Vascular plant colonisation, distribution and vegetation development on Surtsey during 1965–2015

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ABSTRACT

Since Surtsey was formed in 1963–1967, colonisation of vascular plants has been recorded by locating the first colonists of each species within a 1 ha (100x100 m) quadrat grid system of the island. The abundance of individual vascular plant species was further recorded within the grid in 1996-1997, 2005-2006, and 2014-2015 using a three graded abundance scale from rare to common.

During 1965–2015, a total of 74 vascular plant species were found on Surtsey. The colonisation was considerable between 1965–1979 followed by a stagnation period. After the establishment of a dense seagull colony on the southern part of the island in 1986, colonisation increased greatly and peaked between 1992–1995. The colonisation differed greatly between surface types, being highest on sandy lava and barren lava, relatively low on eolian sand and coastal sediments, and none on palagonite tuff. By classification and ordination six main vegetations types were identified over the period 1996–2015, forming a gradient from scattered, species poor pioneer vegetation to a dense, lush vegetation developed under by high nutrient input from breeding seagulls. Over this period major vegetation changes occurred. Areas with pioneer vegetation have greatly decreased, while areas with Honckenya and gravel flat vegetation, and forb rich grassland have increased. The number of species per ha increased on average from 4.8 to 7.2 and 10.4 in the years 1996-1997, 2005-2006, 2014-2015 respectively. Despite the great influence of seabirds within their breeding colony, most of the island still has sparse vegetation cover. The colonising species differed greatly in their rate of dispersal. Species with the greatest rate were *Honckenya peploides, Poa annua* and *Silene uniflora*, followed by *Sagina procumbens, Puccinellia coarctata, Cerastium fontanum, Arabidopsis petraea, Leymus arenarius* and *Rumex acetosella*. They are either pioneers and/or ruderals and are common on the mainland of Iceland, where they grow in sparsely covered, rocky or sandy areas or on land that has been disturbed.

INTRODUCTION

Surtsey was formed in a submarine eruption in 1963–1967 and became the westernmost island of the Westman Islands archipelago and the southernmost island of Iceland. The island was considered unique and therefore it was of great interest to follow geological and geomorphological changes of the island and the colonisation of life and primary succession on the new land (Norrman J.O. 1970, Jakobsson et al. 2000, Baldursson & Ingadóttir 2007, Romagnoli & Jakobsson 2015). Therefore, in 1965, Surtsey was protected by law in order to minimize the effect of human activities (Baldursson & Ingadóttir 2007). Various types of research have been performed on Surtsey and in 2008 the island was accepted onto the UNESCO World Heritage List due to its unique nature and the research activities taking place there (Hermannsson 2009).

Colonisation of plants and animals has been intensively studied on Surtsey ever since the island was formed. The first organisms to establish on the island were probably bacteria and fungi (Schwabe 1970). Vascular plants were also early colonisers with the first individuals found in 1965 (Fridriksson 1966). During the first two decades colonisation and succession was characterised by coastal plants as the species *Honckenya peploides* and *Leymus arenarius*[1] were forming a sparse vegetation in sandy areas (Fridriksson 1992, Magnússon et al. 2009). Mosses were first observed in 1967 and lichens in 1970 (Jóhannsson 1968, Kristinsson 1972). These two groups have formed continuous cover in a few spots on the island. However, vascular plants have been of far greater significance in vegetation development on the island (Kristinsson & Heiðmarsson 2009, Ingimundardottir et al. 2014, Magnússon et al. 2014.

Colonisation by invertebrates and birds has been studied on Surtsey (Ólafsson & Ingimarsdottir 2009, Petersen 2009). The first records of invertebrates were in 1964 (Friðriksson 1964) and the first birds started breeding in 1970 (Petersen 2009).

From 1990 vegetation succession and soil development has been investigated in permanent plots distributed in different habitats on the island (Magnússon & Magnússon 2000, Magnússon et al. 2009, 2014). Subsequently, these plots have also been used for studies of invertebrate fauna, ecosystem functions and density of seabird nests. (Magnússon et al. 2009, Ólafsson & Ingimarsdóttir 2009, Sigurdsson 2009, Sigurdsson & Magnússon 2010, Leblans et al. 2014).

Significant changes have taken place in the vegetation of Surtsey with time, largely due to a breeding colony of seagulls that started forming in 1986 on the southern lava fields of the island. The colony remained spatially well confined during the first years but has since expanded in area (Magnússon et al. 2014). After 1986 the colonisation by new plant species increased significantly on the island (Magnússon et al. 2014). Comparison of plots inside and outside the seagull colony indicate a great influence of the birds on plant succession and soil development. They show an increase in vegetation cover, ecosystem respiration, soil carbon and nitrogen content, lower soil pH and soil temperatures in plots within the colony (Sigurdsson & Magnússon 2010).

Since the formation of the island, colonisation of vascular plants has been closely monitored in annual visits by scientists using a 100 x 100 m grid system, which was established on the island in order to accurately map the location of individual plants (Fridriksson & Johnsen 1968). In 2015 a total of 74 species had been discovered on Surtsey, or 15% of Iceland's native vascular plant flora. Of them 64 were found living that year (Magnússon et al. 2020).

In the years 1996-1997 the abundance of all vascular plants on the whole island was mapped within the grid. This was repeated in 2005-2006 and again in 2014-2015. The purpose of this mapping was to obtain information on the distribution of vascular plants on the island and to monitor the rate of dispersal and distribution of individual species. In this paper we describe the colonisation and distribution of the vascular plant species on Surtsey, where and in what types of land they were found. We also describe the main vegetation types found on the island in 2015 and how the vegetation has changed over time.

STUDY AREA

Surtsey is the southernmost of the Westman Islands and is 32 km off the south coast of Iceland (Fig. 1). It was formed during an eruption from the sea floor that lasted from 1963 to 1967. During the eruption, two main tephra cones were built up from two craters on the northern part of the island, while the southern part was formed by lava flows which are mainly of the smooth pahoehoe type, though rugged aa flows are also found (Baldursson & Ingadóttir 2007). At the end of the eruption in 1967 the island had reached an area of 2.65 km^2 and a height of 174 m a.s.l. (Jakobsson et al. 2000). Over time, the island has changed greatly. Large parts of the lava fields on the southern part have disappeared due to marine abrasion and erosion (Jakobsson et al. 2000, Óskarsson et al. 2020). On the northern and leeward side, a spit was formed by accumulation of eroded costal sediments (Fig. 1). In addition, the tephra cones have gradually been transformed into denser palagonite tuff (Jakobsson et al. 2000, Óskarsson et al. 2020). In 1972 the area of the island had decreased to 2.25 km^2, in 1996 to 1.54 km^2, and in 2014 1.31 km^2 (Fig. 1). In 2014 the highest point on the island was 154 m above sea level and thus was 20 m lower than at the end of the eruption in 1967. During 1972–1996, the island decreased on average by 3 ha per year and by 1.3 ha per year during 1996–2014. These changes have been greatest in areas below 60 meters (Fig. 1). Due to the heavy marine abrasion, high cliffs have formed around the island except at the leeward northeastern side. With time the surface characteristics have also changed considerably. The highest cones around the

1 Nomenclature follows Wąsowicz 2020.

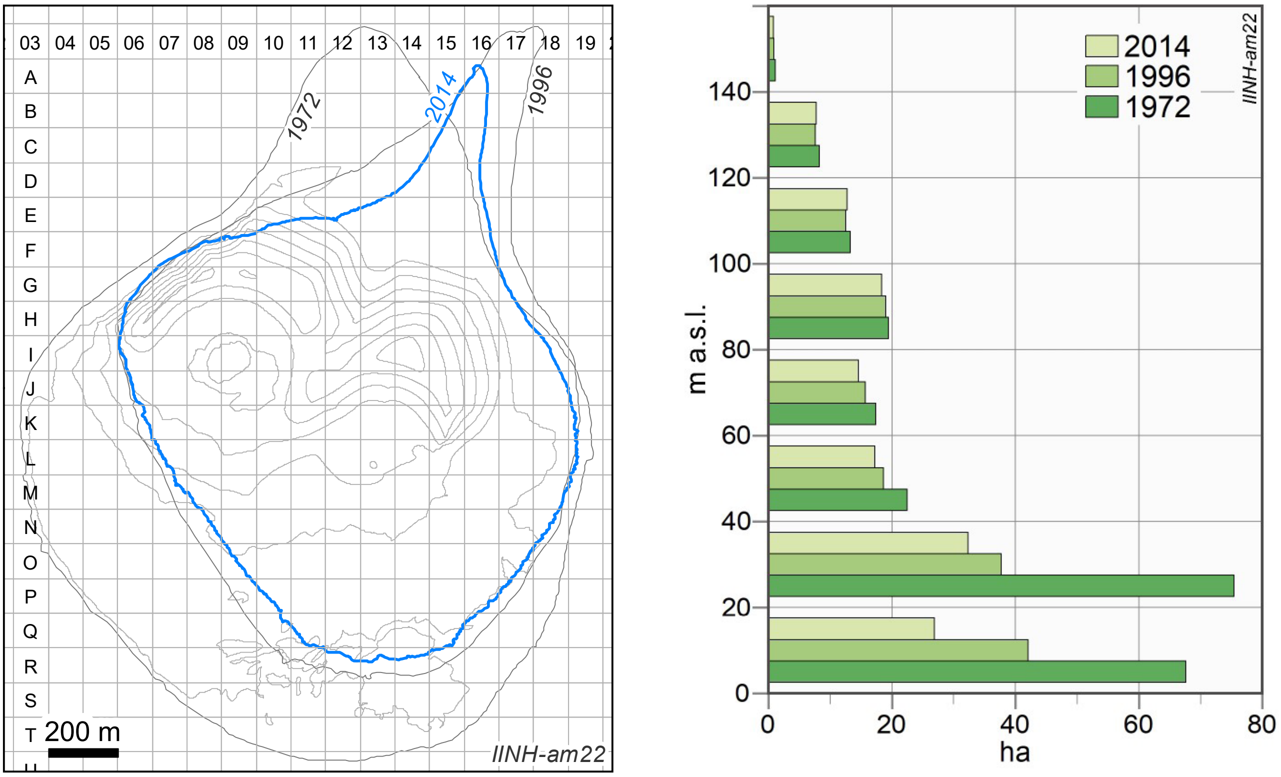


Fig. 1. (A) Map showing the size and outline of Surtsey in 1972, 1996 and 2014. Contour lines (20 m) are based on data from 1972. Also shown is a 100 x 100 m grid system that has been used since the end of the eruption in 1967 to map the distribution of plants on the island. (B) Area of Surtsey by altitude in 1972, 1996 and 2014.

craters now consist of a hard but relatively smooth surface, with a thin layer of gravel and tephra in the most sheltered places. Tephra and sand have also been moved by wind and water from the upper to lower areas and accumulated on lower slopes and the lava below (Óskarsson et al. 2020). However, on the southernmost parts of the lava only fine material is found.

