TERRESTRIAL BIOLOGY

Vegetation succession on Surtsey, Iceland, during 1990-1998 under the influence of breeding gulls

BORGTHÓR MAGNÚSSON[1] & SIGURDUR H. MAGNÚSSON[2]

[1]Agricultural Research Institute, Keldnaholt, 112 Reykjavík, Iceland.
[2]Icelandic Institute of Natural History, Hlemmur 3, PO. Box 5320, 125 Reykjavík, Iceland.

ABSTRACT

Vegetation succession and soil development were studied on Surtsey, in 22 permanent plots that were set up in 1990 to 1995. The plots were on sand or lava substrate and outside or inside a gull colony that started forming on the island in 1986. The formation of the colony was followed by enhancement of plant cover in the breeding area and a sharp rise in rate of colonization of plant species not found previously on the island.

Twenty species of vascular plants were recorded within the plots in 1998, when a total of 47 species was found on the whole island. Plots outside the gull colony had on average 2 species and 6% plant cover. *Honkenya peploides* was the most prominent species in the sand plots but *Sagina procumbens* in the lava plots. Inside the gull colony 9 species were found on average in each plot and total cover was 72%. In sand plots inside the colony *Honkenya peoploids*, *Poa annua* and *Stellaria media* were the dominant species, but *Puccinellia distans* and *Cochlearia officinalis* in the lava plots. The soil outside the colony was high in pH (7.5) and low in total C (<0.1%). Inside the colony the soil pH (6.4) had decreased and total C (1.1%) increased.

Changes in vegetation cover and species richness have been minor in plots outside the gull colony during the study period and the dominant species *Honkenya peploides* appears to have fully colonized the sand areas. Most of the species of these areas are perennials with clonal growth. Within the gull colony plant cover and species richness have, on the other hand, incresed two to threefold. The vegetation of the gull colony is characterized by perennial and annual species adapted to disturbed and nutrient-rich habitats. Most of the species are found in bird colonies on neighbouring islands.

INTRODUCTION

Colonization of life on Surtsey has been studied since the formation of the island. Investigation carried out in the early days revealed that microbial moulds, bacteria and fungi soon become established in the fresh volcanic substrate (Schwabe 1970, Smith 1970, Fridriksson 1975). In the summer of 1965 the first vascular plant was found growing on Surtsey, mosses became visible in 1968 and lichens were first found on the Surtsey lava in 1970 (Fridriksson 1966, Johannsson 1968, Einarsson 1969, Kristinsson 1972).

Plant colonization on Surtsey has been closely studied, the vascular plants in particular as they have been of far greater significance than mosses and lichens in the vegetation development. The island has been visited every summer and a record kept of colonizing species and their fate. Initially, each individual plant that was found on Surtsey was marked on a map and given a label. Measurements were made of its growth and development, through the summer and from year to year. Such detailed observations were possible while the number of plants on the island was relatively small and it was continued until 1978. After that time the focus has been more on particular sites on the island where the general development has been foll-

wed. Colonization of new species has, however, continued to be monitored for the whole island (Fridriksson 1992, 2000, Magnússon *et al.* 1996).

The first twenty years of vegetation colonization and succession on Surtsey were characterized by invasion and spread of the coastal species *Honkenya peploides, Leymus arenarius* and *Mertensia maritima* which formed a simple community on the unfertile, sandy substrate on the island. Of the other seventeen species discovered on the island during that period only seven managed to become established and spread slightly but they were all insignificant in the vegetation (Fridriksson 1992, Magnússon *et al.* 1996).

In 1986 a few pairs of lesser black-backed gull *(Larus fuscus)* were found breeding on a lava terrain on the southern part of Surtsey. In the following years the number of breeding pairs increased greatly and a distinct colony was formed by the lesser black-backed gull, herring gull *(Larus argentatus)* and great black-backed gull (*Larus marinus*) that also had been breeding in the area. The formation of the gull colony marked a new era in plant colonization and succession on Surtsey as these gulls had considerably stronger impact that other breeding birds earlier established on the island.

The present paper describes a study of vegetation succession on Surtsey between 1990 and 1998. The aim of the study is to investigate plant colonization, vegetation composition and soil development under different substrate conditions and influence of birds (Magnússon *et al.* 1996). The study is based on permanent plots that have been set up in different locations on the island.

STUDY AREA

General

Surtsey was formed in a volcanic eruption, lasting from November 1963 to June 1967. At the end of the eruption the island had reached 2.7 km² in total area. During the eruption two large tephra cones were built up on the middle of the island by the main craters (Fig. 1). The highest point on Surtsey, 154 m above sea level, is on the eastern hill. The southern part of the island is formed by lava flows descending from the craters. The lava flows have to a large extent been filled in by drifting tephra sand from the hills above them. The lava in the southeasternmost part of Surtsey is though still mostly free of sand, but airborne dust has settled in hollows and fissures. The northernmost part of Surtsey

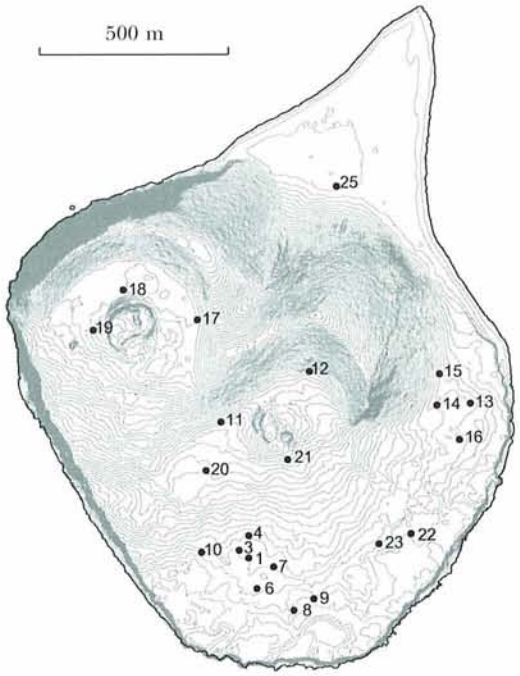

Figure 1. Location of permanent plots on Surtsey, shown on a topographical map of the island from 1998, contour intervals are 2 m. North is up in the figure. (done by: Hans Hansson, Icelandic Institute of Natural History).

is a low ness, formed by eroded material carried by the surf to the leeward side of the island (Jakobsson 1993, Fridriksson 1975, 1994). During winter sea water may wash over the ness area in extreme storms. The coastal erosion has taken its toll of Surtsey and in 1998 the island had been reduced to 1.5 km² (Jakobsson 1998).

