ARCTIC
VOL. 42, NO. 4 (DECEMBER 1989) P. 323-332

Changes to the Climate and Flora of Hopen Island during the Last 110 Years

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(Received 28 June 1988; accepted in revised form 10 March 1989)

ABSTRACT. Hopen, a small island in the Barents Sea, is situated within the polar desert region. Altogether 26 vascular plants have been noted in four inventories conducted between 1873 and 1982. The temperature climate following the Little Ice Age has fluctuated considerably but with a clear warming after 1920. New areas have become available to the plants since permanent snowfields have melted. The number of species has increased from 17 in 1873 to 19 in 1982, but the turnover has been relatively large. Hopen does not show island biogeography equilibrium. Instead, the July mean temperature is probably the determining factor for the number of species. Mainly seed-dispersed species have colonized Hopen during this period. The origin of the vascular flora and the migration mechansims are difficult to interpret if it is considered that the entire Svalbard Archipelago was simultaneously under ice during the Weichsel glaciation.

Key words: vascular flora, polar desert region, climatic fluctuations, dispersal, island biogeography

RÉSUMÉ. Hopen, une petite île de la mer de Barents, se situe dans la zone désertique polaire. On a dénombré un total de 26 plantes vasculaires lors de quatre inventaires menés entre 1873 et 1982. Il y a eu de très grandes variations dans la température à la suite du Petit âge glaciaire, avec un net réchauffement après 1920. De nouvelles zones sont devenues propices à la végétation, suivant la fonte des névés. Le nombre d'espèces est passé de 17 en 1873 à 19 en 1982, mais le roulement a été assez important. Hopen ne montre aucun signe de l'équilibre biogéographique insulaire. Il semble au contraire que la moyenne des températures de juillet soit déterminante pour le nombre d'espèces. Ce sont surtout des espèces disséminées au moyen des graines qui ont colonisé Hopen au cours de cette période. L'origine de la flore vasculaire et les mécanismes de migration sont difficiles à interpréter si l'on considère que l'archipel du Svalbard était tout entier recouvert par la glace, durant la glaciation de Weichsel.

Mots clés: flore vasculaire, région désertique polaire, variations climatiques, dispersion, biogéographie insulaire

Traduit pour le journal par Nésida Loyer.

INTRODUCTION

Plants in the Arctic are adapted to living in a severe climate. Daily variations in temperature and precipitation are, however, small, which implies that the short-term environment is relatively constant. In the Arctic vegetative reproduction through rhizomes and runners is considered to be considerably more common than sexual reproduction and dispersal of seed (Billings and Mooney, 1968; Bliss, 1971). Despite the fact that severe competition in plant communities is not expected in these environments, the arctic vascular plants have several characteristics in common with K-selected species (cf. Stearns, 1976), which can also be associated with stable conditions.

The climate around the Barents Sea has varied considerably following the post-glacial thermal maximum. Climatic changes have occurred during at least two periods (Bray, 1971). Baranowski and Karlén (1976) report that the Werenskioldbreen on the southwestern part of Spitsbergen extended over a tundra vegetation that colonized older glacial deposits. Similar developments are reported in other parts of the Barents Sea area (Grosswald, 1963). This glacial extension took place during the Little Ice Age, which started during the 17th century and continued until about 1900, with a maximum from 1800 until 1850. The temperature curve has fluctuated but has shown an upward trend from the 1730s until the present (Bray, 1971).

Consequently, in a longer perspective, the environment for plants in this area cannot be considered stable. Climatic changes influence the availability of suitable habitats in several ways. The ice melt following the Little Ice Age has resulted in new areas of land being available for colonization. According to the theories of island biogeography (MacArthur and Wilson, 1967), the number of species can be expected to increase with area. The increased population size is assumed to reduce the risk of local extinction of species on islands. In addition, the number of species may increase, since a larger area generally implies a greater diversity in habitat. Rannie (1986) discussed the strong relationship between summer temperature and the number of vascular plants in arctic Canada.

According to these mechanisms the climatic improvement should have resulted in the number of species increasing after the Little Ice Age. The species composition should also have been influenced such that easily dispersed species, which also have an ability to become established, form an increased proportion of the species stock. The immigration of species with only vegetative means of reproduction should proceed more slowly and the establishment should assume more stable conditions. Seed-dispersed species more easily return following an unsuccessful attempt at colonization.