Based on data from an automatic weather station (2009–2019) the climate on Surtsey is relatively mild but windy, with a monthly mean temperature above freezing during all calendar months and wind speed exceeding 20 m/s for 30 days a year on average (Petersen & Jónsson 2020). The warmest month is August with a mean of about 11.3 °C and December the coldest with an average temperature of 3.2 °C. The mean annual precipitation is about 1000 mm, the summer months being the driest and October, on average, the wettest. According to the temperature data, the growing season on Surtsey is long compared to other sites in Iceland as a daily mean temperature above 4 °C generally begins in the middle of April and lasts until November.

METHODS

Plant colonisation and establishment

In 1967 a 100 x 100 m grid system covering the whole island was established in order to map and monitor accurately the location of individual plants (Fridriksson & Johnsen 1968) (Fig. 1). During the first decade all new individuals found were also precisely marked, usually with a wooden stake and given a number. In the first years the fate of all plants was also assessed. By 1979 new individuals had become so numerous that their marking was no longer possible. After that, only the first individuals of new species on the island were systematically marked. From 1998, the location of new colonists has also been recorded by GPS coordinates (Magnússon et al. 2009).

In the present study the relationship between plant colonisation and different surface types on the island was explored by examining in what surface type the first two individuals of each species were found. The classification was based on a modified geological map from 2004 made by Jakobsson (2006). Due to surface changes of the island, this classification is not accurate in all cases, but should still give a good overview of the main types of land in that plants have colonised. Seven of the tagged plant locations were in areas that had been destroyed by marine abrasion before 1996. These places were classified based on a geomorphological map of Surtsey from 1972 (Norrman et al. 1974).

Abundance and distribution

The abundance of individual vascular plant species was systematically examined on the whole island, first in 1996-1997, then in 2005-2006 and finally in 2014-2015. Steep slopes and cliffs not accessible on foot were left out. In each quadrat of the 100 x 100 m grid system the plant species found were classified according to the following abundance scale:

1. Rare - Five or less individuals within a quadrat, or the total cover of a species is less than 2 m^2
2. Medium - More than 5 individuals within a quadrat, or the total species cover ≥2 m^2. Species found within less than half of the quadrat.
3. Common - Species found at several sites and distributed within more than half of the quadrat.

The quadrats by the sea were not all of full size. They were nevertheless examined like other quadrats, but only if their size was at least 1/3 of full size (100 x 100 m). Distribution in these quadrats was assessed in the same way as elsewhere but based on the area that was available.

In the study years 1996-1997, 2005-2006 and 2014-2015, a total of 135, 139 and 116 quadrats were examined respectively. The island had decreased considerably during this period, but according to measurements in 1998, 2006 and 2016, its area was 148.1, 137.7 and 128.3 ha in these years respectively (Icelandic Institute of Natural History unpublished data). Differences in the number of quadrats between surveys is due to the fact that the island is constantly shrinking, but also that areas, especially on steep slopes, are differently accessible mainly depending on weather conditions. In order to display the distribution of individual species on the island, maps were made for each species based on their abundance in the quadrats at the different times.

Data analysis

Relationship between vegetation in individual quadrats and trends in plant succession on Surtsey were analysed by classification and ordination. Data from all the quadrats and years was included, 381 in total and 69 vascular plant species. Classification was performed with the two-way indicator species analysis program TWINSPAN (Hill & Šmilauer 2005) and the pseudospecies cut levels set to 1, 2 and 3 based on how common the species were. Ordination was carried out with the Canoco 5 program (ter Braak & Šmilauer 2012). Abundance of vascular plant species in the quadrats was subjected to detrended correspondence analysis DCA. In the analysis detrending was by segments and downweighting of rare species performed. Five supplemental variables were passively projected into the ordination space, namely: normalized difference vegetation index (NDVI) in 1996, 2006 and 2015; number of species per quadrat; shortest distance to sea; distance from the initial center of the seagull colony; and height a.s.l. As the height a.s.l. of the quadrats had not changed significantly from 1996 to 2015, the height model of 1998 was used for all years. The two distances were based on quadrat midpoints.

NDVI data was downloaded from U.S. Geological Survey (USGS), calculated from atmospheric corrected Landsat 5, Landsat 7, and Landsat 8 satellite images acquired on August 17 1996; July 20 2006 and August 6 2015. The data was cut along shorelines to minimise the impact of the sea and an average calculated for each quadrat based on 30 m pixel size. NDVI is an indicator of the magnitude of photosynthetically active vegetation and is usually given in values from -1 to 1 (Rouse et al. 1974). It is calculated with the formula: NDVI = (R-IR)/(R+IR), where R is red reflectance and IR is infrared reflectance where R is red reflectance and IR is infrared reflectance.

Descriptive statistics were performed using the JMP software 9.01 (SAS Institute Inc. 2010). The relationship between supplemental variables and TWINSPAN-classes were analysed with one way ANOVA. Non-normal parameters were log-transformed prior to analysis followed by Tukey's Pairwise Significant Difference test at $\alpha = 0.05$. When transformation was not sufficient for normal distribution requirements, a non-parametric Wilcoxon test was performed and pairwise comparisons made using rank sum test at $\alpha = 0.05/8 = 0.00625$. The relationship between the different surface types on Surtsey and colonisation of vascular plants was tested with Pearson chi-square test.

RESULTS

Colonisation in time

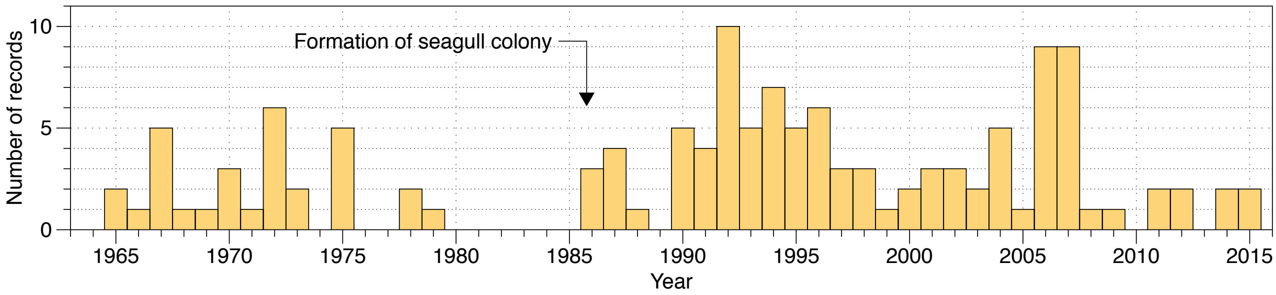


Fig. 2. Vascular plant colonisation on Surtsey during 1965–2015 based on the first two records of each species. Total number of records = 130, of these, 56 species have been recorded at two locations and 18 at one.

During 1965–2015, a total of 74 vascular plant species were found on Surtsey. The results show that plant colonisation has changed over time (Fig. 2). Based on the first two records of each species, the colonisation was considerable between 1965–1979, the first years after the island rose from the sea. Then six years passed without any new colonisation being noticed. Following 1986 there was, however, a sharp increase in colonisation that peaked during 1992–1995 after which it declined again. A new peak occurred in 2006–2007. It should be noted that new plant species are not always found in their first year of growth on the island. In some cases, they may be several years old when they are discovered.

Relationship between surface types and colonisation

The colonisation of plants on Surtsey has varied in time and space (Fig. 4). The first plants (1965–1967) were found on the northern spit of the island and on nearby slopes. During the following years (1968–1980) the colonisation does not seem to be strongly restricted to any particular area but was spread over a large part of the island. However, no colonisation was observed on the highest hills or on steep slopes (Fig. 4).

In the years 1986–1995, after a break of six years, a new period of colonisation began and now the new colonisers were mainly confined to two areas. Firstly, in and around the western crater and secondly, and to a much greater extent, in the southern part of the island where seagulls started nesting in great numbers in 1986. New plant species were also found to the east of that site. From 1995, the main area of colonisation has been within and at the eastern edges of the seagull colony. Limited colonisation has occurred within the western crater area (Fig. 4).

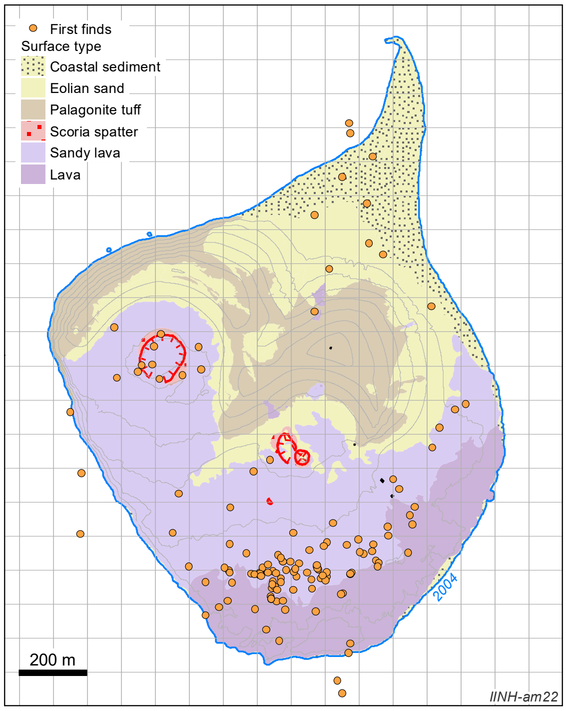


Fig. 3. Map showing the main surface types on Surtsey in 2004, based on Jakobsson (2006) and the sites of first two records for each vascular plant species found on the island 1965-2015. Points outside the coastline of 2004 were on land that had eroded.

Plant colonisation differed significantly between surface types (chi-square = 76,87, n =5, $p < 0.0001$). Colonisation was highest on sandy lava but was also considerable on lava (Fig. 5). No colonisation was observed in areas classified as palagonite tuff and relatively low on aeolian sand and coastal sediments.