Surtsey is the southernmost of the Westman islands, 7 – 35 km off the south coast of Iceland. The climate in the area is mild and oceanic. At the Heimaey weather station, 15 km from Surtsey, the mean annual temperature during 1961-1990 was 4.8°C and the mean annual precipitation was 1590 mm (Fridriksson 1994). The area is generally frost free from the first week of May until the middle of October (Einarsson 1976).

Nesting birds and formation of gull colony

The Westman Islands are known for their abundance of seabirds. In the first weeks of the Surtsey eruption gulls were seen roosting on the shores of the new-born island. Ever since, birds have been important in the development of the ecosystem on Surtsey through enrichment of the soil with their excrements and dispersal of plant seeds to the island (Fridriksson 1975, 1994, 2000, Petersen 1993, Magnússon *et al.* 1996).

Fulmar (*Fulmarus glacialis)* and black guillemot *(Cepphus grylle)* were the first species of birds

Table 1. Breeding bird species on Surtsey, descriptions of nesting sites and relative impact on vegetation development, based on observations. Number of breeding pairs is taken from last bird census in 1990 (Petersen 1993).

Species	Nesting pairs	Nesting in sea cliffs	Nesting inland	Nest made of vegetation and other materials	Effect on plant cover	Effect on colonization of new plant species
Fulmar	120	+	+		considerable	not evident
Black-Guillemot	15	+			none	none
Great Black-backed gull	7		+	+	considerable	not evident
Kittiwake	5	+		+	slight	none
In gull colony:			+	+	profound	profound
Lesser black-backed gull	120					
Herring gull	35					
Great black-backed gull	28					
Glaucous gull						

to nest on Surtsey in 1970 when one nest of each species was found in the cliffs on the southern part of the island. In 1974 great black-backed gull started breeding on Surtsey, kittiwake *(Rissa tridactyla)* in 1975, herring gull in 1981, lesser black-backed gull in 1986 and glaucous gull *(Larus hyperboreus)* in 1993 (Petersen 1993). The effect of the bird species on the vegetation development appears to be related to their population size, selection of nesting sites and the type of nest they build (Table 1). The gull species build nests of vegetation, sea-weed, feathers and other available material while the fulmar and black guillemot do not use nest building materials or only slightly arrange pebbles under their eggs. The nests of the black guillemot and the kittiwake are confined to sea-cliffs of the island, which are very unstable and change considerably between years due to wave erosion. Vegetation has not become established at their nest sites. The kittiwake, however, roosts in great numbers on the northern ness of Surtsey and enriches the soil with excrements. In the early years the nests of the fulmar were mostly confined to the sea cliffs but in the last 15 years it has also established nest sites inland, mainly in the cliffs of the old craters where small concentrations of about 5 – 15 pairs are now found in five different locations on the island. Vegetation has not become established at the fulmar nest sites in the unstable sea cliffs but at the inland sites vegetation cover has increased considerably at most of the sites. New plant species for the island have on the other hand never been found at these fulmar nest sites. The great black-backed gull nests inland on Surtsey. During the early years the pairs were solitary with nests far apart. *Honkenya-* and *Leymus*-plants were frequently selected as nest sites but the birds also gather plants and other suitable material when they build the nest (AE. Petersen, personal communication). Plant vigor and cover was enhanced around the nests (Fridriksson 1994) but these soilitary nest sites have never been centres for colonization of new plant species on the island.

In 1986 the first nests of the lesser black-backed gull were found on a lava flat on the southern part of Surtsey. This marked the initiation of the dense gull colony on the island that now consists of the lesser black-backed, herring, great black-backed and glaucous gull (Table 1). These species, with the exception of the great black-backed gull, usually nest in colonies and the nests can be within a short distance (< 10 m) of each other (Sobey & Kenworthy 1979). They build nests that are mostly made of plant material. In the first years of the colony *Racomitrium*-moss was mainly used by the lesser black backed and herring gull for nest building but with increasing cover of vascular plants in the colony grasses and *Honkenya* have also been used (Petersen, unpublished data). The number of breeding pairs in the colony and the extent of the breeding area has increased greatly. In the last thorough bird census on Surtsey in 1990 (Petersen 1993), there were over 150 pairs in the colony (Table 1), and we estimate that the number had risen to at least 300 pairs in 1999. Most of the birds breed within a 7 ha area. The lower part of the colony is on lava terrain but the upper part on lava that has been filled with tephra sand from the slopes above. The forma-

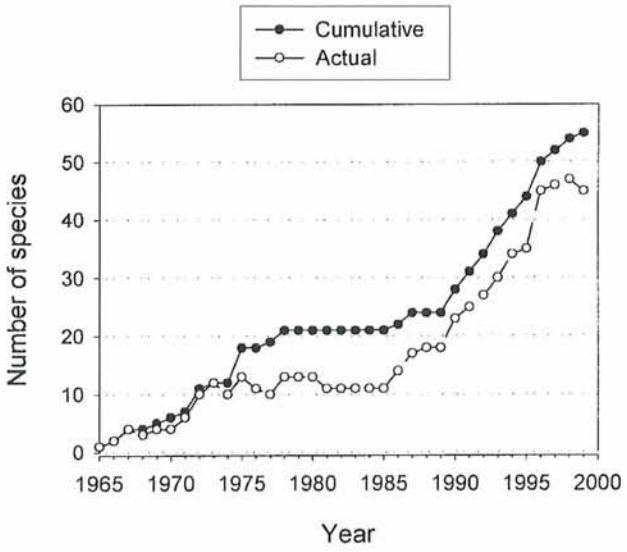

Figure 2. Number of vascular plant species found on Surtsey during 1965-1999, (based on Fridriksson & Magnusson 1992, Fridriksson 1994, 2000).

tion of the colony had immediate effects on vegetation cover within the breeding area. This gull invasion was also followed by a sharp rise in colonization of new plant species on the island (Fig. 2) and most of them were initially found within the colony area (Fridriksson 1994, 2000, Magnússon *et al.* 1996).

METHODS

Permanent plots

During 1990 to 1995 permanent plots, 10 x 10 m in size, were set up on Surtsey. The location of the plots was chosen subjectively with respect to substrate types (sand or lava) and the influence of the gulls on vegetation development in their colony on the southern part of the island. The first five plots were set up in the gull colony area in 1990, in 1994 fourteen plots were added and six in 1995 (Fig. 1, Table 2). Two of the plots (no. 2 and 5) set up in 1990 were taken out of use in subsequent years and one plot on the northern part of the island (nr. 24) was destroyed by sea-floods during the winter of 1997-1998. Therefore 22 permanent plots are currently on the island.

