, in table marked -AL (e.g. P-AL, K-AL), are extracted by standard AL-solution (0.10 M NH₄-lactate, 0.40 M acetic acid). Values from 2.0 M HCl extractions (e.g. P-HCl, K-HCl) also include stored constituents.

In comparison to the soil samples of Surtsey from localities No. 14 (lava sand) and No. 18 (tephra sand), both about 40 m above sea level, mean values from six Swedish wheat fields from the surroundings of Uppsala are included (Table 3).

The soil samples of Surtsey and the Swedish ones represent the upper surface layers.

RESULTS

Biological nitrogen fixation *in situ*

The analytical results, together with a short description of the 13 investigated localities, are recorded in Table 1. The resulting *in situ* values, 0.2-64.5 ng N₂ cm⁻² h⁻¹, show biological nitrogen fixation at all localities studied and verify the assertion that active nitrogen fixation is established on Surtsey. It was found by enrichment cultures that the nitrogen fixing activities could be attributed to the presence of nitrogen fixing blue-green algae in the soil. The algae were unevenly dispersed in the surface layer of the soil, which is reflected in the varying nitrogen fixing values. For the same reason some of the enrichment cultures did not contain any nitrogen algae at all in spite of the occurrence of nitrogen fixation, since the sampling spots for the algal cultures were not the same as the spots used for the measurement of nitrogen fixation. As in earlier investigation (Henriksson et al. 1972 b) the cosmopolitan *Nostoc muscorum* Ag. and *Anabaena variabilis* Kütz. were recorded. This coincides with the observations of Schwabe (1974),

who has found them well dispersed over the island. The values here reported are probably not typical for the whole island, since several of the sites were selected with the intention of obtaining positive results for nitrogen fixation. Conditions favouring the occurrence of nitrogen fixing algae are, for instance, moist soil and presence of mosses (Schwabe 1974).

Biological nitrogen fixation in Surtsey soil in comparison to volcanic soils of the mainland and to Swedish uncultivated and cultivated soils

The determinations of nitrogen fixation performed *in situ* show the actual activities under present conditions of water content, temperature, light, and nutrient constituents. Since the conditions in nature are varying, the values received under field conditions fluctuate and depend on the water and weather conditions. However, biological nitrogen fixation in a soil can be more precisely stated by capacity measurements at standard conditions, and the results of such measurements from soils of different districts will be comparable (Henriksson et al. 1972 c). For that reason soil samples from 9 localities on Surtsey were analysed in 1970. The analyses showed values between 2.54 ng fixed N_2 $g^{-1} h^{-1}$ at 20°C and 3000 Lux (Henriksson et al. 1972 b). The intention is to follow up the development of nitrogen fixation on the island continuously.

In order to have some idea of the development of biological nitrogen fixation on Surtsey, samples from three Icelandic lava flows from Hekla, formed in 1766, 1878, and 1913 respectively, were analysed. This was performed under laboratory conditions, and the technique was exactly the same as for the samples of Surtsey. The results from these newly formed Icelandic soils are also compared with results from uncultivated and cultivated soils from the surroundings of Uppsala in Sweden. The results are brought together in Table 2. From these values it is evident that nitrogen fixation is relatively high on Surtsey compared to the nitrogen fixation found in the volcanic soils of Hekla, but low compared to the soils of Uppland (Sweden). The lava flows of Hekla are all well colonised by mosses and lichens. The pH is 6.1-6.9, and the structures are of the same specially sandy character as that of Surtsey. The lower values of Hekla may be explained by higher competition in older lava flow. The same tendency may occur later on Surtsey, when biological life there is established to the same level. Anyhow, the Swedish soils of

precambrian provenience show capacity values of much higher dimensions.

In this experiments little or no nitrogen fixation occurred in the dark showing that heterotrophic nitrogen fixing bacteria such as *Azotobacter* and *Clostridium* are of very little or no importance. In addition, the enrichment cultures of *Azotobacter* showed negative results, which is also in accordance with the investigation of Schwartz and Schwartz (1972). It is, however, possible that photosynthetic bacteria with ability to fix nitrogen may be of certain smaller importance (Henriksson 1971, Stewart 1973).