Given that the seagulls clearly have a great influence on the colonisation of new species on Surtsey, it was interesting to explore whether colonisation differs on the land types before and

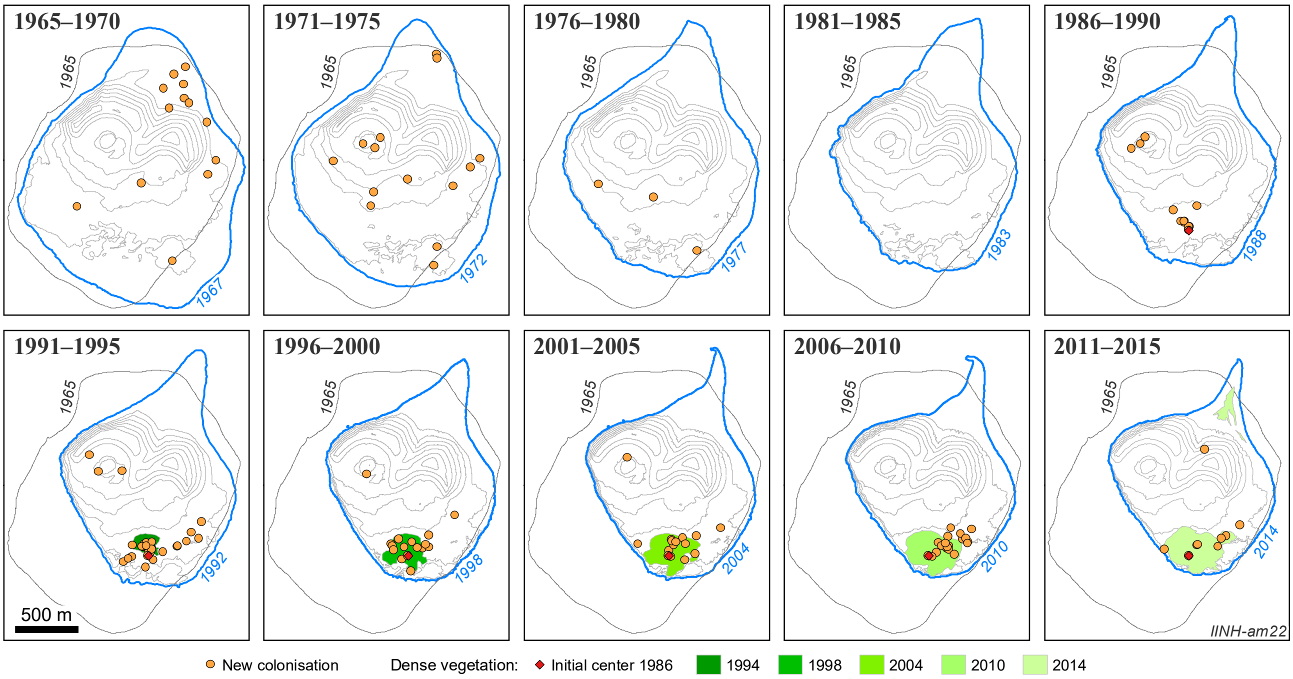


Fig. 4. Maps showing colonisation locations of vascular plants on Surtsey at five years intervals, based on the first two records of each species. The red spot indicates the initial center of the seagull colony established in 1986. The green areas indicate the development of dense vegetation on the island, outlined from aerial photographs.

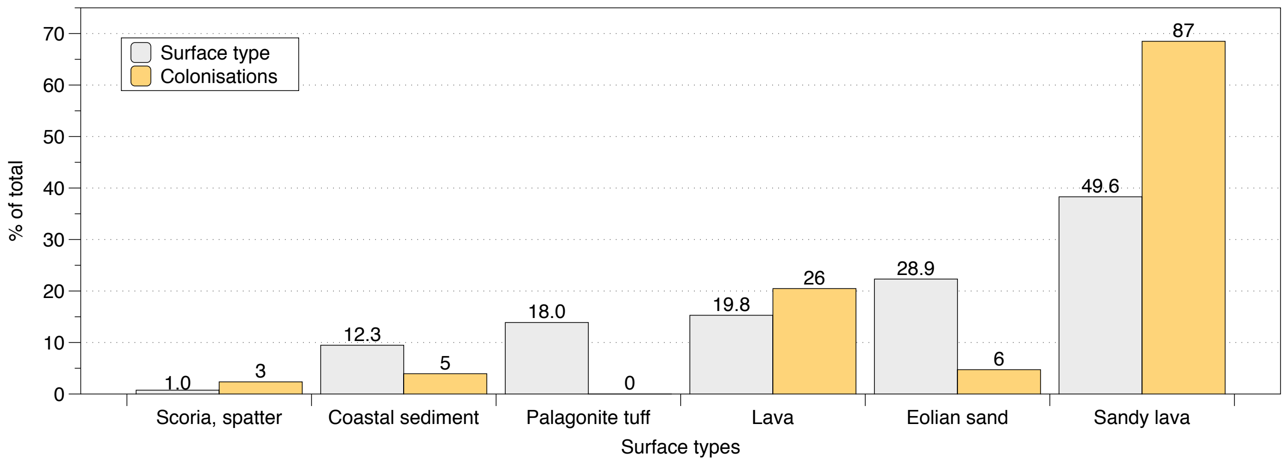


Fig. 5. The relationship between area of different surface types on Surtsey and colonisation of vascular plants. Colonisation is based on the first two records of each species during the period 1965–2015. The area of different surface types is calculated from the size of the island in 2004 and based on map from Jakobsson (2006). Note that records in eroded areas outside the island (6 in total) at that time are excluded (see Fig. 3). Numbers above bars show the area of the different surface types (total size of island 2004 is 129.6 ha) and records of colonisation respectively (127 in total).

after the formation of the seagull colony in 1986. Due to few records (low expected values) it was only possible to compare the colonisation on lava and sandy lava. The results, however, did not show a significant difference between these categories after the arrival of the birds (chi-square = 1.01, df = 1, Ns).

The vegetation types on Surtsey

TWINSPAN-classification of the 381 quadrats studied revealed a great difference in the vegetation of the island (Fig. 6). In the first division two main groups were formed with seven species as positive indicators. Therefore, two main types of vegetation can be recognized. The first (TW1-TW4, 172

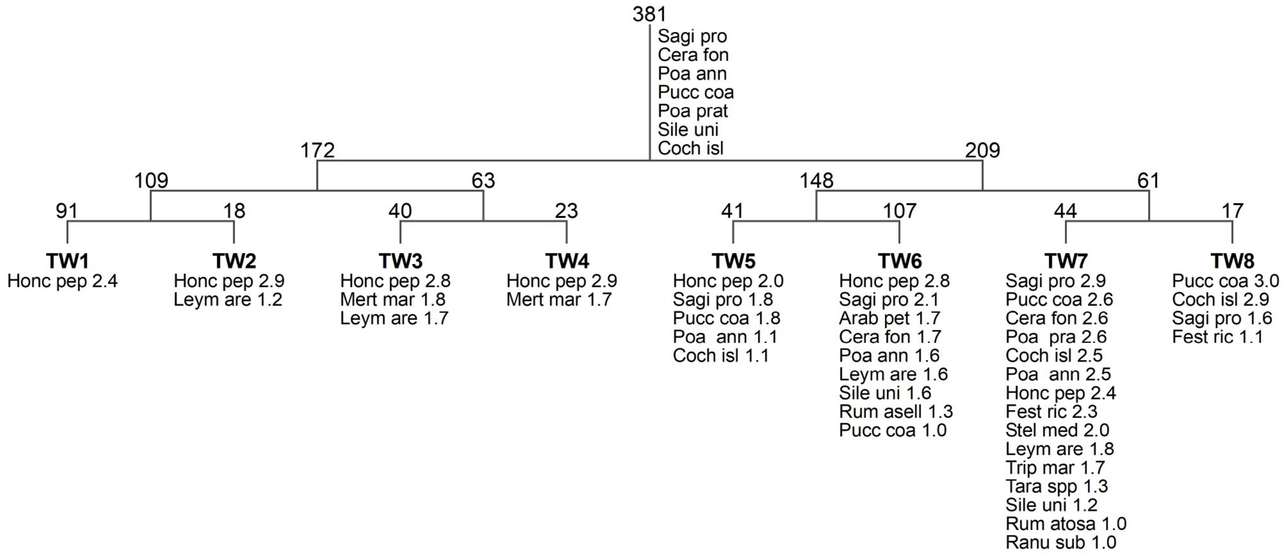


Fig. 6. Result of a TWINSPAN-classification of all quadrats studied on Surtsey based on the abundance of vascular species in 1996-1997, 2005-2006 and 2014-2015. The number of quadrats in each class is shown and so are indicator species for the first division. For each class, the most common species are shown based on average abundance (≥1.0) for each species.

quadrats) is characterized by the pioneer species *H. peploides, Mertensia maritima* and *L. arenarius*. In the second (TW5-TW8, 209 quadrats) the pioneers of the first main group are still part of the vegetation but several other species characterize the vegetation like the forb species *Sagina procumbens, Cerastium fontanum, Silene uniflora* and *Cochlearia islandica* but also the grass species *Poa annua, Puccinellia coarctata and Poa pratensis.* Further divisions resulted in eight classes TW1-TW8 (Fig. 6). The five environmental parameters tested show that there was a great variation between the groups (Table 1). Species richness was very low in TW1 but slightly higher in TW2 or 1.8 and 2.8 species/quadrat respectively. Although low, the richness was significantly higher in TW3 and TW4 (4.1 and 4.7 species/quadrat). The species richness was higher in groups TW5 and TW8 (5.7 and 6.8) and still higher in group TW6 (9.7). However, the group TW7 had by far the highest richness or 18.1 species/quadrat.

Table 1. The six vegetation types on Surtsey and the averages ± SE for vegetation and supplemental variables for the eight TWINSPAN-classes, TW1-TW8. Numbers within parentheses are min-max. Capital letters indicate if differences are significant between classes. Examples of the vegetation types are shown in Fig. 7.

	Honckenya pioneer vegetation		*Honckenya-Mertensia-Leymus* vegetation		*Honckenya-Sagina-Puccinellia* vegetation	*Honckenya* and gravel flat vegetation	Forb rich grassland	*Cochlearia* see-cliff vegetation
	TW1 n=91	TW2 n=18	TW3 n=40	TW4 n=23	TW5 n=41	TW6 n=107	TW7 n=44	TW8 n=17
Number of species*	1.8±0.08E (1-4)	2.8±0.26D (2-6)	4.1±0.19C (3-7)	4.7±0.23C (3-7)	5.7±0.33C (1-11)	9.7±0.29B (4-18)	18.1±0.82A (10-31)	6.2±0.83C (2-13)
NDVI**	-0.019±0.005 E (-0.164-0.076)	0.004±0.008 CDE (-0.078-0.050)	0.051±0.022 C (-0.442-0.520)	-0.017±0.015 E (-0.311-0.061)	0.026±0.006 CD (-0.045-0.122)	0.044±0.006 C (-0.130-0.382)	0.420±0.031 A (0.020-0.804)	0.198±0.039 B (-0.046-0.548)
Height a.s.l. m**	48±3.7CDE (4-138)	55±5.2BC (10-92)	32±6.4EF (4-146)	91±5.7A (14-136)	49±6.8CD (2-146)	71±3.3B (18-146)	26±0.8D (18-42)	21±0.4DF (18-24)
Distance from shore, m**	217±16AB (0-570)	188±33ABC (14-441)	146±23C (0-535)	239±25AB (59-534)	189±27ABC (0-522)	245±12A (6-522)	157±12BC (14-309)	30±10E (0-121)
Distance from the initial center of gull colony, m**	839±31A (235-1491)	605±43BC (348-1055)	908±47A (295-1370)	764±43AB (386-1057)	616±32BC (189-953)	610±22C (173-1057)	191±20D (36-809	232±23D (113-429)

* ANOVA
** Nonparametric comparisons, Wilcoxon.