Hopen Island in the Barents Sea offers possibilities to test these theories.

Previous Investigations

The vascular flora of Hopen has been inventoried on four different occasions, in 1873, 1924, 1970 and 1982 (Eaton, 1876; Iversen, 1926; Engelskjøn *et al.*, 1972; Skye, 1986). Altogether 26 species have been noted (Table 1). None of the investigations has covered the entire island. The most comprehensive appears to have been the inventory in 1924 (Iversen, 1926). The island was again visited in 1929 and 1930 (Iversen, 1941), when notes were also made, but no new species were discovered. Schweitzer (Engelskjøn *et al.*, 1972) made an inventory of the southern part of the island (1970) from the radio station. In 1982 the present author visited most parts of the island apart from the northernmost area, where oil prospecting influenced the natural plant cover. As can be seen from the maps of dispersal in Skye (1986), the

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TABLE 1. Vascular plants on Hopen noted by Eaton, 1873 (Eaton, 1876); Kofoed, 1924 (in Iversen, 1926), Schweitzer, 1970 (Engelskjøn *et al.*, 1972) and Skye, 1982[1]

	1873	1924	1970	1982		
1. *Ranunculus sulfureus* Sol.	✓	✓	✓	✓	C	S
2. *Papaver dahlianum* Nordh.	✓	✓	✓	✓	A	S
3. *Saxifraga tenuis* (Wahlenb.) H. Sm.	✓	✓	✓	✓	C	S
4. *S. cernua* L.	✓	✓	✓	✓	C	SV
5. *S. cespitosa* L.	✓	✓	✓	✓	A	S
6. *Alopercurus alpinus* Sm.	✓	✓	✓	✓	C	SV
7. *Cerastium regelii* Ostf.	?	✓	✓	✓	A	SV
8. *Cochlearia officinalis* L.	?	✓	✓	✓	C	S
9. *Saxifraga oppositifolia* L.	?	✓	✓	✓	C	SV
10. *S. rivularis* L.	?	✓	✓	✓	C	SV
11. *Phippsia algida* (Sol.) R. Br.	?	✓	✓	✓	C	S
12. *Poa arctica* var. *vivipara* (Malmg.) Schol.	✓			✓	A	V
13. *Draba alpina* L.	✓	✓	✓		C	S
14. *Deschampsia alpina* (L.) R.&S.	✓	✓			A	V
15. *Potentilla hyparctica* Malte.	✓				C	S
16. *Luzula confusa* (Hartm.) Lindb.	✓				C	S
17. *Puccinellia phryganodes* (Trin.) Scribn. & Merr.	✓				C	V
18. *Ranunculus pygmaeus* Wahlenb.		✓	✓	✓	C	S
19. *Saxifraga nivalis* L.		✓	✓	✓	C	S
20. *Cerastium alpinum* L.		✓			A	S
21. *Poa alpigena* var. *vivipara* (Malmg.) Schol.			✓	✓	C	V
22. *P. alpina* var. *vivipara* L.			✓	✓	A	V
23. *Cerastium arcticum* Lge.			✓	✓	A	S
24. *Festuca vivipara* (L.) Sm.			✓		A	V
25. *Oxyria digyna* (L.) Hill.				✓	C	S
26. *Draba adamsii* Ledeb.				✓	C	S

[1]The nomenclature follows Rønning, 1979. A = amphiatlantic plants, C = circumpolar plants, S = sexual reproduction, V = vegetative reproduction, SV = both sexual and vegetative reproduction.

southern part of the island is richer in species than the northern parts. No details are given about the areas visited during Eaton's expedition to the island in 1873 (Eaton, 1876). However, it is probable that largely the same areas were visited as in other investigations.

Eaton's list of species requires a number of comments. *Papaver dahlianum* is called *Papaver nudicaule* L. and *Potentilla emarginata* Pursh is a synonym of *P. hyparctica* Malte. As regards *Saxifraga caespitosa* L., *S. groenlandica*, Eaton said that "The Hope Is. specimen is a dwarf not 1/4 inch high, . . ." *Luzula arcuata*, Wahl is *L. confusa* (Hartm.) Lindb. As regards *L. arcuata*, Rønning (1979) said that *L. arcuata* is not found in typical forms on Svalbard. He further indicated that *L. arcuata* in some cases may be confused with *L. confusa*. Eaton mentioned *Aira alpina* L. ??, with Hopen as the only place where this species was found. This is regarded by me as *Deschampsia alpina* (L.) R. et S., since this species is included in a later inventory. Eaton was also doubtful about *Glyceria maritima* Walh. var. *festuciformis* Hartm., which was also only noted from Hopen. I consider it to be *Puccinellia phryganodes* (Trin.) Scribn. & Merr.