Eight of the plots (no. 1, 3, 4, 6-10) are within the gull colony on the southern part of the island, four plots (no. 20-23) are a short distance above or to the east of the colony where the effects of the gulls were less pronounced when the plots were established, four plots (no. 13-16) are on the easternmost part of the island, five plots (no. 11-12, 17-19) are up in the crater area and one plot (no. 25) is on the lowland ness to the north of the hills (Fig.1). The plots are 5 – 100 m above sea level, ten of the plots are on lava and twelve on sand or sand filled lava (Table 2). The plots replaced older transects set up in 1987 (Magnússon *et al.* 1996).

Table 2. Location, substrate and sampling frequency for permanent vegetation plots on Surtsey.

Plot no.	Year of sampling	Substrate type	Location
1, 3, 4	1990, 1992, 1994, 1996, 1998	sand-filled lava	inside gull colony
6-10	1994, 1996, 1998	lava	inside gull colony
11, 12, 15	1994, 1996, 1998	sand	outside gull colony
13, 14, 16-19	1994, 1996, 1998	sand-filled lava	outside gull colony
20, 21	1995, 1996, 1998	sand-filled lava	outside gull colony
22, 23	1995, 1996, 1998	lava	outside gull colony
25	1995, 1996, 1998	sand	outside gull colony

Vegetation sampling

Vegetation sampling in the plots has generally been carried out every second year (Table 2). Five 10 m line-transects were laid across each plot, parallel at 1, 3, 5, 7 and 9 m from their western edge. Plant cover was determined by line-intercept method. All vascular plant species intercepting the line were recorded and measured and also the total cover of mosses, lichens and bare ground. Additional vascular species within the plots not intercepted by the line were also recorded.

Soil sampling

In 1998 soil samples were taken from all the permanent plots. Four random samples were taken in each plot with a soil corer (7 cm diameter) down to 10 cm depth. After sampling the four samples were mixed to make a composite sample for each plot. In the laboratory the samples were dried at 40°C and sieved through a 2 mm mesh. Measurements of pH were made in an approximate 1:1 mixture with distilled water, content of organic carbon (C%) was determined using a carbon analyser (Leco Carbon Determinator, C–12) and nitrogen (N%) by the Kjeldahl method.

Data analysis

DECORANA-ordination (Hill 1979) was used to investigate the vegetation similarity between individual plots and successional trends based

on the data from the different sampling years. In the input data, species mean cover values were used. The CANOCO-program (ter Braak 1987) was used for the ordination analysis, selecting square-root transformation of the data and downweighing of rare species.

RESULTS

VEGETATION AND SOIL IN 1998

Species richness and cover

Twenty plant species were recorded in the 22 permanent plots in Surtsey in 1998 (Table 3) when a total of 47 species was found on the whole island. Of the 20 species, 9 were found in plots outside the gull colony and 15 in plots inside it. Only 4 species were found in plots in both areas (Table 3). The most abundant species in the permanent plots in 1998 were *Honkenya peploides, Sagina procumbens* and *Puccinellia distans*. These were the only species occurring in half of the plots or more (Fig. 3).

Vegetation cover in the plots in 1998 was around 30% on the average, with vascular plants dominating and mosses and lichens only contributing around 1% (Table 4). *Honkenya peploides* had the highest mean cover, followed by *Puccinellia distans, Poa annua, Stellaria media* and *Cochlearia officinalis*, which all reached over 1% cover.

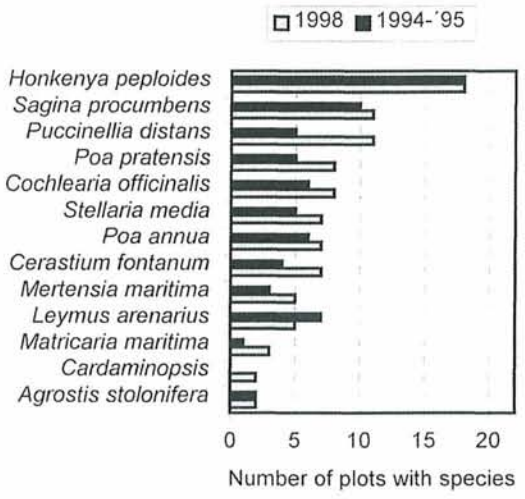

Figure 3. Relative frequency of vascular species in 22 permanent plots in Surtsey at establishment of all plots in 1994 to 1995 and in 1998. Only those species occurring in ≥ 2 plots in 1998 are shown.

Table 3. Vascular plants recorded in permanent plots on Surtsey in 1998 and their occurrance with respect to gull colony. Nomenclature follows Kristinsson (1986).

Species	Plots outside gull colony n=14	Plots inside gull colony n=8
Monocots:		
Agrostis stolonifera		x
Agrostis capillaris		x
Agrostis vinealis		x
Festuca richardsonii		x
Juncus alpinus	x	
Leymus arenarius	x	x
Poa annua		x
Poa pratensis		x
Puccinellia distans	x	x
Dicots:		
Armeria maritima	x	
Cardaminopsis petraea	x	
Cerastium fontanum		x
Cochlearia officinalis		x
Empetrum nigrum		x
Honkenya peploides	x	x
Matricaria maritima		x
Mertensia maritima	x	
Sagina procumbens	x	x
Silene uniflora	x	
Stellaria media		x
Total no. of species	9	15

There was a profound difference in vegetation between plots outside and inside the gull colony (Figs 4-6). Outside the colony the vegetation cover was on average only 5.5% (±2.6 s.e.) and 2.2 (±0.4 s.e.) species were found in each plot. In this area *Honkenya peploides*, was the only species with substantial cover on sand or sand-filled lava (Figs 5 and 10). *Leymus arenarius* and *Mertensia maritima* were most often associated with *Honkenya* but their cover was insignificant. In the two lava plots (no. 22 and 23) located outside the gull colony (Table 2) *Sagina procumbens* was the most prominent species but its cover was very low (<1%).

Within the plots of the gull colony the vegetation cover had reached 71.5% (±11.7 s.e.) in 1998 and 8.6 (±0.8 s.e.) plant species were found in each plot on average (Fig. 11). In the colony *Honkenya* was very abundant in plots with sandy substrate, where its cover was substantially higher than in comparable plots outside the colony. There were however signs of that *Honkenya* had begun to degenerate in the oldest plots in the colony and was giving way to competing species that had invaded the area (Fig. 5). *Poa annua* and *Puccinellia distant* have become very abundant in plots within the gull colony where they were the main dominants with *Honkenya*. *Puccinellia* was more confined to

Table 4. Average plant cover (%) of vascular species, mosses, lichens and bare ground in the 22 permanent plots in Surtsey in 1994 -'95 and 1998, + indicates that cover was not measureable.