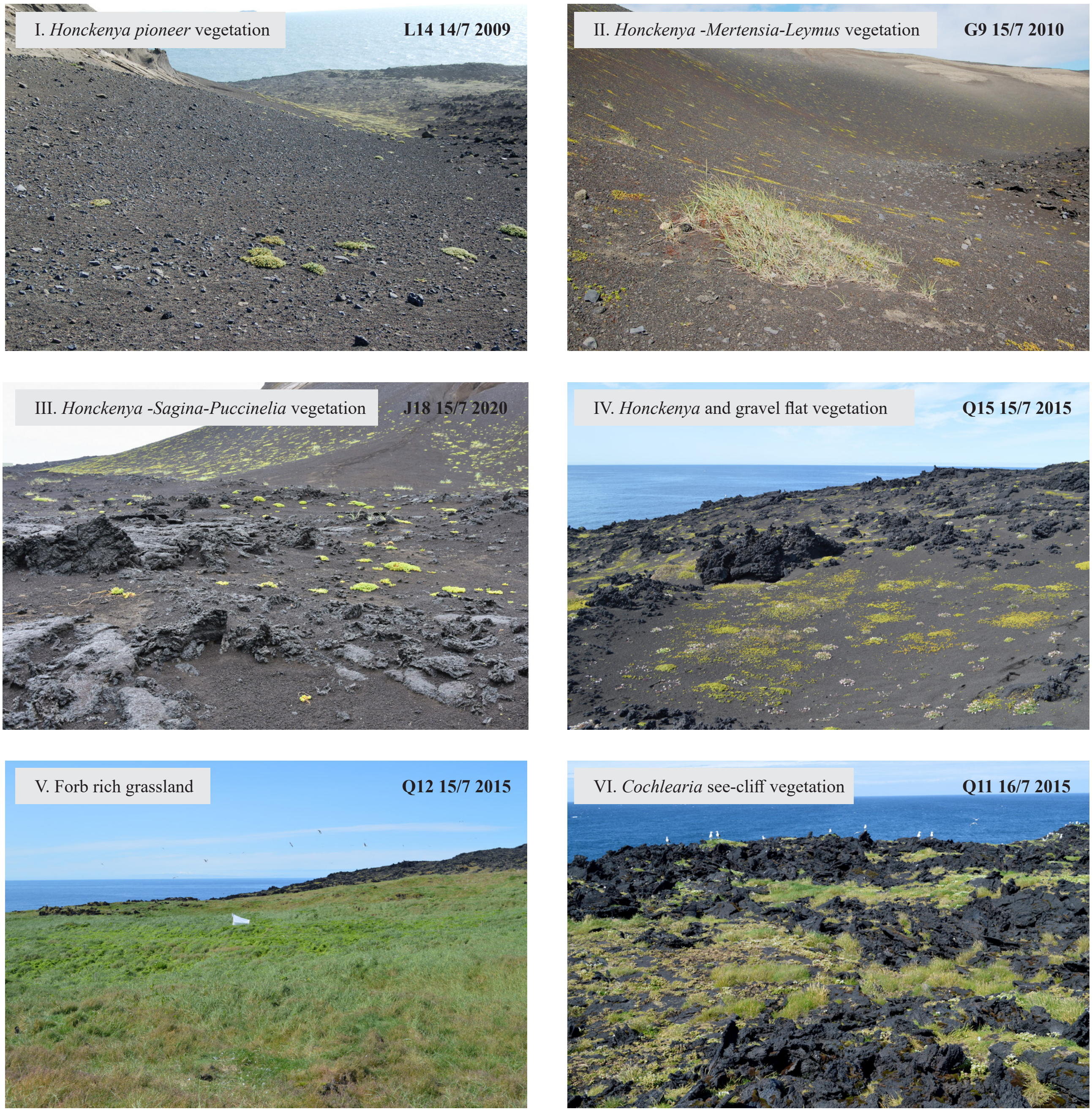


Fig. 7. Examples of the six main vegetation types on Surtsey in 1996–2015. Information on species richness and dominating species is given in Table 1 and Fig. 6.

NDVI values were very different by groups (Table 1). They were lowest in group TW1, TW4 and TW2 (- 0.019, -0.017 and 0.004). Groups TW5, TW6 and TW3 all had fairly similar values, or in the range 0.026–0.051. Much higher values were in category TW8 (0.198). NDVI values were by far highest in group TW7 (0.420).

Based on species composition and abundance of the vascular plants measured in the quadrats between 1996 to 2015, six main vegetation types can be identified on the island (Fig. 7).

I. *Honckenya* pioneer vegetation. This type is represented by the TWINSPAN-classes TW1-TW2. Although very sparse *H. peploides* is the only abundant species in this type.

II. *Honckenya-Mertensia-Leymus* vegetation. The next vegetation type is represented in groups TW3-TW4. This vegetation is closely related to type I but is considerably richer in species. In addition to *H. peploides*, *Mertensia maritima* and *L. arenarius* are common.

III. *Honckenya-Sagina-Puccinellia* vegetation. The third type consists of group TW5. *H. peploides* and *S. procumbens* are abundant, but also the grass species *P. coarctata* and *P. annua*.

IV. *Honckenya* and gravel flat vegetation. The fourth vegetation type is represented by group TW6. *H. peploides* is common as well as *S. procumbens*, but this type is characterised by *Arabidopsis petraea*, *S. uniflora* and *Rumex acetosella,* all common species on gravel flats in Iceland (Kristinsson 2010).

V. Forb rich grassland. The fifth vegetation type corresponds to the group TW7. It differs significantly from all other vegetation types on Surtsey mainly due to high species richness and production. Many coastal plants are still present but additional species adapted to nutrient rich habitats are found. Grass species are common such as *P. pratensis, P. annua, Festuca richardsonii* but also forbs such as *C. fontanum, Stellaria media, Rumex acetosa* and *Ranunculus subborealis.*

VI. *Cochlearia* see-cliff vegetation. The sixth vegetation type on Surtsey is represented by group TW8. The most common species are *P. coarctata, C. islandica, S. procumbens* and *F. richardsonii*.

Ordination

The ordination revealed the variation in the vegetation on Surtsey and the changes that have occurred from 1996-1997 to 2014-2015 (Fig. 8). The eigenvalues for the first three axes were 0.36, 0.14 and 0.10 respectively. The main difference in the vegetation is along Axis 1, which clearly separates the quadrats in the species poor and sparsely vegetated quadrats (TW1-TW4) from those species richer and with denser vegetation (TW7-TW8) (Fig. 8). Intermediate along the axis are quadrats of the classes TW5-TW6. The diagram shows that they have much in common with the quadrats with high scores on Axis 1. Axis 2 mainly separates quadrats in TW5 and TW8 from other classes but both of these classes have relatively low values on the axis. The species *P. coarctata, C. islandica* and *S. procumbens* are relatively common in the quadrats (Fig. 9).

Based on the ordination and the environmental variables tested the main gradient in the vegetation data is related to NDVI, species number and distance to the initial center of the seagull colony (Fig. 9). On average both the number of species and NDVI increased along axis 1, but the opposite was true for the distance to the initial center of the seagull colony. The correlation between NDVI and coordinates on axis 1 was 0.61 ($r^2 = 0.37$; $n = 381$; $p < 0.0001$) but the corresponding coefficients for number of species and distance from the initial center of the seagull colony were 0.69 ($r^2 = 0.48$; $n = 381$; $p < 0.0001$) and -0.48 ($r^2 = 0.60$; $n = 381$; $p < 0.0001$) respectively. Distance from shore and h.a.s.l showed much lower correlation with the two ordination axis.

There are also some differences in vegetation depending on the location on the island (Table 1; Fig. 6 & 10). The quadrats in group TW4 are mainly found in the relatively high-lying areas. In addition, the quadrats belonging to TW8 are unique as they are generally close to the shore, or on average 30 m. It is also clear that the vegetation on the island is strongly related to the distance from the initial center of the seagull colony, but the quadrats classified in TW8 and TW7 are on average close to the site where the gulls began to nest in 1986 or 232 and 191 m respectively.

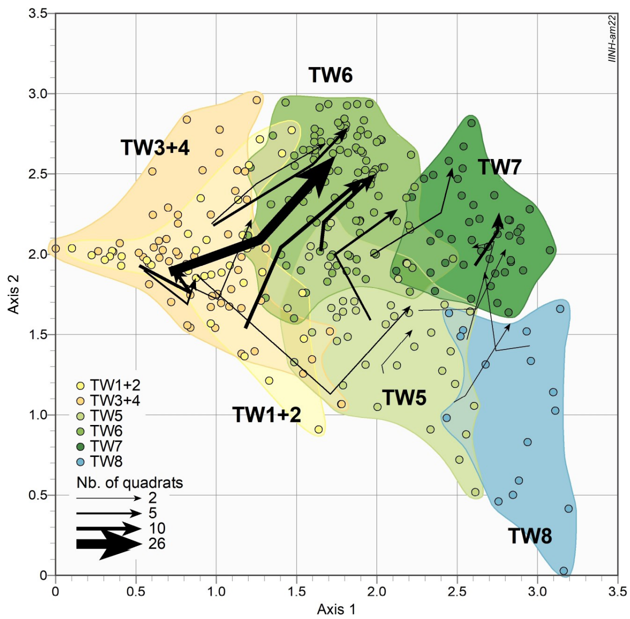


Fig. 8. DCA-ordination of quadrats on Surtsey based on abundance of vascular plant species in quadrats sampled in 1996-1997, 2005-2006 and 2014-2015. Lines enclose the six vegetation types: TW1-TW2, TW3-TW4, TW5, TW6, TW7 and TW8. The arrows denote the main vegetational change with time representing quadrats which transfer between TW-classes in a similar way. Arrow thickness is proportional to the number of quadrats behind each arrow.