Nitrification and denitrification processes on Surtsey

The nitrifying processes caused by *Nitrosomonas* and *Nitrobacter* are known to be most favourable in soils at a pH of about 7. Higher alkaline conditions support the activity of *Nitrosomonas* and retard that of *Nitrobacter*, resulting in a nitrite accumulation in the soil, which, however, can be reduced by present denitrifying organisms (Campbell and Lees 1967). On the other side, the activity of these organisms is inhibited in acid conditions. The Surtsey soils show pH reactions of very slight acidity, near the neutral point (Table 3). This fact indicates a good environment for nitrogen reducing organisms, which are also activated in more or less anaerobic conditions, which are common in a normal soil.

The intention of the reported investigation is to give some indication of the dispersion of these two significant groups of organisms. The results are given in Table 1. In every sample tested, activities of nitrogen reducing organisms were found, also from the stranded wood. After 8 weeks no traces of the nitrate, supplied to the culture medium, could be recovered. The analyses after 3 and 6 weeks showed that the expected processes were going on.

In the case of *Nitrosomonas* and *Nitrobacter* the results showed the presence of these organisms in all surface layers except localities No. 5, 9, 12 B, 14 C, and 18 B, where no evidence was observed at all. Samples No. 14 C and 18 B represent deeper layers in the soil, where aerobic conditions, necessary for the organisms involved, are suppressed. On the other side, in the rhizosphere of *Honkenya peploides* (No. 13) the organisms were represented.

No traces of NH_4^+ , NO_3^- , or NO_2^- were recorded after 8 weeks in the cultures of No. 2, 4, 13, 14 A, and 18 A, indicating a total conversion

of NH_4^+ to N_2 . The analyses after 3 and 6 weeks showed that the expected processes were going on.

The soil analyses of Surtsey compared to cultivated Swedish soils

The hitherto published chemical analyses of the lava of Surtsey (Thorarinsson et al. 1964, Jakobsson 1968) show primarily the mineralogical state. However, those results do not represent the actual nutrient availability for biological requirements. In respect to this, analyses in the agricultural chemical way appear to be more useful (Table 3).

One of the most remarkable differences between the virgin Surtsey-soils and the Swedish ones is the very high content of readily available iron on Surtsey. This iron, derived from the alkali olivine basalts (about 13% olivine), will certainly be reduced as time goes on. The olivine components will then be transformed to more insoluble compounds. The copper analyses of the Surtsey samples show also very high values; the recorded Swedish ones are more typical. On the other hand, boron shows low values in the soils of Surtsey.

The presence of high quantities of available sodium on Surtsey can be explained by contributions from the sea. In addition, magnesium and calcium show high values, especially in the stored fractions. In the case of Mg-HCl and Ca-HCl it is evident that these constituents are present in less soluble forms, magnesium in olivine and calcium as CaSO_4 . Calcium is enriched in the soils of Surtsey by salt spray from the sea and precipitates as sulphate (Sigvaldason and Fridriksson 1968).

The phosphorus content on Surtsey is high compared to common uncultivated soils in the northern temperate zone, and the values recorded are of the same magnitude as in fertilized cultivated Swedish soils.

Regarding sulfur, the analyses of the lava show surprisingly low values, as much higher could be expected on account of the frequent smell of hydrogen sulfide. However, this sulfur-fraction is easily lost at the time of sampling, and is therefore not included in these actual analyses.

Compared to the Swedish soils the most striking, but not unexpected, observation is the extremely low content of nitrogen compounds available for biological life on the island. In uncultivated soils nitrogen deficit is common, but in the virgin soils of Surtsey it is definitely pronounced. On the other hand, the $\text{NO}_3\text{-AL}$ value

(26.5 mg/ 100 g soil) for the Swedish cultivated soils is high and can be explained by fertilizer application shortly before the sampling. However, this NO_3 -value will shortly be reduced by rain, drainage, and by assimilation.

The pH of the Surtsey soils shows values just under neutrality, and the specific conductances of the soils are of the same order as those of the cultivated Swedish ones. However, on Surtsey the composition of the salt mixture in the soil can be easily changed by leaching rainfalls and repeated deliveries from the sea. Sigvaldason and Fridriksson (1968) found 121.5 mg dissolved salts per 100 g tephra after thoroughly leaching with distilled water. Their sample was from the same area as locality No. 18.

At present time the Surtsey soils contain negligible quantities of organic matter and are free from humus and subsoil. These organic compounds are a requirement for many microorganisms and higher plants, not only for their growth but also for sufficient water holding capacity. Pure lava is not characterized by this latter quality, but on Surtsey the low water retention can be balanced by the high air humidity and normally abundant rainfalls.