	1994 -'95	1998
Monocots		
Agrostis stolonifera	0.05	0.09
Agrostis capillaris	0.01	0.01
Agrostis vinealis	absent	+
Festuca richardsonii	+	0.91
Juncus alpinus	+	+
Leymus arenarius	0.01	0.66
Poa annua	1.84	4.67
Poa pratensis	0.17	0.48
Puccinellia distans	1.72	7.61
Dicots:		
Armeria maritima	absent	+
Cardaminopsis petraea	absent	+
Cerastium fontanum	0.14	0.97
Cochlearia officinalis	0.53	2.03
Empetrum nigrum	absent	+
Honkenya peploides	9.25	9.89
Matricaria maritima	+	+
Mertensia maritima	+	+
Sagina procumbens	0.72	0.74
Silene uniflora	+	+
Stellaria media	0.05	2.66
Vascular plants total:	13.71	28.71
Mosses	1.32	0.79
Lichens	+	0.01
Bare ground	85.49	73.28

the lava plots while *P. annua* had higher cover in the sandy plots (Fig. 5). Other species that were common in plots of the gull colony and attained considerable cover in one or more plots were *Stellaria media, Cochlearia officinalis, Sagina procumbens, Cerastium fontanum, Festuca richardsonii, Leymus arenarius* and *Poa pratensis* (Table 4).

Ordination results

The results of the ordination also show a clear distinction in vegetation between sand and lava areas and the vegetation changes that have occurred within the gull colony (Fig. 7). Tightly clustered to the right on the ordinatation diagram, with the highest scores on axis 1, are plots from sand or sand-filled lava. These plots represent the initial stage in the vegetation succession on sand on Surtsey. It can be described as the *Honkenya*-stage as *H. peploides* is the only species commonly occurring in the plots and with substantial cover (Figs 5 and 10). Other species that were recorded with measureable cover in one or more these plots were *Leymus arenarius, Mertensia maritima* and *Sagina procumbens*. In the lava plots the initial stage of plant succession is characterized by colonization of *Sagina procumbens*, and may therefore be described as the *Sagina*-stage. The two plots (no. 22 and 23) representing this stage have the highest scores on axis 2 on the ordination diagram (Fig. 7). The cover of *Sagina* is, however, very low at this stage as described above.

The changes from these initial stages affected by the breeding gulls are clearly demonstrated on the diagram (Fig. 7). All the plots within the gull colony are far removed from the initial stages. The changes appear greater in the lava plots and their vegetation is also more diverse than in the sand plots within the colony. In the sand plots (1, 3 and 4) *Honkenya peploides, Poa annua* and *Stellaria media* were the dominant species and other species recorded with relatively high cover in one or more of these plots were *Cerastium fontanum, Leymus arenarius* and *Poa pratensis*. Species of less prominence but occurring in all the sand plots in the colony were *Cochlearia officinalis, Sagina procumbens* and *Puccinellia distans*. One of the lava plots (10) is

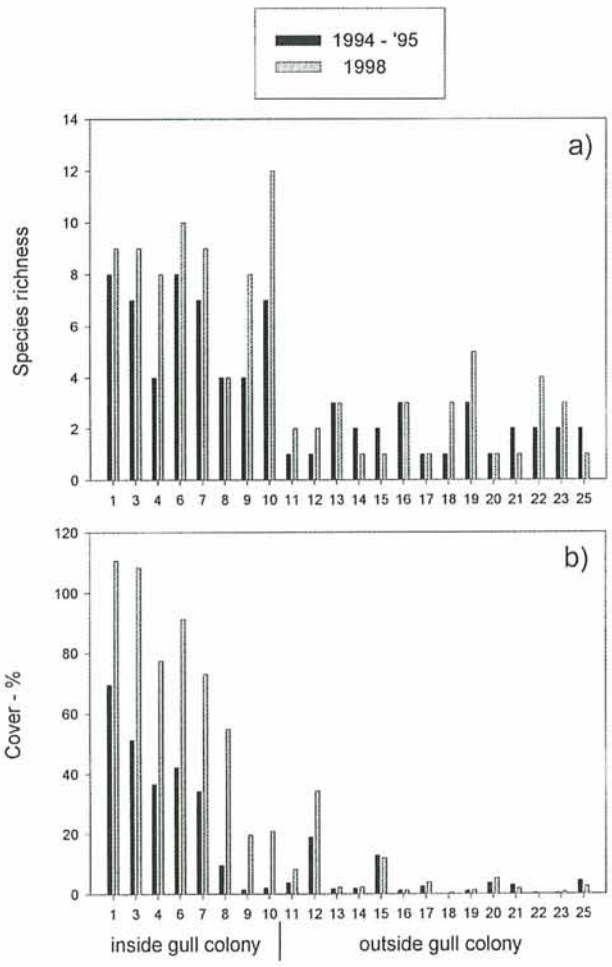

Figure 4. Species richness (a) and vascular plant cover (b) in permanent plots in Surtsey in 1994 -'95 and in 1998. Plots no. 1-10 are inside gull colony, plots no. 11-25 are outside it.