Four of the most common species in 1982 were not reported in 1873, for example, *Cerastium regelii, Cochlearia officinalis, Phippsia algida* and *Saxifraga oppositifolia.* They are now extremely common over the entire island. However, it appears probable that they had been forgotten. Eaton included them in his list from other parts of Svalbard. None of the other plants that were later noted from Hopen is mentioned by Eaton. Eaton was not a botanist but a skilled entomologist, which gives a certain assurance of correct observations. Unfortunately, his herbarium, if he had one, cannot be found.

During Iversen's journey in 1924, the zoologist E. Kofoed was responsible for the notes and collection of plants, whereas Johannes Lid was responsible for the species determinations. He found that 8 species were new to Hopen and that the total had now reached 20 (Iversen, 1926:28 ff.).

Schweitzer's list includes 18 species (Engelskjøn *et al.*, 1972). He stated that Eaton would have determined *Saxifraga tenuis* incorrectly and called it *S. nivalis*, a puzzling comment since Eaton does not mention *S. nivalis* but indeed *S. tenuis.* He also suspected that Eaton's *Poa arctica* R. Br. was what he himself called *P. pratensis* L. agsp. *alpigena* (Fr.). The reason for this falls outside my judgement, since I have myself found both species.

Obviously, none of the inventories can claim to have included all species present. However, all four must be regarded as serious and largely reflecting the actual conditions present at the time of the inventory.

In addition to these four inventories, there are reports of other individual finds, e.g., *Minuartia rubella* (herb. O.) and *Ranunculus hyperboreus* (Herb. TROM). Henrik Österholm (pers. comm. 1983) told me that on his visit to Hopen in 1966 he found *Oxyria digyna.* As regards his information (Österholm, 1968) on finds of *Silene acaulis, Diapensia lapponica* and *Saxifraga stellaris*, it can be stated that *Silene acaulis* and *Diapensia lapponica* may be *Cerastium regelii* and *Saxifraga caespitosa* respectively, whereas *S. stellaris*, which is not noted from Svalbard, may possibly be *S. tenuis.*

THE POSITION AND NATURAL CONDITIONS OF HOPEN

Hopen Island is part of the Svalbard Archipelago (Fig. 1) and is situated in the Barents Sea about 220 km to the east of the southernmost tip of Spitsbergen. The Hopen radio station, situated at 76°30′N, 25°04′E, is on the eastern side of the island about 10 km from the southern tip. Hopen is 34 km long and 2.5 km wide at its widest point, with an area of 47 km^2 (Norderhaug, 1982). The island may be regarded as a flat horst drawn out in a NNE-SSW direction and slightly placed on edge, sloping towards the NNE. Topographically, Hopen may be said to consist of seven different elements: mountain plateaus broken by "skards," steep slopes (bird cliffs), screes, ravines, shore meadows and beaches of sand and gravel.

The plateaus are covered by a layer of fine-grained and frequently water-saturated soil that in places may be extremely stony. The "skards," i.e., the depressions between the plateaus, have similar soil conditions. Drier areas, frequently sloping gently and characterized by gelifluction, are found between the waterlogged areas. Vegetation is relatively sparse, with larger or smaller unvegetated areas between the cushion-like plants.