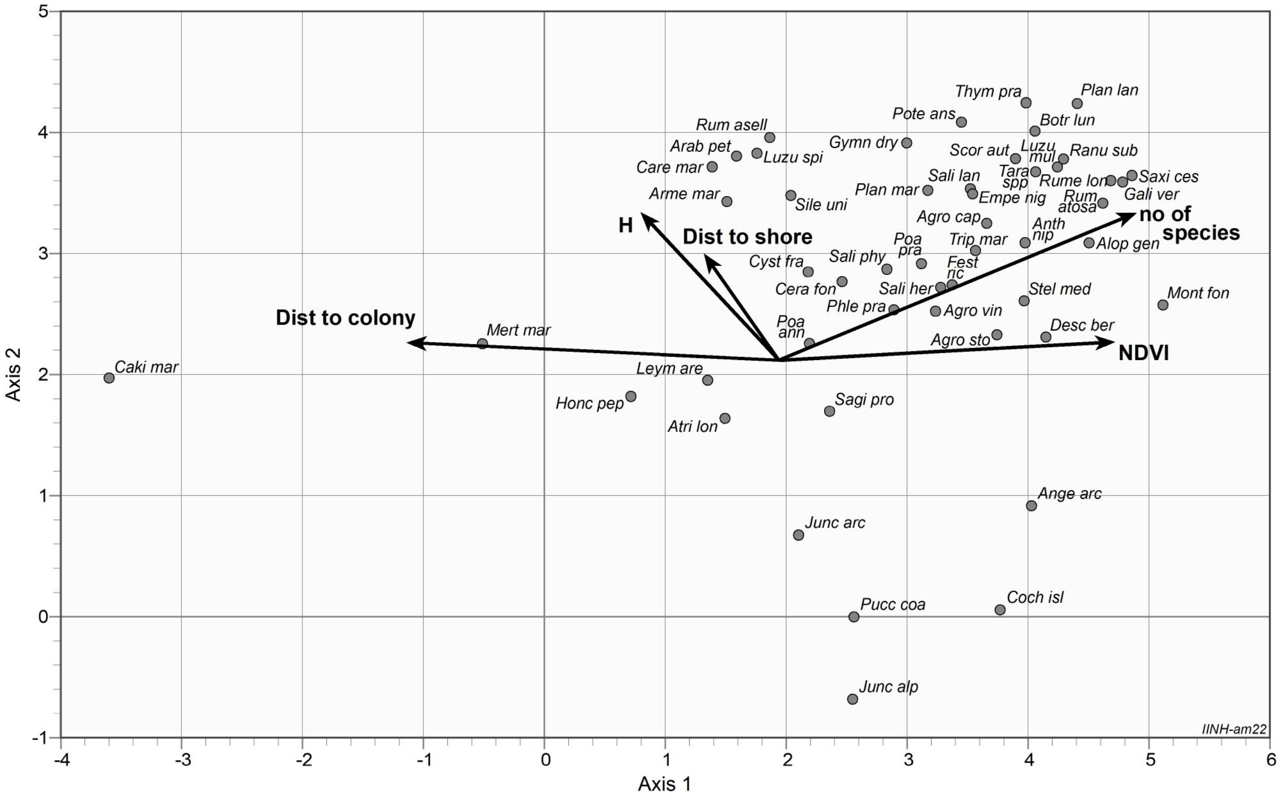


Fig. 9. Results of DCA-ordination of species based on species abundance in quadrats measured in 1996-1997, 2005-2006 and 2014-2015. Only 50 species with the greatest effect on the ordination are shown. Relationship between environmental variables and the DCA-ordination is denoted with arrows where arrow length indicates the relative importance of the variables in explaining the vegetational variation. H is the hight (m) above sea level measured in 1998. Full names of the species are given in Appendix I.

Vegetation changes in time and space

During the study period, major vegetational changes took place on Surtsey, but they vary depending on the location (Fig. 8 & 10).

In the years 1996-1997 the entire northern part of the island had either *Honckenya* pioneer vegetation or *Honckenkia-Mertensia-Leymus* vegetation (classes TW1-TW4). Better vegetated and more species-rich areas (TW5-TW8) were at that time mostly confined to an area on the southern part of the island mainly close to and around the seagull colony (Fig. 10).

Over time, the distribution of the species poor pioneer vegetation (TW1-TW4) has decreased significantly. In 2014-2015 it was only found in the northeastern part of the island (Fig. 10). Instead, other and more species rich vegetation types increased considerably on the island. The most fertile and species-rich areas (TW7) had e.g., increased from about 10 ha in the years 1996-1997 to almost 18 ha in 2014-2015. The largest increase was in *Honckenya* and gravel flat vegetation (TW6), which covered only about 14 ha in the first survey in 1996-1997 but was found in more than 60 ha in 2014-2015 and covered more than half of the island (Fig. 10).

The transfer of quadrats between TW classes provides a good overview of the main vegetation changes that have taken place on Surtsey (Figs. 8 and 10). Changes can be divided into three categories. First, areas that have hardly changed. These are mainly quadrats in classes TW1 and TW2, *Honckenya* pioneer vegetation, which are high on the southeastern slopes of the island and in coastal quadrats on the west side. There conditions are extremely severe due to erosion and transport of sand and tephra. Only very few species can survive under these conditions. e.g. *H. peploides* and *L. arenarius.* Secondly, many quadrats of almost all TWINSPAN-classes all over the island had developed to varying degree towards vegetation class V that characterizes the seagull colony. There the vegetation is relatively dense and rich in species (Fig. 8 & 9). Thirdly, there were a few quadrats by the south coast where the sea constantly erodes the island and affects the vegetation so that salt-tolerant species such as *C. officinalis, P. coarctata and S. procumbens* dominate (*Cochlearia* see-cliff vegetation) while others retreat (Fig. 10).

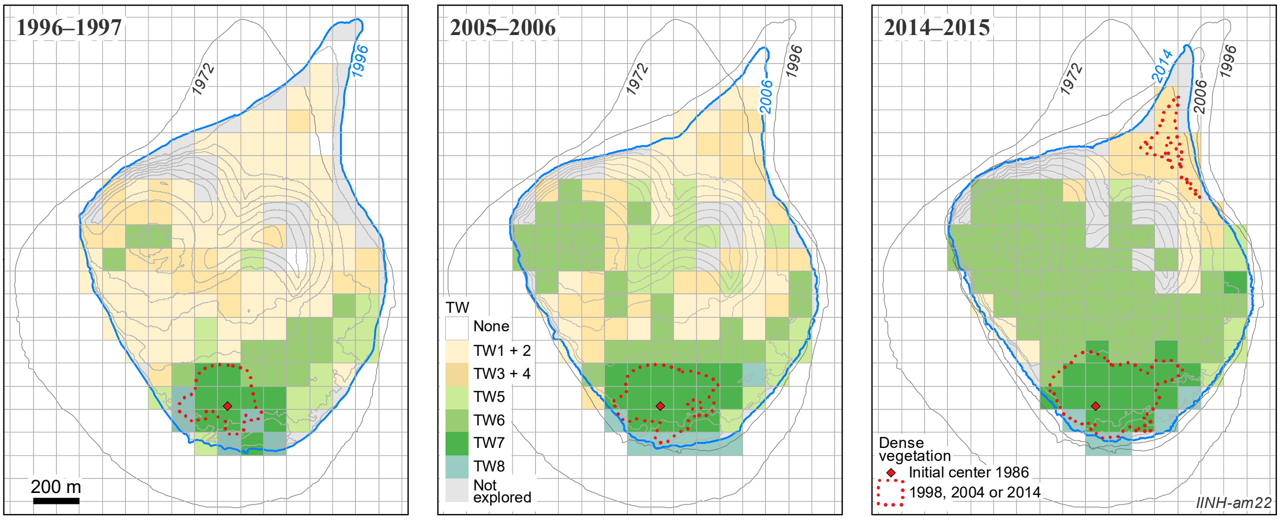


Fig. 10. Maps showing changes in the distribution of the TW-classes on Surtsey. The red dot indicates where the seagulls started to nest on the island in 1986. The dotted lines enclose areas with dense vegetation estimated from aerial photographs.

Changes in the number of species

On Surtsey, the number of species per quadrat has increased substantially during the study period (Fig. 11). In the quadrats that have been sampled in the three surveys (n = 113), the average number of species has increased from 4.8 (min-max 0-22) species/quadrat in the years 1996-1997 to 7.2 (1-26) in the years 2005-2006 and to 10.4 (1-31) in the years 2014-2015. The largest increase occurred on the southern part of the island where the seagulls began to nest, especially in an area extending 300–400 meters to east of the site. A substantial increase also occurred within and around the large crater on the northwestern part of the island (Fig. 11). The increase in species numbers was relatively low on the northeastern part of the island, especially on the low spit and on the steep slopes of the palagonite tuff crater. However, a decrease was found in some quadrats, especially in the western part of the seagull colony and in quadrats close to the sea to the west of that site. There, the number of species declined the most by 8 species per quadrat (from 17 to 9).

There was a strong relationship between the distance from the initial center of the seagull colony and the number of species (Fig. 12). The number of species was highest close to the seagull colony but decreased with increasing distance from that site. In 1996-1997, these effects were visible up to 500 m from the site, and with time they increased and were approximately 600 m at the end of the study period.

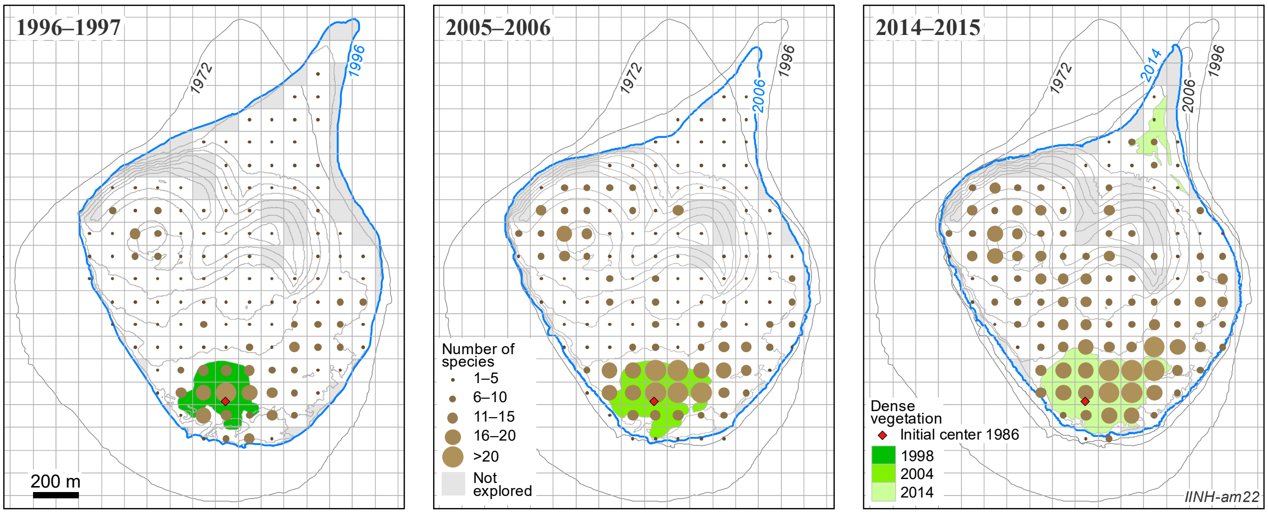


Fig. 11. Maps showing the number of species in quadrats at different times on Surtsey. A red dot indicates where seagulls started nesting on the island in 1986. The green areas denote a dense vegetation estimated from aerial photographs.