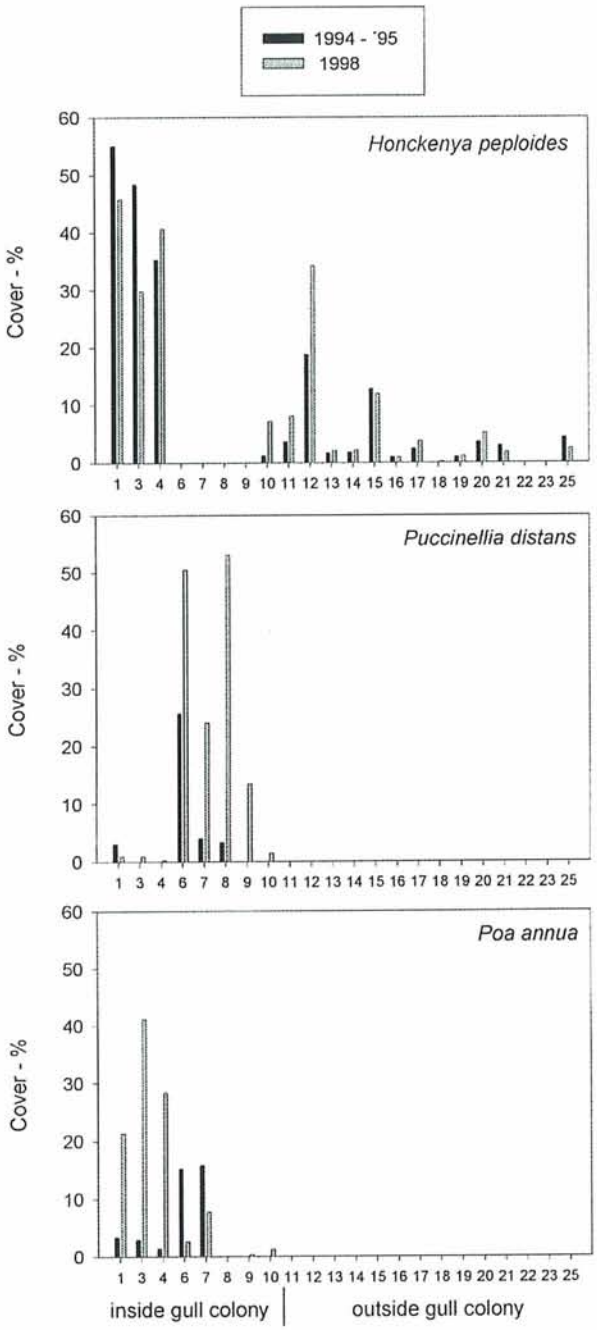

Figure 5. Cover of *Honkenya peploides, Puccinellia distans* and *Poa annua* in permanent plots in Surtsey in 1994 -'95 and 1998. Plots no. 1-10 are inside gull colony, plots no. 11-25 are outside it.

positioned close to the sand plots in the ordination results (Fig. 7). In the plot there is slight sand, which has enabled *Honkenya* to grow in it. In 1998 it was the dominant species in the plot, but otherwise the species were more characteristic of the vegetation of the gull colony. The other lava plots (6, 7, 8 and 9) of the gull colony are separated further to the left on the ordination diagram (Fig. 7). In all of these plots *Puccinellia distans* was the dominant (Fig. 5) and other species that were common to the plots was the initial colonizer *Sagina procumbens* and *Cochlearia officinalis* and *Poa pratensis*. Other species that had considerable cover in one or more of these four plots in 1998 were *Cerastium fontanum, Stellaria media, Festuca richardsonii* and *Poa annua*. It should be noted that *Honkenya* was not found in any of these plots.

Soil results

In the soil sampled in 1998 and analysed for pH, total C and N, there was a considerable difference between plots outside the gull colony and inside it. The soil from the gull colony was lower in pH and higher in C and N (Table 5). In plots outside the colony the pH was in the range of 6.83 – 8.04 compared to 6.17 – 6.69 inside. C and N content of the samples taken outside the colony were in most cases below limits of quantification of the methods used (0.105% for C and 0.004% for N). In samples from inside the colony total C ranged from 0.37 – 3.33% and the total N 0.03 – 0.26% (Table 5). The highest C and N levels were from plots (6 and 7) that were in the oldest part of the colony where the first breeding gull pairs were found in 1986.

Table 5. Results of analysis of soil samples taken from permanent plots in Surtsey in 1998. Plots 1-10 are inside gull colony, plots 11-25 outside it. For carbon the limit of quantification was 0,105% and 0,004% for nitrogen.

Plot	pH	C %	N %
1	6.38	0.647	0.057
3	6.38	0.576	0.054
4	6.69	0.366	0.037
6	6.28	2.534	0.228
7	6.17	3.329	0.257
8	6.38	0.827	0.069
9	6.51	0.427	0.034
10	6.61	0.429	0.035
11	8.04	< 0.105	< 0.004
12	7.57	< 0.105	< 0.004
13	7.52	< 0.105	< 0.004
14	7.55	< 0.105	< 0.004
15	7.56	< 0.105	< 0.004
16	7.39	< 0.105	< 0.004
17	8.00	< 0.105	< 0.004
18	7.50	< 0.105	< 0.004
19	7.44	< 0.105	< 0.004
21	7.60	< 0.105	< 0.004
22	6.83	< 0.105	0.008
23	6.88	< 0.105	0.006
25	7.67	< 0.105	0.011
Average:			
1-10	6.42	1.141	0.096
11-25	7.50	(<0.105)	(<0.004)

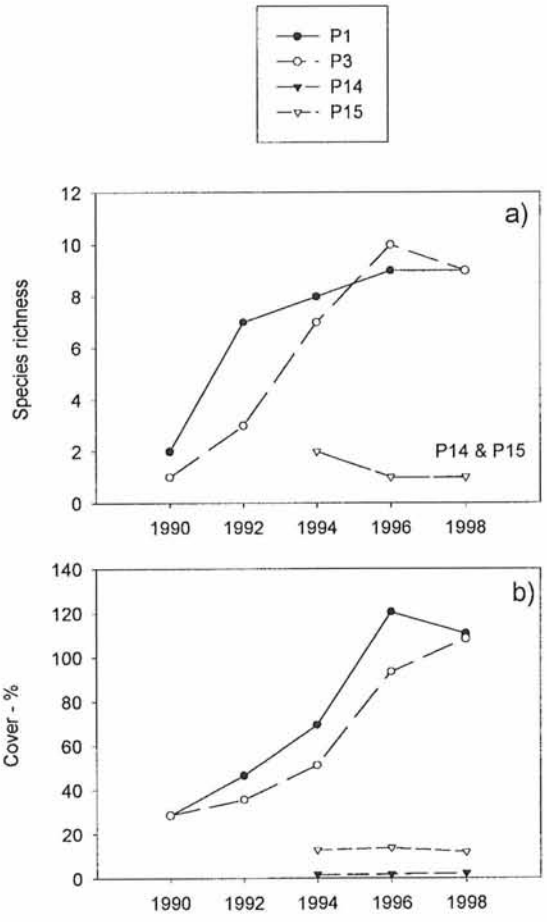

Figure 6. Changes in species richness (a) and cover (b) in plots inside (P1, P3) and outside (P14, P15) gull colony during 1990 – 1998.

The close relationship between vegetation and soil development on Surtsey and how it is affected by the breeding gulls is also demonstrated on Fig. 8, where the results of soil carbon analysis have been superimposed on the ordination results.

VEGETATION CHANGES FROM 1990

The first permanent plots in Surtsey were set up in a sandy area of the gull colony in 1990. Repeated measurements of vegetation in these plots and other plots set up on the island in subsequent years showed a steady increase in species richness and vegetation cover. This increase is, however, mostly confined to plots within the gull colony. Outside the colony they are not as distinct (Fig. 4-6). There was only a substantial increase in cover in one plot (no. 12) outside the gull colony (Fig. 4). The plot is within 40 m of a small crater where fulmars have been nesting in increasing numbers in the last few years and are probably affecting the site.

When the first plots were established in the gull colony in 1990 the effects of the gulls on the vegetation were noticable. At that time only one to two species were found in each plot and vegetation cover was around 30% (all *Honkenya*) which was high for the island at that time. In 1998 the number of species in the plots had risen to between eight and ten and several species in addition to *Honkenya*, e.g. *Poa annua, Stellaria media, Leymus arenarius* and *Poa pratensis,* had attained a high cover in the plots. Total vegetation cover in the plots at that time had reached 100% (Figs. 6 and 11). In comparable plots, set up in 1994 outside the gull colony, there has not been an increase in species number. *Honkenya* was the only species in these plots in 1998 and its cover has not changed from 1994 (Fig. 6). The two plots (14, 15) shown in the example are from one of the oldest *Honkenya*-areas on Surtsey that was initially colonized by the species in 1968 (Fig. 10).