The differences between the recorded analyses of the elements of the lava sand (No. 14) and tephra (No. 18) are remarkably small, and the two types of soil will probably be of about the same initial qualities with respect to biological development.

The analyses show that the preliminary limiting factor for general plant development on Surtsey is the very low content of nitrogen compounds. For this reason the Surtsey pioneers must have extremely small requirements for available nitrogen in the soil.

DISCUSSION

The vascular plants on Surtsey registered up to 1972, have been located on the shores or on those parts of the lowlands which are flooded by rough sea. In the locations they are frequently destroyed by sea and wind erosion or by becoming totally covered by light sand.

However, on other parts of the island mosses and lichens are stationary botanical pioneers (Fridriksson et al. 1972). 18 different species of mosses on 120 localities and 3 species of lichens on 2 localities were registered in 1970, and this development has increased during the last years.

In addition, the microflora is represented by algae, fungi, and bacteria, which has been verified by a number of investigations.

The content of nitrogen compounds of biological interest has not increased in time since the preliminary analyses of Ponnampertuma et al. (1967) were carried out. Consequently only those organisms which have small requirements for available nitrogen compounds are suited to be stationary and active pioneers on this island, and for that reason the photoautotrophic nitrogen fixing microorganisms are especially well-qualified.

The mosses and lichens are well-known to have low requirements for nutrients. Schwabe (1974) has demonstrated a general close association between mosses and nitrogen fixing blue-green algae on Surtsey. It is also evident from other investigators that mosses are supplied with nitrogen by nitrogen fixing blue-green algae (Vlassak et al. 1973) and *Azotobacter* (Snyder and Wullstein 1973). The latter have also made similar observations on lichens in pioneer ecosystems.

As a result of this investigation blue-green algae seem to be an important contributor of combined nitrogen to the studied ecosystem. However, Brock (1972, 1973) declared after visual observations on Surtsey, and microscopical examinations of soil samples in the laboratory, that "blue-green algae are quite unimportant as primary colonizers of Surtsey. Mosses and lichens are of greater importance, and coccoid algae (*Chlorophyta*) are of lesser importance." Brock neglects in that way the elementary significant physiological activity of the nitrogen fixing blue-green algae on Surtsey. Especially as considerable growth of only blue-green algae was observed in our cultures, where redistilled water or nitrogen-free nutrient solution was added to the soil samples.

Several of the investigated Surtsey localities (Table 1) show biological nitrogen fixation of the same order as has been measured from other soils. Henriksson (1971) and Henriksson et al. (1972 a) found in *in situ* determinations of uncultivated Swedish soils a nitrogen fixation of 1-450 ng N₂ cm⁻² h⁻¹, of which the high value was measured under special conditions. Stewart and Harbott (published in Fogg et al. 1973) recorded 4 ng N₂ cm⁻² h⁻¹ for arable and 14 ng N₂ cm⁻² h⁻¹ for pastureland in Scotland.

The demonstrations of general occurrence of nitrifying and denitrifying organisms on Surtsey will not give any informations about their activities *in situ*, but the results indicate the presence of these catabolic parts of the nitrogen cycle.

Finally, blue-green algae are of essential importance for the asymbiotic development of hete-

rotrophic microorganisms in virgin soil and for the primary stages of soil formation (Harley 1970, Shtina and Nekrasova 1971, Vlassak 1972). Because of them the floristic and faunistic colonization of Surtsey will accelerate (Lindroth et al. 1973).

ACKNOWLEDGEMENTS

The authors had the good fortune to visit Surtsey as members of the *Swedish Biological Surtsey Expedition* in the summer 1972. For this privilege we are deeply indebted to the leader, Prof. Carl H. Lindroth, University of Lund. We are also grateful to Prof. Nils Fries, Head of the Institute of Physiological Botany, University of Uppsala, for his valuable interest and provision of facilities, to Dr. Bo Thente, Uppsala, for valuable discussions and to Mr. Ágúst H. Bjarnason, Reykjavik, for collecting the samples from Hekla. Our thanks are also due to Dr. Howard Bonnett, Uppsala, for careful revision of the English of our manuscript.

Support for travel to Surtsey was provided by the *Swedish Natural Research Council* and accommodation on Surtsey by the *Surtsey Research Society*.

