Nitrogen fixing blue-green algae as pioneer plants on Surtsey 1968—1973

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Nitrogen is the most critical limiting major nuttrient in the terrestrial area of Surtsey (Henriksson & Henriksson 1974). If the water supply is sufficient, nitrogen undoubtedly limits the development of the algal vegetation. This finding is, among other things, supported by several hundred enrichment cultures which were kept in our laboratory during the study period. The cultures were set up on N-poor media, and were compared with controls containing sufficient N, in which the typical substrate types of Surtsey (lava, tephra of different grain sizes, fine fractions of windblown dust and sediments scoured out by precipitation) were tested in varying quantities added to the nutrient medium. The resulting number of species and the total production in all cases increased with the N-content of the medium, at least up to concentrations of about 30 mg N (as NO_3) per 1000 ml.

Under these conditions, biological N-fixation is of great importance both in soil formation and in ecogenesis. It has been apparent since 1968 that compared with nitrogen compounds, all other mineral nutrients are present in plentiful supply — some trace elements in toxic excess. The *Cyanophyta,* among which many are nitrogen fixers, were collected and propagated in N-deficient enrichment cultures. The results of this work are only summarised here under the heading of N-fixing species since the processing of all the data will require more time.

At the place of collection, sterile plates and nutrient solutions were inoculated with substrate samples. Other samples of the same substrate were also taken to the laboratory in Plön and cultivated in different media and under different conditions of light and temperature.

The collections on the island were made during 7 visits:
28-30 July 1968, 29 July - 1 August 1969, 21 May 1970, 5-7 August 1970, 15-17 July 1971, 8-11 July 1972, 25-27 July 1973.

For the collections, all substrate types above the high water mark on the shore which could be distinguished visually were considered from the first visit. Close attention was given to the sites which, as shown by examination with a hand lens, were seen to be colonized with Cryptogams (algae, mosses), or obviously had a good water supply (steam fissures, secondary craters, temporary pools, rock pools etc.). Algal developments have been followed in situ with a hand lens or microscope since 1968. Populations of algae were at first found by direct observation only in the immediate vicinity of steam vents, mostly (although not always) near moss plots (especially *Funaria hygrometrica).* These consisted mainly of members of the group *Schizothrix-Plectonema* (with trichome diameter less than 2.5μm) and sometimes also of pennate diatoms which formed shiny brownish deposits up to about 1 mm in diameter. Up to the summer of 1973, such small algal deposits, often only visible with a hand lens and usually consisting of several species, occurred in open areas apparently only periodically or temporarily. There are two independent causes for this fact:

1. The predominant species in such stands are actively motile (Behre & Schwabe 1970), so that they can avoid the occasional dry periods by withdrawing below the surface of the substrate.

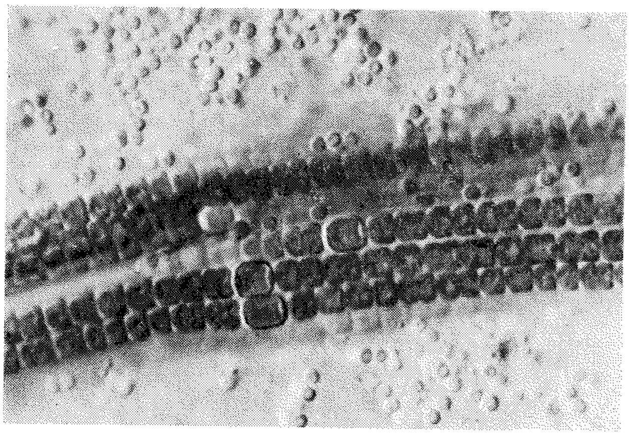

Fig. 1. *Nodularia harveyana Thur.* Together with *Aphanocapsa* cf. *elachista* (2-2,5 μmΦ). From the lava flow in Surtur I (8.8.1970).

Fig. 2. *Hapalosiphon hibernicum* W. et G. S. West. Typically branched primary trichome and secondary trichomes. From Strompur (5.8. 1970).

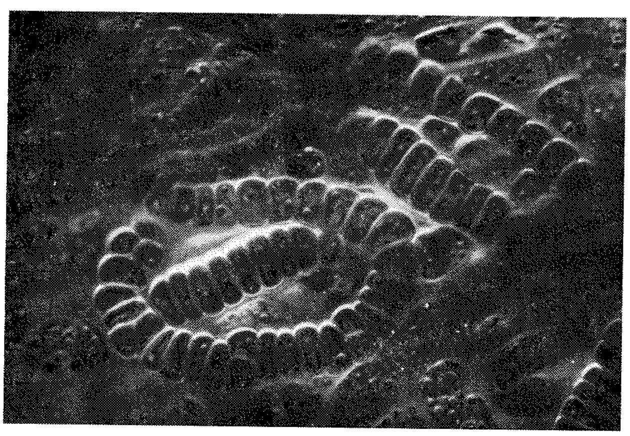

Fig. 3. *Hapalosiphon hibernicum* W. et G. S. West. An older culture. The trichomes almost completely transformed into chains of akinetes. From Strompur (5.8.1970).