In the gull colony a similar trend to the sandy plots can also be seen in the lava plots when different years are compared, although the sampling period is shorter. Total vegetation cover in the lava plots in 1998 was generally lower than in the sandy plots but the species richness was comparable (Fig. 4). As described above *Sagina procumbens* was the initial colonizer of the lava plots but in the colony *Puccinellia distans* has become the main dominant. Several other species also occurred in the plots.

The relative vegetation changes in the permanent plots from 1990 to 1998 are also revealed by the ordination, when the placement of the

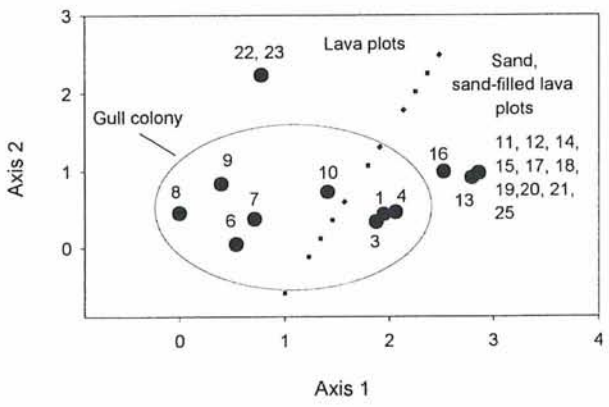

Figure 7. DECORANA-ordination results of the permanent plots on Surtsey for the year 1998.

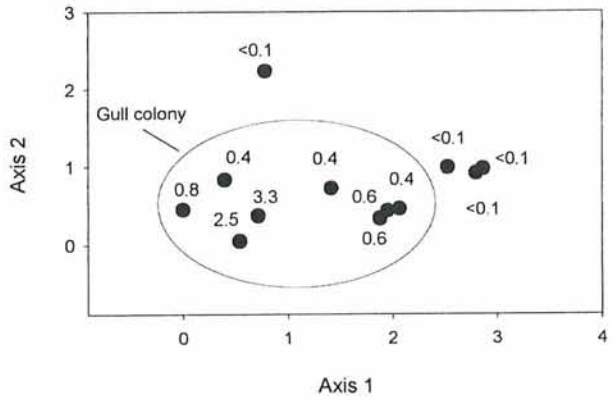

Figure 8. Results of analysis of soil carbon content in permanent plots in 1998 (C%) superimposed on the DECORANA-ordination results. Placement of plots is the same as shown on Fig. 7.

same plot in different years was studied (Fig. 9). The first two DCA axes accounted for 90% (72+18) of the variation extracted by the four axes given in the analysis. As shown on Fig. 7 and described above, the plots with the highest scores on axes 1 and 2 represent the initial stages of vegetation succession on sand (*Honkenya*-stage), (Fig. 10) and lava (*Sagina*-stage) on Surtsey. Changes or movement of plots from these stages represent successional changes influenced by the gulls in the breeding colony. The movement of plots between years on the ordination diagram (Fig. 9) are caused by changes in species composition and relative cover. Changes in species composition are due to new colonization as species have generally not been outcompeted in the plots yet. The ordination results indicate that the vegetation changes have been greatest during the first years, but slow down with increasing species richness and cover in the plots (Fig. 9).

DISCUSSION

Succession outside gull colony

On most of Surtsey relatively small vegetation changes took place in the permanent plots during the study period. The sand areas had already been colonized by coastal species, mainly *Honkenya peploides, Leymus arenarius* and *Mertentsia maritima* which all are clonal perennials (Davy & Figueroa 1993) adapted to the nutrient-poor habitats. The vegetation cover of this simple community is low (< 20%) and has generally not increased in the last years, which was also found in previous monitoring of the sand areas on eastern Surtsey during 1987 and 1994 (Magnússon *et al.* 1996). *Honkenya peploides* has been the most successful colonizer and is the dominant species on the sand (Fig. 10). The population growth of *Honkenya* on Surtsey was fast in the early years but individuals of the species started producing seeds on the island in 1971, which compares to 1977 for *Mertensia* and 1979 for *Leymus* (Fridriksson 1992, Magnússon *et al.* 1996). *Armeria maritima, Cardaminopsis petraea* and *Silene uniflora* were all recorded in permanent plots outside the gull colony in 1998. These species, which are very common on infertile gravel and sandy flats in Iceland, did not become established on the island until the period 1986-1991 (Fridriksson 1994). They have all been producing seeds on the island for a number of years and will probably become more prominent members of the sand community in the near future.

The permanent plots in the bare lava areas, outside the gull colony, have mostly been devoid of vascular plants. Only *Sagina procumbens* and *Puccinellia distans* have spread onto the lava, but total plant cover remains extremely low (< 1%). The spread of both species onto the lava areas has probably been facilitated by their high abundance within the gull colony where seeds may have been dispersed from.

The soil of Surtsey, apart from the gull colony, is poorly developed and has a relatively high pH and very low content of C and N, comparible to mobile coastal dunes (Lundberg 1987). In spite

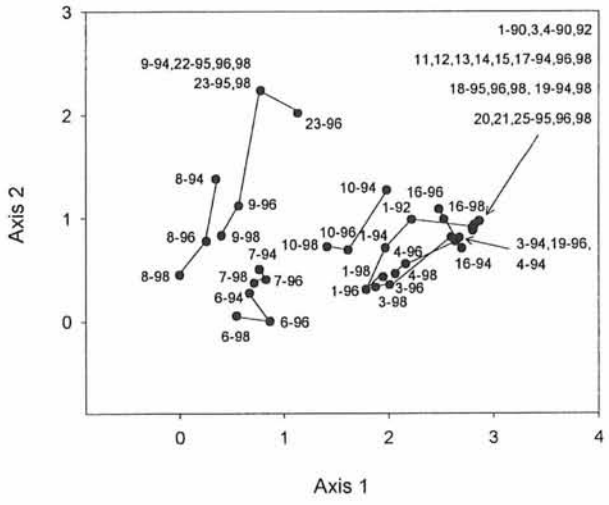

Figure 9. DECORANA-ordination results for permanent plots in the different sampling years. Lines show relative vegetation changes in individual plots between years, 1-90: plot 1 in 1990, etc. (The 1998 plots have the same positions on this diagram as on Fig. 7).