ABSTRACT

Nitrogen fixation in *in situ* determinations at 13 locations on Surtsey amounted to 0.2–64.5 ng N₂ cm⁻² h⁻¹. The algae involved were *Anabaena variabilis* and *Nostoc muscorum*. *Azotobacter* were not found in either these 13 or in the other 5 locations studied. On the other hand, nitrifying and denitrifying organisms were found to be commonly occurring. The nitrogen fixing capacities of Surtsey soil samples were higher than those of soils from earlier lava flows formed by Hekla in 1766, 1878, and 1913, but much lower than the nitrogen fixing capacities of uncultivated precambrian Swedish soils. Lava and tephra sand were analysed by agricultural chemical methods, and the nutrients available for plants are discussed. The values are also compared with similar ones from Swedish wheat fields. At the present time a pronounced deficit of nitrogen compounds characterizes the Surtsey soil.

References

- Aaronson, S., 1970: Experimental microbial ecology. — Acad. Press. N.Y. 236 pages.
- Behre, K. and Schwabe, G. H., 1970: Auf Surtsey/Island im Sommer 1968 nachgewiesene nicht marine Algen. — Schr. Naturw. Ver. Schleswig-Holst. Sonderband Surtsey: 31–100.
- Brock, T. D., 1972: Microbiological observations on Surtsey,