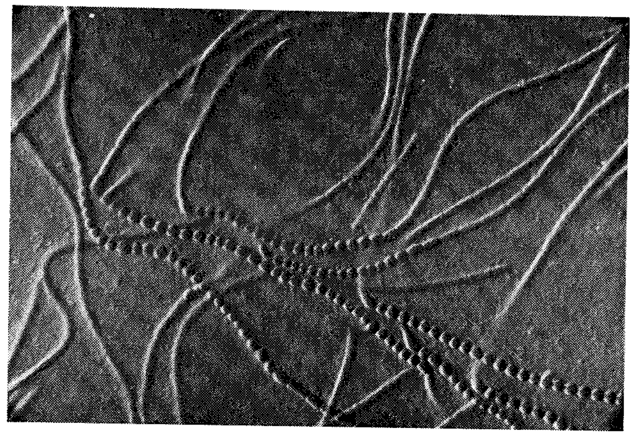

Fig. 4. *Mastigocladus laminosus* Cohn. In full development with typically differentiated trichomes. From the main crater of Surtur II, steam vent (16.7.1971).

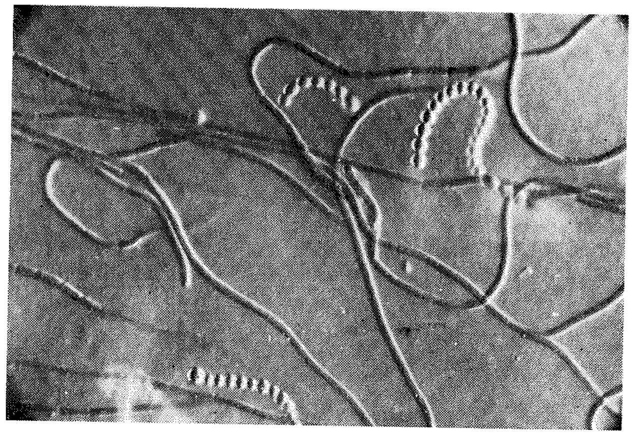

Fig. 5. *Mastigocladus laminosus* Cohn. An older culture with characteristic formation of akinetes in chains. From same locality as in Fig. 4.

Fig. 6. *Tolypothrix tenuis* Kütz. f. *terrestris* Boye-Pet. From the same place as *Mastigocladus* (16.7.1971) in Fig. 4. On warm, moist substrate together with musci.

2. The mineral dust deposited by weak winds straight on the damp surfaces completely covers such algal stands with a very thin layer for some time.

In the last few years we have often watched, with a hand lens, such changes in algal stands occurring within a few hours in places supplied with capillary water. N- fixers could not, however, be seen in situ, but were found in abundance in cultures of the substrates. Their N-fixing activity has been demonstarted by Henriksson et al. (1972, 1974). Large patches of algae (up to more than $0.1m^2$) occurred since 1968 only on the inner sides of hollows with sufficient light (secondary craters, more or less perpendicular lava walls), which are continuously moistened by steam. Several nitrogen fixers have been found here also in situ since 1970 (*Nostoc* sp. A. *"Nostogloea"* ad interim, *Mastigocladus). Different* N-fixers show a strong affinity for moss stands, particularly for *Funaria,* attached themselves to the protonemata. The joint occurrence of mosses and *Anabaena* is so marked and regular that it is possible to speak of a facultative symbiotic relationship. In the last two years it was only on exceptional occasions that stands of moss turfs were not associated with *Nostacaceae.* — In contrast to other musci, *Rhacomitrium* seems to hinder or completely suppress the development of the *Cyanophyta.* — *Nodularia* sp. shows, at least in early development, a strong affinity for protonemata, but then it spreads extensively. It has been noticed that at the place where the species is most abundant (on the southern side of "Lýsuhóll"), the moss turfs are also widely distributed. The *Nodularia* strains from there are different from the other *Nostocaceae* found on Surtsey in many respects:

1. Since 1970 the species has been found at only a few places in the young lava of the large crater Surtur I, and appears to be absent from the entire remaining region.

2. Both the places where it occurs most abundantly ("Lýsuhóll" and "Funaria-fissure" in the southern part of the main crater Surtur) I occasionally are resting-grounds for birds. About half way between these two places is another rather dense stand of *Nodularia;* birds were often found at the plastic tubs installed here some years ago.

3. One conspicuous feature distingunishes the strains of *Nodularia* collected on Surtsey from those on Heimaey and on Iceland itself, and from all the other *Nostocaceae* on Surtsey: under varying culture conditions, akinetes were generally not produced at all, or late and in small numbers.

From these findings it can be concluded that, unlike the other blue-green algal pioneers, *Nodularia* is not brought to Surtsey by wind, but probably by birds. — The thermophilic species *(Mastigocladus laminosus* (cf. Fig. 4 and 5) etc.) had no relationship with moss stands but were distributed on steam vents under 50° also in mixed stands with other species. *Rivulariaceae* have hitherto not been found. Until the summer 1973 *Scytonemataceae* have been represented by only one species *(Tolypothrix tenuis,* cf. Fig. 6).