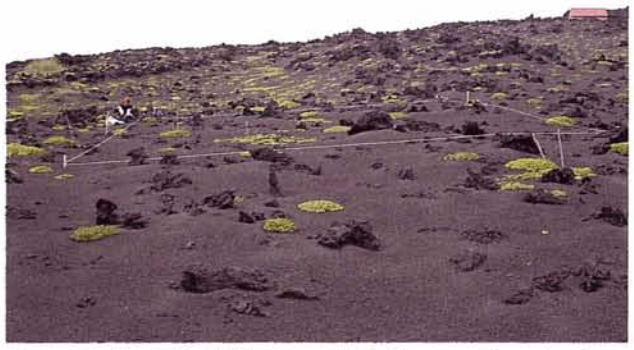

Figure 10. Plot 14 in 1998, on sand-filled lava outside gull colony. *Honkenya peploides*, had 2% cover and was the only species in the plot.

of the poor development the soils of the simple *Honkenya*-community in Surtsey have been shown to have higher root, microbial and microfaunal activity and carbon content than sand areas without vegetation on the island (Magnússon 1992, Frederiksen 1999).

Succession within gull colony

There were profound changes in vegetation in permanent plots within the gull colony where vegetation cover and species richness increased greatly over the study period (Fig. 11). The driving force of these changes is the nutrient enrichment of the soil by the gulls and introduction of new plant species, which also appears to be related to the activity of the gulls. At their breeding sites gulls deposit faeces and regurgitate pellets, fish and marine invertebrates are spilled on the ground during feeding of young and corpses of young and adult birds that die within the colony decompose at the sites. Nest material may also be brought into the sites. The most significant of these for the vegetation development are the faeces that have a relatively high content of nitrogen, phosphorus, potassium and minerals (Sobey & Kenworthy 1979).

The rise in the rate of colonization of new plant species on Surtsey, mostly within the gull colony, following the invasion of the lesser black-backed and the herring gull is more difficult to explain and only a speculative attempt can be made. If the colonization is primarily due to improved nutrient status of the soil within the colony, then why have the more dispersed inland nest sites of the great black-backed gull and of the fulmar never been the hotspots of colonization of new plant species? The explanation may be found in the feeding ecology of these bird species.

Both lesser black-backed and herring gull are frequently seen in grassland and hayfields in coastal areas in southern Iceland where they feed on insects and earthworms. Plant seeds may also be selected and eaten directly or indirectly with earthworms. Viable seeds have been found in the digestive tract and casts of earthworms (Grant 1983, Reest & Rogaar 1988, Thompson *et al.* 1994). Some such seeds are from the same species or genus (e.g. *Sagina procumbens, Cerastium fontanum, Stellaria media, Epilobium, Poa annua, Agrostis spp., Capsella bursa-pastoris, Taraxacum ssp.* and *Rumex spp.*) that have been found within the gull colony of Surtsey. In a study of vegetation of gull colonies (lesser black-backed, herring, great black-backed gull) on islands in Britain, Gilham (1956) found that gulls can disperse plant seeds. In regurgitated pellets viable seeds of barley and wheat were found that the gulls had carried from at least 15 – 20 km distance. In the pellets viable seeds of *Cerastium, spp., Festuca, spp., Poa annua, Polygonum aviculare, Rumex, spp., Stellaria media* and other species were also found (Gilham 1956, 1970).

The great black-backed gull depends more on fish, carcasses and spill and feeds more on the shore or out at sea than the two other gull species (Petersen, personal communication). The fulmar gets all its food from the sea and does not visit other inland areas than nesting sites. It may also matter here that the lesser black-backed and the herring gull tend to build as bulky nests as the great black-backed gull, not to mention the fulmar which does not collect material for its nest scrap (Table 1). In a study of the nest-building activities of herring gulls in Scotland it was found that the birds collected most of the plant material used for nest building near the nest sites within the colony area. A few birds, however, brought in material from outside the colony (Sobey & Kenworthy 1979). In the first years of the gull colony in Surtsey grass cover on the island was so scarce that it may have forced some of the gulls to visit the neighbouring islands (≥5 km) to collect plant material for their nests.

The vegetation succession on Surtsey has changed considerably after the formation of the gull colony. A number of new plant species have colonized the island, the nutrient status of the soil has improved which has enabled nutrient demanding plants to become established and also improved the conditions of older species on the

island. The main species that have taken advantage of the improved conditions within the colony area are *Sagina procumbens, Poa annua, P. pratensis, Puccinellia distans, Cerastium fontanum, Cochlearia officinalis* and *Stellaria media*. Most of these species prefer disturbed and/or nutrient-rich habitats and have high seed production (Kristinsson 1986, Grime *et al.* 1988). *Poa annua* and *Stellaria media* are annuals, but annual species had not been able to become firmly established on Surtsey before the formation of the gull colony.

In the oldest plots in the center of the gull colony, changes in vegetation composition and cover between years appear to have slowed down in the last few years (Figs 6 and 9). With the formation of a closed sward it will be more difficult for new species to colonize the area and plants of small stature may be outcompeted. In some of the lava plots the cover of *Sagina procumbens* has started to decrease but the species has not disappeared in any of the plots yet. The vegetation of the outer Westman islands is characterized lush grassland and forb communities that are species poor and under strong influences of seabirds (Fridriksson & Johnsen 1967). All the key species of these communities, with the exception of *Angelica archangelica,* have now become established within the gull colony on Surtsey. The vegetation development within the colony will probably be into the direction of the communities found on the other islands. *Festuca richardsonii* is the dominant species in grass swards on the islands (Fridriksson & Johnsen 1967) but in the gull colony on Surtsey the species is rather infrequent in comparison to *Puccinellia distans* and *Poa annua* (Table 4). Where *Festuca* is found within the gull colony it forms very dense patches by vegetative expansion. Only one of the permanent plots (6) contains *Festuca* where its cover increased from less than 1% in 1994 to 20% in 1998, which may be indicative of the growth potential of the species.

The results of the soil analysis showed that there has been a considerable build-up of soil organic matter within the gull colony in the 13 year period from its formation (Table 5). However, the carbon content of the soil within gull colony in Surtsey is still relatively low in comparison to freely drained grassland soils in Iceland where the organic carbon is commonly in the range of 5-15% (Helgason 1968). Recent studies of the soil biota on Surtsey have demonstrated that the activity and diversity of soil organisms is much higher in the gull colony than in other habitats on the island (Frederiksen 1999, Gjelstrup 2000, Sigurdardóttir 2000).

Figure 11. Plot 1 in 1998, on sand-filled lava inside gull colony. The plot had 9 plant species in 1998 and extent of bare ground was only 8%. *Honkenya peploides* was the dominant species with 46% cover, *Poa annua, P. pratensis, Stellaria media, Cerastium fontanum* and *Leymus arenarius* had also a relatively high cover in the plot.