1970. — Surtsey Research Progress Report 6: 11–13.
- Brock, T. D., 1973: Primary colonization of Surtsey, with special reference to the blue-green algae. — *Oikos*, 24: 239–243.
- Campbell, N. E. R. and Lees, H., 1967: The nitrogen cycle. — In *Soil Biochemistry* (ed. McLaren, A. D. and Peterson, G. H.). Marcel Dekker, Inc. N.Y. 509 pages.
- Castenholz, R. W., 1972: The occurrence of the thermophilic blue-green alga, *Mastigocladus laminosus*, on Surtsey in 1970. — Surtsey Research Progress Report 6: 14–19.
- Clendenning, K. A., Brown, T. E. and Eyster, H. C., 1956: Comparative studies of photosynthesis in *Nostoc muscorum* and *Chlorella pyrenoides*. — *Canad. J. Bot.* 34: 943–966.
- Cunningham, A., 1947: Practical bacteriology. — Oliver and Boyd. Edinb. 222 pages.
- Fogg, G. E., Stewart, W. D. P., Fay, P. and Walsby, A. E., 1973: The blue-green algae. — Acad. Press. London. 459 pages.
- Fridriksson, S., Sveinbjörnsson, B. and Magnússon, S., 1972: Vegetation on Surtsey — summer 1970. — Surtsey Research Progress Report 6: 54–63.
- Gebhardt, L. P. and Andersson, D. A., 1958: Laboratory instructions in microbiology. 2nd ed. — C. V. Mosby Co. St. Louis. 261 pages.
- Geitler, L., 1932: Cyanophyceae von Europa unter Berücksichtigung der anderen Kontinente. — Rabenhorts Kryptogamenflora 14. Leipzig. 1162 pages.
- Gorham, P. R., MacLachlan, R., Hammer, U. and Kim, W. D., 1964: Isolation and culture of toxic strains of *Anabaena flos-aquae* (Lyngb.) de Bréb. — *Verh.int. Ver. Limnol.* 15: 796–803.
- Harley, J. L., 1970: Importance of microorganisms to colonising plants. — *Trans. Bot. Soc. Edinb.* 41: 65–70.
- Henriksson, E., 1971: Algal nitrogen fixation in temperate regions. — *Plant and Soil*, Spec. vol. Biological nitrogen fixation: 415–419.
- Henriksson, L. E., Enckell, P. H. and Henriksson, E., 1972 c: Determination of the nitrogen fixing capacity of algae in soil. — *Oikos* 23: 420–423.
- Henriksson, E., Englund, B., Hedén, M.-B. and Was, I., 1972 a: Nitrogen fixation in Swedish soils by blue-green algae. — In *Taxonomy and Biology of Blue-green Algae* (ed. Desikachary, T. V.). Univ. Madras. 591 pages.
- Henriksson, L. E. and Henriksson, E., 1974: Occurrence of fungi on the volcanic island of Surtsey, Iceland. — *Acta Bot. Icelandica* 3: 82–88.
- Henriksson, E., Henriksson, L. E. and DaSilva, E. J., 1975: A comparison of nitrogen fixation by algae of temperate and tropical soils. — In *Nitrogen Fixation in the Biosphere* (Eds. Stewart, W. D. P. and Nutman, P. S.). Cambridge Univ. Press. p: 199–206.
- Henriksson, E., Henriksson, L. E. and Pejler, B., 1972 b: Nitrogen fixation by blue-green algae on the island of Surtsey, Iceland. — Surtsey Research Progress Report 6: 66–68.
- Holmberg, O. and Pejler, B., 1974: On the terrestrial microfauna of Surtsey during the summer 1972. — Surtsey Research Progress Report 7: 17–19.
- Jakobsson, S., 1968: The geology and petrography of the Vestman Islands. — Surtsey Research Progress Report 4: 113–130.
- Lindroth, C. H., Andersson, H., Böldvarsson, H. and Richter, S. H., 1973: Surtsey, Iceland. The development of a new fauna, 1963–1970. Terrestrial invertebrates. — *Entomol. Scand. Suppl.* 5. 280 pages.
- National Swedish Board of Agriculture, 1965: Royal proclamation regarding the stipulations for soil analyses and methods. (In Swedish.) Proclam. No. 1 with suppl. Stockholm.
- Ponnamperuma, C., Young, R. S. and Caren, L. D., 1967: Some chemical and microbiological studies of Surtsey. — Surtsey Research Progress Report 3: 70–80.
- Schwabe, G. H., 1970 a: On the algal settlement in craters on Surtsey during summer 1968. — Surtsey Research Progress Report 5: 68–69.
- Schwabe, G. H., 1970 b: Zur Ökogenese auf Surtsey. — *Schr.d. Naturw. Ver. Schleswig-Holst. Sonderband Surtsey*: 101–120.
- Schwabe, G. H., 1971: Die Ökogenese im terrestrischen Bereich postvulkanischer Substrate, schematische Übersicht bisheriger Befunde auf Surtsey/Island. — *Peterm. Geograph. Mitt.* 115: 268–273.
- Schwabe, G. H., 1974: Nitrogen fixing blue-green algae as pioneers on Surtsey 1968–1973. — Surtsey Research Progress Report 7: 22–25.
- Schwabe, G. H. and Behre, K., 1972: Algae on Surtsey in 1969–1970. — Surtsey Research Progress Report 6: 85–89.
- Schwartz, W. and Schwartz, A., 1972: Geomikrobiologische Untersuchungen. X. Besiedelung der Vulkaninsel Surtsey mit Mikroorganismen. — *Zeitsch. f. allg. Mikrobiol.* 12: 287–300.
- Shtina, E. A. and Nekrasova, K. A., 1971: The direct and indirect contribution of soil algae to the primary production of biocoenoses. — *Int. Nat. de la Recherche Agronomique*, Paris, 71: 37–45.
- Sigvaldason, G. and Fridriksson, S., 1968: Water soluble leachate of volcanic ash from Surtsey. — Surtsey Research Progress Report 4: 163–164.
- Snyder, J. M. and Wullstein, L. W., 1973: Nitrogen fixation on granite outcrop pioneer ecosystems. — *The Bryologist* 76: 196–199.
- Stewart, W. D. P., 1968: Acetylene reduction by nitrogen fixing blue-green algae. — *Arch. Mikrobiol.* 62: 336–348.
- Stewart, W. D. P., 1973: Nitrogen fixation by photosynthetic microorganisms. — *Ann. Rev. of Microbiol.* 27: 283–316.
- Stewart, W. D. P., Fitzgerald, G. P. and Burris, R. H., 1967: *In situ* studies on N₂ fixation using the acetylene reduction technique. — *Proc. Nat. Acad. Sci. Wash.* 58: 2071–2078.
- Stewart, W. D. P., Mague, T., Fitzgerald, G. P. and Burris, R. H., 1971: Nitrogenase activity in Wisconsin lakes of differing degrees of eutrophication. — *New Phytol.* 70: 497–509.
- Thorarinsson, S., Einarsson, T., Sigvaldason, G. and Elisson, G., 1964: Submarine eruption off the Vestmann islands. — *Bull. Volc.* 27: 444.
- Vlassak, K., 1972: Biologische Stikstoffixatie (Biological nitrogen fixation) (In Dutch). — *Agricultura* 4: 4–52.
- Vlassak, K., Paul, E. A. and Harris, R. E., 1973: Assessment of biological nitrogen fixation in grassland and associated sites — *Plant and Soil* 38: 637–649.