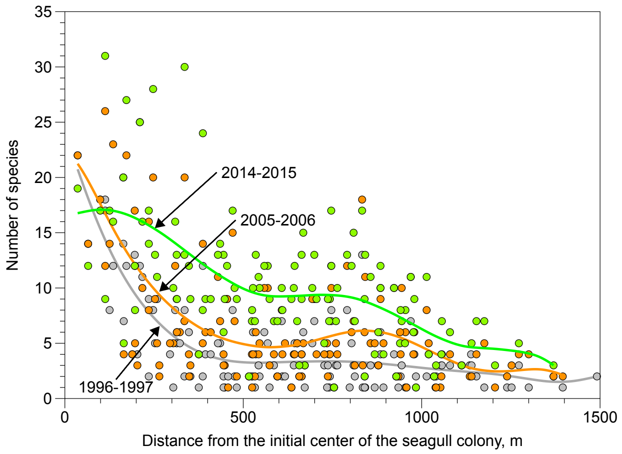


Fig. 12. Changes in the number of species with time related to distance from the initial center of the seagull colony on Surtsey. The lines are fitted with the LOESS method (locally estimated scatterplot smoothing).

NDVI and distance from the seagull colony

The results showed that the NDVI-values were very variable on the island. They were highest within the seagull colony but decreased rapidly with increasing distance (Fig. 13). At ca 500 m distance the effect had become rather low. The NDVI-values have increased over time, especially from 2006 to 2015. The results also showed that NDVI had risen sharply at a distance of 1100–1300 m.

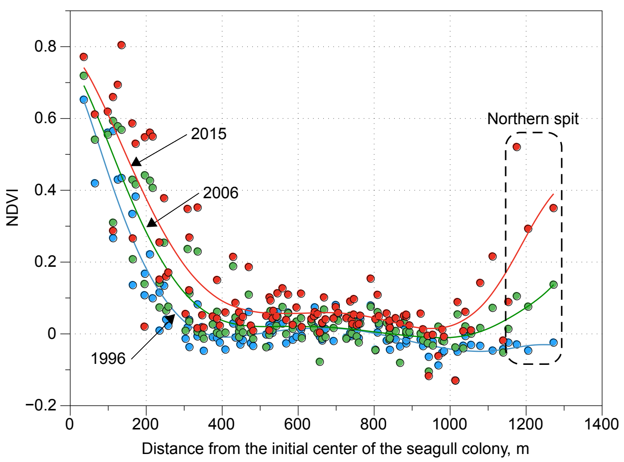


Fig. 13. NDVI-values on Surtsey 1996, 2006 and 2015 related to distance from the initial center of the seagull colony. Data is only shown for those quadrats that were sampled in the three surveys. Quadrats on the northern spit are marked with a rounded box. The lines are fitted with the LOESS method (locally estimated scatterplot smoothing).

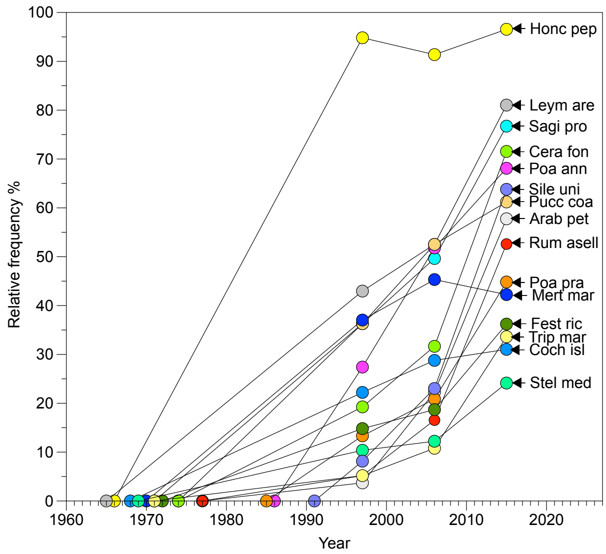


Fig. 14. Relative frequency of the 15 most common vascular plant species on Surtsey in 2014-2015 related to their year of colonisation. The frequency is shown as a percentage of quadrats with species out of the total number of quadrats inspected in, 1996-1997, 2005-2006 and 2014-2015. In these years 135, 139 and 116 quadrats were inspected respectively. Full names of the species are given in Appendix I.

Distribution of species

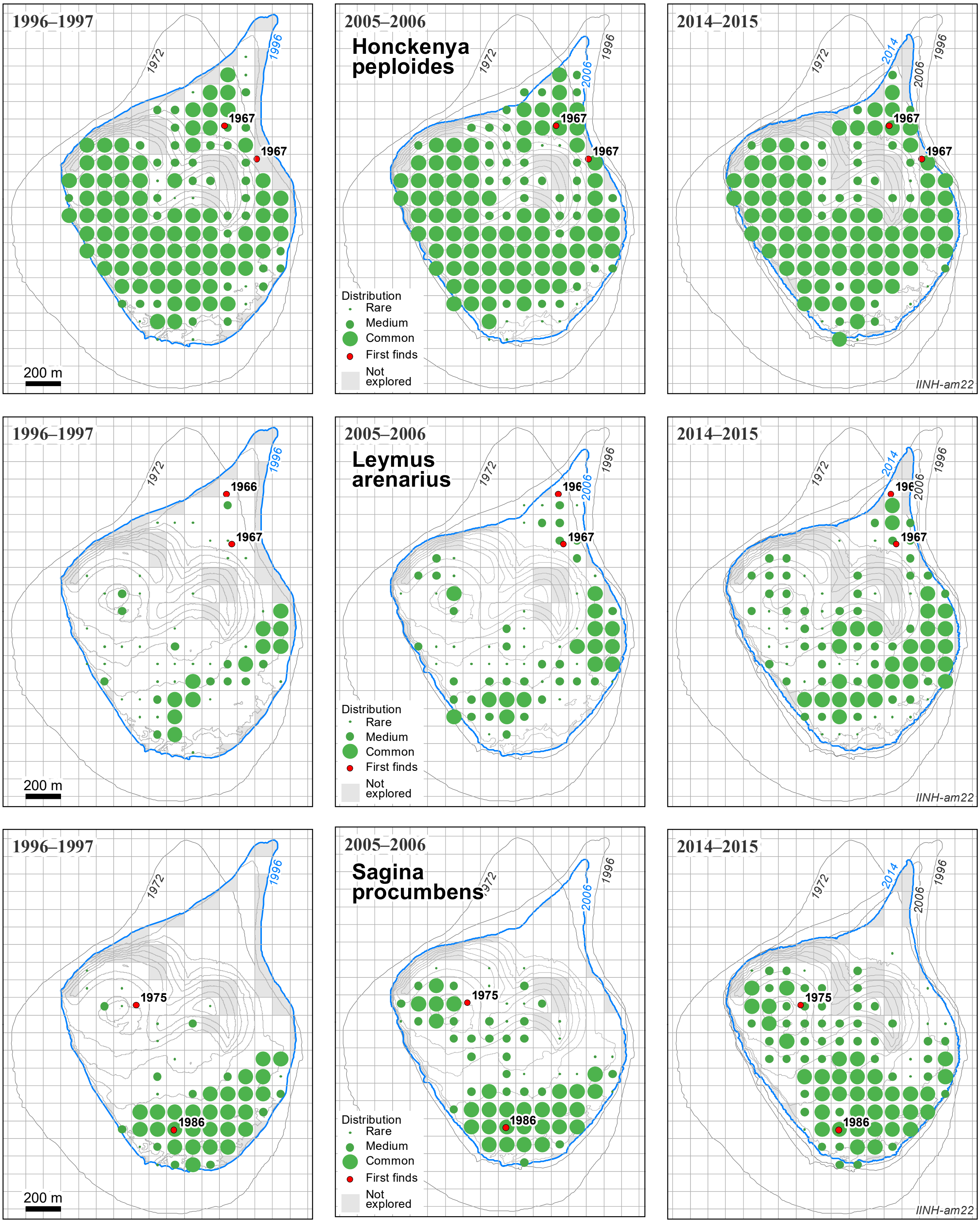
The results shown on Figs. 14 & 15 illustrate how the distribution of the most common species in 1996-1997 has increased during the subsequent study periods, and the largest increase generally occurring between 2006 and 2015. *H. peploides* is an exception, as the species had more or less colonised the whole island in 1996-1997. Then it was already found in 95% of the quadrats studied and its distribution has not changed considerably from that time. (Fig. 14). The species next in rank, *L. arenarius, S. procumbens* and *C. fontanum* had a much lower distribution in our first survey, but they have all spread widely during the research period as they were found in over 70% of the quadrats in the last survey. Other common species were *P. annua, S. uniflora, P. coarctata, A. petraea* and *R. acetosella*, all of which were found in over 50% of the quadrats studied in the last survey. The other exception to the general trend was *Mertensia maritima*, but its distribution decreased slightly from 2006-2007 to 2014-2015 (Fig. 14).

Based on frequency of the species on Surtsey they can roughly been divided into four categories:

I. High dispersal rate species. This category includes *H. peploides, P. annua* and *S. uniflora*, which had spread to over 50% of quadrats in less than 20 years.

II. In the second category are species that had reached this level in 35–40 years, namely *S. procumbens, P. coarctata, C. fontanum, A. petraea, L. arenarius* and *R. acetosella*. *P. pratensis* could also be included in this category, as the species showed similar rate of dispersal, but it had only been on the island for 29 years in the last survey (Fig. 14).