ACKOWLEDGEMENTS

The Surtsey Research Society has provided logistic support for the study. The initiation of the project was funded by the Icelandic Research Council. Ásrún Elmarsdóttir, Áslaug R. Áslaugsdóttir and Jón Gudmundsson assisted with the field work and Hans Hansson with graphic work. AEvar Petersen provided information on the birds and made remarks on the manuscript. Sturla Fridriksson has contributed to the project in various ways. The first author worked on this paper during a stay at the Botanical Institute of the University of Copenhagen.

References

Davy, A.J. & M.E. Figueroa 1993. The colonization of strandlines. *In* Miles, J. & D.W.H. Walton (eds). Primary Succession on Land. Special publication nr. 12 of the British Ecological Society. Blackwell Sci. Pub., Oxford, pp. 113-131.

Einarsson, E., 1973. Invasion of terrestrial plants on the new volcanic islands Surtsey. *In* Ecology and Reclamation of Devasted Land. (Papers of an International Symposium on Ecology and Revegetation of Drastically Disturbed Areas, held in August 1969 at The Pensilvania State University, U.S.A.). London, pp. 253-270.

Frederiksen, H.B., 1999. Soil microbiota responses. Effects of plants, soil properties and elevated CO_2. Part II. Microbiota on Surtsey. Ph.D.-Thesis, Zoological Institute, Dept. of Terrestrial Ecology, Universtiy of Copenhagen, Denmark, 66 pp.

Fridriksson, S., 1966. The pioneer species of vascular plants in Surtsey *Cakile edentula*. Surtsey Res. Progr. Rep. II: 63-65.

Fridriksson, S. 1975. Surtsey. Evolution of life on a volcanic island. Butterworths, London, 198 pp.

Fridriksson, S. 1992. Vascular plants on Surtsey 1981-1990. Surtsey Res. Progr. Rep. 10: 17-30.

Fridriksson, S. 1994. Surtsey. Lífríki í mótun. Hið íslenska náttúrufræðifélag og Surtseyjarfélagið, Reykjavík, 112 pp.

Fridriksson, S. 2000. Vascular plants on Surtsey 1991-1998. Surtsey Res. 11:21-28.

Fridriksson, S., & B. Johnsen 1967. The vascular flora of the outer Westman Islands. Societas Scientiarum Islandica, Greinar IV (3): 37-67.

Fridriksson, S. & B. Magnússon 1992. Development of the ecosystem on Surtsey with references to Anak Krakatau. GeoJournal 28(2): 287-291.

Gilham, M.E., 1956. Ecology of the Pembrokeshire Islands. V. Manuring by the colonial seabirds and mammals, with a note on seed distribution by gulls. Journal of Ecology 44: 429-454.

Gilham, M.E. 1970. Seed dispersal by birds. *In* F. Perring (ed.) The Flora of Changing Britain, Botanical Society of the British Isles, Cambridge, pp. 90-98.

Gjelstrup, P. 2000. Soil Mites and Collembolans in Surtsey, Iceland, 32 years after the eruption. Surtsey Res. 11: 43-50.

Grant, J.D. 1983. The activities of earthworms and the fates of seeds. *In* J.E. Satchell (ed.) Earthworm Ecology , Chapmann & Hall, London, p. 107-122.

Grime, J.P., J.G. Hodgson & R. Hunt 1988. Comparative Plant Ecology. A Functional Approach to Common British Species. Unwin Hyman, London.

Helgason, B. 1968. Basaltic soils of south-west Iceland. II. J. Soil Sci. 19: 127-134.

Hill, M.O. 1979. DECORANA – A FORTRAN program for Detrended Correspondence analysis and Reciprocal averaging. Ecology and Systematics, Cornell University, Ithaca, New York.

Jakobsson, S.P. 1993. Surtseyjareldar 1963-1967 og jarðfræðirannsóknir í Surtsey 1967-1993. *In* S.P. Jakobsson, S. Friðriksson & E. Hauksson (eds). Surtsey 30 ára. Surtseyjarfélagið, Reykjavík, p. 1-7.

Jakobsson, S.P. 1998. Surtsey 35 ára. Náttúrufræðingurinn 68: 83-86.

Jóhannsson, B. 1968. Bryological observation on Surtsey. Surtsey Research Progress Report 4: 61.

Kristinsson, H. 1972. Studies on lichen colonization in Surtsey 1970. Surtsey Res. Progr. Rep. 6: 77-78.

Kristinsson, H. 1986. Plöntuhandbókin. Blómplöntur og byrkningar. Bókaútgáfan Örn og Örlygur, Reykjavík.

Lundberg, A. 1987. Sand dune vegetation on Karmøy, SW Norway. Nordic Journal of Botany 7: 453-477.

Magnússon, B. 1992. Soil respiration on the Volcanic Island Surtsey, Iceland in 1987 in Relation to Vegetation. Surtsey Res. Progr. Rep. 10: 9-16.

Magnússon, B., S.H. Magnússon & J. Gudmundsson 1996. Vegetation succession on the volcanic island Surtsey. Búvísindi, Icel. Agr. Sci. 10: 253-272. (In Icelandic with an English summary).

Petersen, AE. 1993. Fuglar. *In* S.P. Jakobsson, S. Fridriksson & E. Hauksson (eds). Surtsey 30 ára. Surtseyjarfélagið, Reykjavík, p. 14.

Reest, P.J. van der & H. Rogaar 1988. The effect of earthworm activity on the vertical distribution of plant seeds in newly reclaimed polder soils in the Netherlands. Pedobiologia 31: 211-218.

Schwabe, G.H. 1970. On the algal settlement in craters on Surtsey during summer 1968. Surtsey Res. Prog. Rep. 5: 68-69.

Sigurdardóttir, H. 2000 Status of collembolans (Collembola) on Surtsey in 1995 and first encounter of earthworms (Lumbricidae) in 1993. Surtsey Res. 11: 51-55.

Smith, H.G. 1970. An analysis of Surtsey substratum for Protozoa. Surtsey Res. Progr. Rep. 5: 78-79.

Sobey, D.G. & J. B. Kenworthy 1979. The relationship between herring gulls and the vegetation of their breeding colonies. Journal of Ecology 67: 469-496.

ter Braak, C.J.F. 1987. CANOCO - a Fortran programme for canonical community ordination by correspondence analysis, principal component analysis and redundancy analysis. TNO Institute of Applied Computer Science. Statistics Department Wageningen, The Netherlands.

Thompson, K., A. Green & A.M. Jewels 1994. Seeds in soil and worm casts from neutral grassland. Functional Ecology 8: 29-35.