At present, three N-fixing species (including the variety-rich collective species *Nostoc muscorum)* are distributed over the entire island surface, one (*Nodularia,* cf. Fig. 1) is common only in the lava fields of Surtur I, and four are restricted to thermal sites or areas permanently moistened by steam. The distribution area of *Anabaena* and *Nostoc muscorum* is at least as large as that of the moss stands (except *Rhacomitrium*) or perhaps larger. From these observations a definite close association between the two groups is clear. Up to now, the ecogenesis has obviously proceeded more rapidly in the young lava flows of Surtur I than in the older ones of Surtur II (compare moss distribution to that of *Nodularia;* see also Behre & Schwabe 1970). The reasons for this. are not known.

The expansion of *Anabaena* and the *Nostoc* species on the island, which are not markedly thermophilic, is strongly influenced by the abundance and very rapid development of resting spores (akinetes). All the initial colonizers (strains) of these species found on Surtsey show this characteristic in the early development stages. Furthermore the akinetes of these pioneers, which are formed in chains, separate promptly from each other so that a short period of drying out enables further dispersal. Viable resting spores are commonly found in the so far completely uncolonized accumulations of wind-transported material everywhere on the island. *Nodularia* is the only exception.

Typical resting spores of *Hapalosiphon hibernicum* (cf. Fig. 2 and 3) are also frequently found, whereas *Tolypothrix tenuis* forms occasional hormocysts which likewise favour its local dispersion. The distribution of these two species is presumably restricted by their ecological requirements. Briefly, it can be stated that, at least since 1970, several N-fixing *Nostocaceae* are distributed over the entire island surface covered by lava above the high water mark, and are always frequently found in local associations of typical soil algae.

The above listed species thrive together in media extremely poor in nitrogen, and respond to additions of nitrate (1 to 50 mg N/1000 ml) with a reduction in the relative frequency of heterocysts and often also with a marked general reduction in growth (> 10 mg N/1000 ml). Since 1968, N-fixing blue-green algae have occurred regularly in association with moss stands

SPECIES	1968	1969	1970	1971	1972	1973
Anabaena variabilis	××	×××	×××	×××	×××	×××
Nostoc muscorum 1)	..	[×]	××	×××	×××	×××
Nostoc sp. A	..	×	××	×××	×××	×××
Nostoc sp. B (t) 4)	..	[×]	××	××	××	××
Nodularia harveyana	..	[×]	××	×××	×××	×××
Mastigocladus laminosus (t) 2)	..	×× 2)	××	××	××	××
"Nostogloea" (ad int.) (t) 3)	..	×× 3)	××	××	××	××
Hapalosiphon hibernicum	..	..	×	..	××	..
Tolypothrix tenuis	..	..	..	×	××	××
Scytonema sp. 403	..	..	..	..	[×]	..
Cylindrospermum c.f. *muscicola*	..	..	..	..	[×]	..

1) Definitely a collective species which cannot be satisfactorily separated using the normal taxonomic methods. The variety of forms has increased markedly since 1970.
2) Originally discovered by Castenholz (1972).
3) As in (2) above and described as "non-branching form of *Mastigocladus laminosus*".
4) Perhaps identical with Castenholz's "*Mastigocladus laminosus* short filament type" (1969, a).

[×] found once
× only distributed in one locality
×× only distributed in a few stands
××× widely distributed
(t) thermophilic/or thermobiont.

(except *Rhacomitrium*), so that one may speak of a facultative symbiosis. Nitrogen is at present the most critical limiting factor in the plant nutrient supply on Surtsey (see Henriksson & Henriksson 1974), so that blue-green algae play an essential role in the progression of ecogenesis. Nitrogen fixation by blue-green algae was already known on Surtsey in 1970 (Henriksson & Henriksson 1972). They have recently shown that N-fixation by blue-green algae was much greater on Surtsey than in similar substrates on Hekla. The results of Henrikson et al. and those presented here complement and confirm each another.

The effects of the rapidly spreading *Cyanophyta* on Surtsey since 1968 are certainly not restricted to N-fixing but are also shown in the mechanical aspect of soil formation, a feature also of very great importance. All the species found to date produce, to a greater or lesser extent, mucous coatings, which together with the movement of those species which form long trichomes result in fixation of the fine rock and mineral fractions of the soil into porous structures (crumb formation). In contrast to the stands of the *Chlorococcales* which have been spreading rapidly since 1969/1970, and which are conspicuous because of their green colour, the *Cyanophyta* cannot be seen with the naked eye from distances greater than 1 m and generally they can not be found by microscopical examination of the natural substrate. This can easily lead to the underestimation of the role of the *Cyanophyta, Diatoms* and a few other groups, because in places with a suitable microlimate (adiabatic humidity) the typical aerophytes spread out superficially, while the genuine soil-building algae remain unvisible (compare T. D. Brock 1972, 1973). Here, the ecological and physiological distinction between genuine soil algae and aerophytic algae strongly bound only on the surface of lava or tephra (resembling those on tree bark and rock surfaces) should be emphasized.

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