III. In the third category are several species that



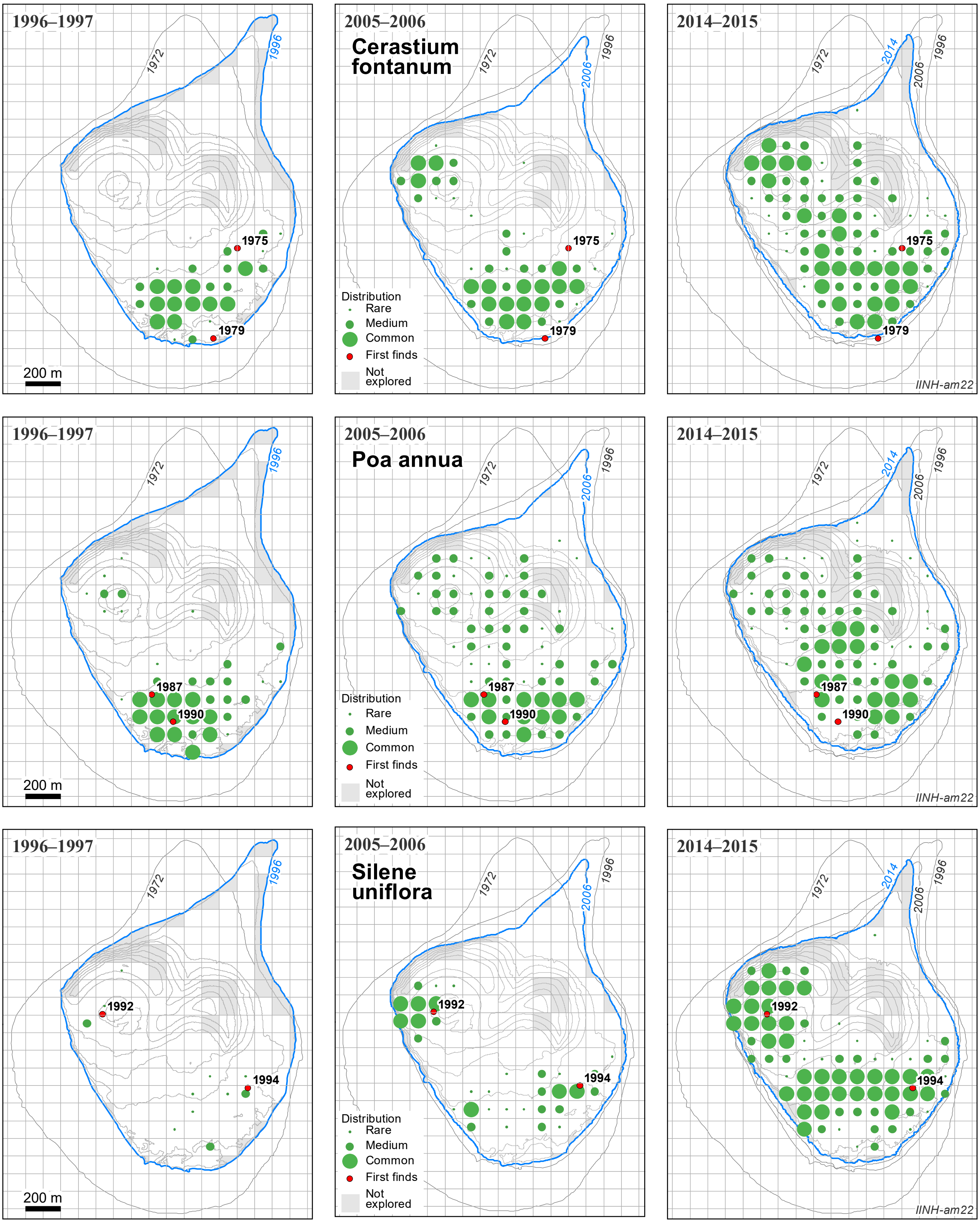


Fig. 15. A-B Map showing development in distribution of the six species that had become most common on Surtsey in the survey of 2014-2015; The red dots indicate the locations of the first two findings of the species on the island. Note that distribution maps for all plant species are given as supplementary information.

all had been on the island for over 40 years but spread rather slowly. In the last survey they were in 17–42% of the quadrats. These are the species, *Carex maritima, S. media, C. islandica, Tripleurospermum maritimum, F. richardsonii* and *Mertensia maritima.*

IV. In the fourth category are species that have either been on Surtsey for a long time without spreading to any extent or species that have been on the island for a relatively short time. Therefore, it is not known yet how they will respond. In the first group are e.g., *Cystopteris fragilis, Cakile maritima* and *Armeria maritima*. The habitats for the first two are of rather limited extent on Surtsey. *C. fragilis*, a perennial species, is found mainly in caves and caverns, while *Cakile maritima*, which is an annual, is confined to the northern coastline.

In the second group are e.g., *Taraxacum spp., Empetrum nigrum, R. acetosa, Ranunculus subborealis* and *Scorzoneroides autumnalis.* In the last survey in 2014-2015 these species had been for 20–25 years on the island and had limited distribution.

DISCUSSION

Dispersal routes

In 2015, a total of 74 vascular plant species had been registered on Surtsey, which is about 16% of the native vascular flora of Iceland, which includes about 480 species (Kristinsson 2010). That means that the potential species pool for Surtsey is limited. Dispersal to Surtsey is certainly limiting for plant colonisation not least due to the isolation and distance from the nearest seed sources.

Northeast of Surtsey are older islands (4.8–16.4 km distance) formed in a similar way as Surtsey (Magnússon et al. 2014). They have all undergone major geomorphological changes, differ in area (0.02–0.25 km2) and are species poor (4–24 species/island). On these islands a total of 27 species of vascular plants has been recorded (Magnússon et al. 2014). Of these, only one (*Saxifraga rivularis*) has not been found on Surtsey by 2015. Therefore, of the species registered on Surtsey by 2015, at least 49 originate from a greater distance than 17 km.

Further away but in the same direction are three islands, Heimaey (18.3 km), Bjarnarey (25.5 km) and Elliðaey (27.1 km). Heimaey is by far the largest of all the Westman Islands (13.4 km^2). More than 180 species of vascular plants have been recorded there (Icelandic Institute of Natural History 2022). On Bjarnarey (0.32 km^2) and Elliðaey (0.46 km^2), a total of 33 species of vascular species have been registered, all but one (*Epilobium hornemanii*) also found on Heimaey. When the flora of Surtsey is compared to the flora of all these islands, it can be assumed that at least seven species (*Calamagrostis neglecta, Eleocharis quingeflora, Juncus alpinus, Gymnocarpium dryopteris, Salix arctica and Salix lanata*) originate from the mainland of Iceland as none of them have been recorded on the other Westman Islands.

Dispersal mode for individual species to Surtsey is not known, but the main transport is by sea, wind and birds (Magnússon et al. 2014). Human-mediated dispersal may have occurred although strong measures have been taken to prevent it. The location of the first colonisers, which all were coastal plants and found near the northern shore, strongly indicates that they were dispersed by sea (Fridriksson 1966, Magnússon et al. 2014). It can also be assumed that bird-mediated dispersal has been very important as species colonisation greatly increased after the formation of a seagull colony on the island (Magnússon et al. 2014, Fig. 2–4). Wind has probably been an active transport agent since the island was formed. Due to the long distance, however, it is not likely that many species have been wind-dispersed. The most likely are *Epilobium, Salix and Taraxacum* or species with particularly light seeds such as *Platanthera* and also the cryptogames like *Cystopteris, Equisetum, Botrychium* and *Polypodium*.

Both on Surtsey and Heimaey, easterly winds prevail (Petersen and Jonsson 2020, Veðurstofa Íslands 2015) which means that large-scale wind-dispersal from Heimaey or from the mainland of Iceland to Surtsey is not very likely. Seed rain is also generally highest in September and October, a period of high precipitation, which will reduce the possibility of transporting seeds by wind over long distances. Based on data from 2013 it has been estimated that about 9% of species in Surtsey were dispersed by sea, 75% by birds and 11% by wind (Magnússon et al. 2014).

Surface characteristics and plant colonisation

Colonisation of plants on Surtsey has varied in space and time (Fig. 4). It is clear that both the import of seeds to the island and the conditions for colonisation have changed since the first plants were found in

1965. Although this study did not explore seedling establishment it is clear that surface characteristics are very important for establishment of plants (Fig. 3).

Save sites for seedling establishment differ greatly by surface type. Palagonite tuff is clearly a difficult place for plants to establish. Although the surface has narrow cracks in places, it is usually smooth and without soil. These areas are relatively high on the island and are often steep. Therefore, seeds that land on palagonite tuff are likely to move elsewhere with wind and water. Erosion, infertility and desiccation are all negative factors preventing successful establishment on palagonite tuff.

Eolian sand is mainly found on the steep slopes below the palagonite tuff areas (Fig. 3). These sites are also very severe habitats for seedling establishment. Surface stability is very low and abrasion by sand movement and accumulation of sand are factors that work against seedling establishment. This habitat is also nutrient poor which makes the establishment of plants difficult (Sigurdsson & Leblans 2020). On sandy lava and lava, the conditions for colonisation are clearly better than on palagonite tuff or on aeolian sand (Fig. 3–5). However, on sandy lava there is a lot of sand that drifts and tears or abrades plants. In sheltered places such as in the western crater, seeds accumulate to some extent and moisture conditions are better that in the more exposed habitats which explains the relatively high colonisation (Fig. 3).

Although there is a significant variation within lava areas, the conditions for colonisation on this surface type are relatively favourable (Fig. 5). In depressions fine material, sand and ash will accumulate and make favourable conditions for plant establishment. On the aa or block lava close to the sea on the southern part of the island this kind of sedimentation is limited. There is also a large effect of salt spray, which probably has unfavourable effects on plant colonisation (Maun 2009).

There was a great increase in species colonisation following the establishment of the seagull colony in 1986 (Fig. 4). This can be attributed to increased import of diaspores and to improved conditions for seedling establishment (Magnússon et al. 2014). As vegetation became denser in the seagull colony, new plant colonisation however slowed down but increased in sparsely vegetated or semi-vegetated areas on the outer edge of the colony, especially to the east. This indicates continued import of new species and a presence of suitable microsites for seedling establishment. Outside this area new colonisation was rather low and sporadic (Fig. 4).

Vegetation types and changes in time

The present study showed that during the research period 1996–2015 there has been very large vegetation changes on Surtsey. As previous studies have shown seabirds were the main drivers of plant succession (Magnússon et al. 2009, Magnússon et al. 2014). The birds have clearly had a great impact on the soil fertility and created conditions for species which otherwise could hardly thrive on the island

The six main vegetation types on Surtsey described in this article reflect results of previous analysis of vegetation on the island, based on small permanent plots (10x10 m) (Magnússon et al. 2009, Magnússon et al. 2020). The present study, however, describes conditions on the whole island and how they have changed over time. The vegetation types I, II and III are all quite similar, i.e. species poor pioneer vegetation (Fig. 6 & 7). The three types were under relatively low influence from seabirds and its area decreased on the island during 1996–2015 (Fig. 10). While vegetation that is clearly affected by the birds, i.e. types V and VI, had expanded significantly.

In general, there was a clear increase in NDVI from 1996 to 2015, which indicates that chlorophyll had increased almost over the whole island (Fig. 13).

The areas on the island that do not seem to have changed over time are steep slopes in the north-eastern part of the island. There the vegetation is still at its early stages (Fig. 10) due to ongoing erosion from the slopes which maintains pristine conditions on that part of the island (Óskarsson et al. 2020).

The increase of dense vegetation has not only occurred within and around the seagull colony. A change has also been observed on the northern spit mainly after 2006 (Fig. 10 & 11, 13). This occurred without a considerable change in plant species number (Fig. 11 & 12). The reasons for this increase can partly be traced to seals breeding on the spit and their transfer of nutrients from sea to land (Magnússon et al. 2020). The fact that this has not yet had a significant effect on species number can maybe be attributed to the fact that seals, unlike seagulls, probably do not carry plant diaspores into the area. Also, the area is flooded by seawater in winter, conditions that few plants are adapted to.

Table 2. The main characteristics of the fast-spreading species on Surtsey.

	Life-form	Established strategy	Vegetative reproduction	Seed production	Coastal species	Gravel flat species	Invasive
Arabidopsis petraea	Perennial					× [a]	
Cerastium fontanum	Perennial	R CSR [b]		High [c]	× [a]		× [d, e]
Honckenya peploides	Perennial		High [f, g]		× [a, h]		
Leymus arenarius	Perennial		High [i]		× [a, i]		× [j]
Poa annua	Annual	R [b]		High [k, l]			× [e, m]
Puccinellia coarctata	Perennial				× [a, h]		
Rumex acetosella	Perennial	CSR-stress tolerant ruderal [b]	High [n, o]	High [n]		× [a]	× [n, p, q]
Sagina procumbens	Perennial	R CSR [b]		High [b, e, r]			× [r, s, e, t]
Silene uniflora	Perennial				× [a]	× [a, h]	

[a] Magnússon, S.H. et al. 2016
[b] Grime, J.P. et al. 1988
[c] Salisbury, E.J. 1964
[d] Global Invasive Species Database 2022a
[e] Ryan, P.G. et al. 2003
[f] Sánchez-Vilas, J. et al. 2012
[g] Sánchez-Vilas, J. & R. Retuerto 2017
[h] Kristinsson, H. 2010
[i] Hubbard, C.E. 1968
[j] Midwest Invasive Species Information Network
[k] Hutchinson, C.S. & G.B. Seymour 1982
[l] Warwick, S. 1979
[m] Global Invasive Species Database 2022b
[n] Stopps, G.J. et al. 2011
[o] Houssard, C. et al. 1992
[p] Global Invasive Species Database 2022c
[q] Ferreiro, N. et al. 2020
[r] Cooper, J. et al. 2011
[s] Visser, P. et al. 2010
[t] Global Invasive Species Database 2022d

Characteristics of individual species

On Surtsey, the species *H. peploides, P. annua* and *S. uniflora* have spread relatively fast. The same can be said of the species *S. procumbens, P. coarctata, C. fontanum, A. petraea, L. arenarius* and *R. acetosella* (Fig. 14 & 15). Although vegetation conditions on Surtsey have changed considerably since the island was formed, it can be concluded that conditions for germination, seedling establishment and growth have in general been relatively suitable for these species. Which are the main characteristics of these species? All are common on the mainland of Iceland. They usually grow in sparsely covered, rocky or sandy areas or on land that has been disturbed. The species are either pioneers and/or ruderals (Table 2). Many of them are also coastal plants such as *H. peploides, S. uniflora, P. coarctata* and *L. arenarius* and are therefore adapted to soil salinity to some extent. Others are common on gravel flats, even far from the sea, such as *A. petraea* or are found close to the sea but also further inland, like *S. uniflora* and *R. acetosella* (Table 2, Magnússon e.t. al 2016). Based on the behaviour of these species on Surtsey, it is clear that they can withstand harsh conditions like strong winds, unstable and nutrient poor soils, and drought.

Two of the fast-spreading species are short-lived, i.e., *P. annua* which is annual and *S. procumbens* which has been classified as perennial or perhaps even winter-annual (Grime et al. 1988) but the others are long-lived. The species *C. fontanum*, *P. annua*, *R. acetosella* and *S. procumbens* are all known for high seed production (Table 2). Personal observations on Surtsey also suggest that the same is also true for *H. peploides, S. uniflora, P. coartata, A. petraea* and *L. arenarius* especially at the margins of seagull colony.

Many of the fast-spreading species on Surtsey do not only spread by seed but also vegetatively. *H. peploides, L. arenarius* and *R. acetosella* have a great potential to spread vegetatively (Table 2). However, the distribution of species on Surtsey is probably mostly due to seed dispersal, although the increase in vegetation cover can in many cases be attributed to vegetative spread.

Many of the species with the highest distribution rate on Surtsey have in general high colonisation ability elsewhere. The species *C. fontanum, P. annua, R. acetosella* and *S. procumbens* have all proved to be active colonisers in areas outside their natural ranges, especially in the southern hemisphere, and have there been classified as invasive (Table 2). For example, *C. fontanum, P. annua* and *S. procumbens* have all spread in the Sub-Antarctic region (Ryan et al. 2003). There they have affected the native flora of the subantarctic Prince Edward Island which is of relatively recent volcanic origin. *R. acetosella*, which is native to Europe and southwestern Asia, has spread throughout many regions of the globe and is considered very invasive in several areas (Stopps et al. 2011, Ferreiro et al. 2020, Global Invasive Species Database 2022c). *L. arenarius*, native to Europe, has been introduced at sites by the Great Lakes in North America. There it has been described as invasive on beaches and dunes (Midwest Invasive Species Information Network 2022).

At least three of the species that have established on Surtsey seem to be very dependent on the seagull colony as they are almost exclusively found within it. These are *Ranunculus subborealis, R. acetosa* and *Taraxacum* spp. All are common on the mainland of Iceland where they grow mainly in nutrient rich grasslands and pastures and in a habitat type classified as Atlantic sea-cliff communities (Kristinsson 2010, Magnússon et al. 2016). Outside Iceland, these species are also common in meadows and pastures, often in fertile, disturbed habitats (Grime et al. 1988).

Future prospects

Despite the great influence of seabirds on the vegetation of Surtsey and some influence of seals, the island is far from being fully vegetated. Most of the island has still very sparse vegetation. It is expected that the vegetation cover will gradually increase, mainly due to the fertilizing effects of birds.

The results of this study indicate that the birds have significantly increased the number of plant species. This is not surprising as seabirds are powerful environmental modulators, generating major changes in soil properties and vegetation in of their breeding colonies (De La Peña-Lastra et al. 2021). Relatively low bird density can increase biodiversity, plant biomass and plant height, as well as to enhance seed dispersal (Anderson & Polis 1999, Sánchez-Piñero & Polis 2000, Otero et al. 2018). Examples of this can now be seen in and at the edges of the seagull colony on Surtsey. However, it is likely that high density of birds will gradually lead to a reduction in species number due to “eutrophication”. This can already be seen in the area where the seagull colony started on Surtsey in 1986. There *F. richardsonii and P. pratensis* have become completely predominant (Magnússon et al. 2009, Magnússon et al. 2014). If the effects of birds become even greater, i.e., increased eutrophication together with increased bird activity like burrowing, trampling and uprooting of plants, it is likely to lead to increase ruderal and nitrophilous species (Kamijo & Hoshino 1995, Baumberger et al. 2012, De La Peña-Lastra et al. 2021). Examples of this can be found in puffin colonies on the older Westman islands (Magnússon et al. 2014).

ACKNOWLEDGEMENTS

The Surtsey Research Society has provided logistic support for the study, and transport to the island was in the hands of the Icelandic Coastguard. Anette Th. Meier and Sigmar Metúsalemsson assisted with diagrams and maps, Járngerður Grétarsdóttir helped with statisticcal analysis. Bjarni D. Sigurdsson, Erling Ólafsson and Starri Heidmarsson have taken part in biological expeditions to the island in recent years and contributed in various ways. Robert Alexander Askew revised the language.

SUPPLEMENTAL INFORMATION

Maps showing development in distribution of individual species of vascular plants found on Surtsey in 2014-2015 are available in Supplement S1.

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Global Invasive Species Database, 2022c. Species profile: Rumex acetosella. Downloaded from http://www.iucngisd.org/gisd/species.php?sc=1342 on 23-03-2022.

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APPENDIX I

Abbreviations and full names of species

Agro cap	*Agrostis capillaris* L.
Agro sto	*Agrostis stolonifera* L.
Agro vin	*Agrostis vinealis* Schreb.
Alop gen	*Alopecurus geniculatus* L.
Ange arc	*Angelica archangelica* L.
Anth nip	*Anthoxanthum nipponicum* Honda
Arab pet	*Arabidopsis petraea* (L.) V.I. Dorof.
Arme mar	*Armeria maritima* (Miller) Willd.
Atri lon	*Atriplex longipes* Drejer
Botr lun	*Botrychium lunaria* (L.) Sw.
Caki mar	*Cakile maritima* Scop.
Care mar	*Carex maritima* Gunnerus
Cera fon	*Cerastium fontanum* Baumg.
Coch isl	*Cochlearia islandica* Pobed.
Cyst fra	*Cystopteris fragilis* (L.) Bernh.
Desc ber	*Deschampsia beringensis* Hultén, Fl. Kamtchatka
Empe nig	*Empetrum nigrum* L.
Fest ric	*Festuca richardsonii* Hook.
Gali ver	*Galium verum* L.
Gymn dry	*Gymnocarpium dryopteris* (L.) Newman
Honc pep	*Honckenya peploides* (L.) Ehrh.
Junc alp	*Juncus alpinoarticulatus* Chaix
Junc arc	*Juncus arcticus* Willd.
Leym are	*Leymus arenarius* (L.) Hochst.
Luzu mul	*Luzula multiflora* (Ehrh.) Lej.
Luzu spi	*Luzula spicata* (L.) DC.
Mert mar	*Mertensia maritima* (L.) Gray
Mont fon	*Montia fontana* L.
Phle pra	*Phleum pratense* L.
Plan lan	*Plantago lanceolata* L.
Plan mar	*Plantago maritima* L.
Poa ann	*Poa annua* L.
Poa pra	*Poa pratensis* L.
Pote ans	*Potentilla anserina* L.
Pucc coa	*Puccinellia coarctata* Fernald & Weath.
Ranu sub	*Ranunculus subborealis* Tzvelev
Rum asell	*Rumex acetosella* L.
Rum atosa	*Rumex acetosa* L.
Rume lon	*Rumex longifolius* DC.
Sagi pro	*Sagina procumbens* L.
Sali her	*Salix herbacea* L.
Sali lan	*Salix lanata* L.
Sali phy	*Salix phylicifolia* L.
Saxi ces	*Saxifraga cespitosa* L.
Scor aut	*Scorzoneroides autumnalis* (L.) Moench
Sile uni	*Silene uniflora* Roth
Stel med	*Stellaria media* (L.) Vill.
Tara spp	*Taraxacum spp*
Thym pra	*Thymus praecox* Opiz
Trip mar	*Tripleurospermum maritimum* (L.) W.D.J. Koch