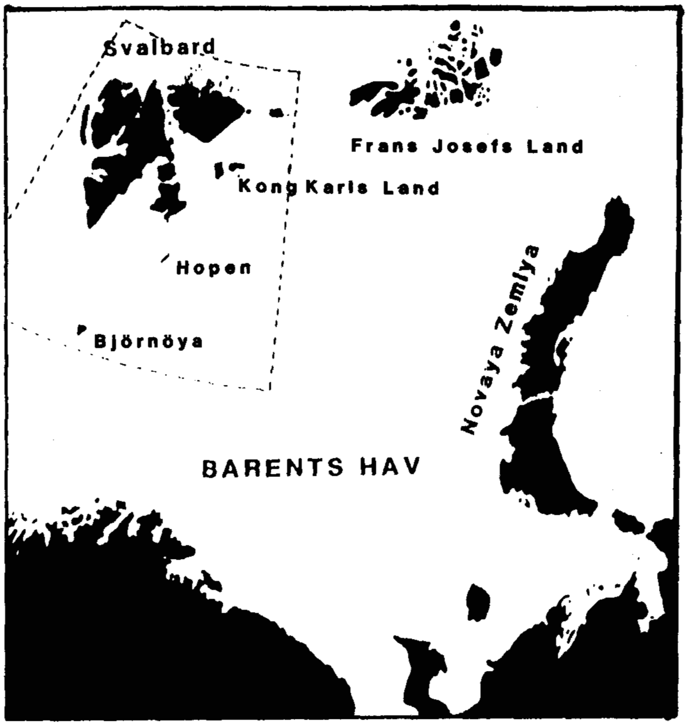

FIG. 1. The Barents Sea and neighbouring areas of land. Hopen is situated in the southeastern part of the Svalbard Archipelago between Bjørnøya and Kong Karls Land.

The substratum of talus deposits consists of weathered gravel mixed with marine sediment. Some areas are more or less unvegetated, mainly on account of landslip. Large amounts of sand and gravel are also transported by meltwater, leading to formation of deep ravines.

In stabilized areas of the landslips there are coherent carpets of mosses containing most of the vascular plants present on the island. The landslip areas below the bird cliffs are frequently rich in ornitocoprophilous species (plants favoured by birds' dung).

The shore meadows and the plains are usually covered with moss in which vascular plants occur fairly abundantly. Organic material that has drifted ashore and remnants from slaughter places are mixed in the mineral soil, which favours the vascular flora. The farther north on the island one progresses, the sparser the vegetation becomes. The recent shores are unvegetated, since waves and ice push keep the fairly coarse material in motion and prevent plants from becoming established.

Permanent snowfields occur in places on Hopen and the meltwater keeps the soil moist on large parts of the island throughout most of the growing period. At present, such snowfields occur on the plateaus, mainly on the steep western side of the island. During the summer, permafrost is found at about 30 cm deep in the soil.

The mean temperature is above ±0°C for about 90 days. "Night" temperatures below 0°C occur occasionally throughout the entire growing period (Steffensen, 1969, 1982).

Aleksandrova (1980) divided the Arctic into tundra and polar desert regions. In her opinion the polar desert region is narrower and more fragmentary in the Arctic than was proposed by, for example, Gorodkov (1958). According to Aleksandrova, the southern border of the polar desert corresponds well to the July isotherm for +2°C. She regarded the southern belt of the polar desert region as a transitory zone to the northern belt of the arctic tundra. Young (1971) and Edlund (1983) also discussed whether the vegetation zones in the Arctic can be related to certain isotherms.

The July mean temperature on Hopen for the period 1951-80 is +2.0°C, with variations from +4.2 to +0.5°C. The August mean temperature for the same period is 0.3°C higher.

As the vegetation on the island is sparse, with larger or smaller unvegetated areas between solitary vascular plants or cushions of one or several species (Skye, 1986), it fits well into the High Arctic area distinguished by Rønning (1969).

Aleksandrova (1980) drew the border between the northern belt of the arctic tundra and the southern belt of polar desert between Nordaustlandet and Spitsbergen. She also included the island groups Kong Karls Land and Storøya and Kvitøya in the polar desert (Fig. 2). With regard to both the appearance and composition of the vegetation, as well as to the temperature conditions, Hopen should be included within Aleksandrova's polar desert region, as should Edgeøya (cf. Neilson, 1970) and probably also Barentsøya.

THE CLIMATE AND ITS FLUCTUATIONS

A Swedish polar expedition was in the neighbourhood of Hopen at midsummer 1898 (Nathorst, 1898). They tried to land on 22 July but were unable to because of the swell. No drift-ice of any importance was present. The photographs taken from the ship show that large areas of the island were snow covered.

During the summer of 1924 Hopen was visited by E. Koefoed and T. Iversen (Iversen, 1926). On 9 July the island was snow covered, but by August large parts were snow free.

On the visit in September 1929 (Iversen, 1941) there was considerably more snow and the mountain slopes were also covered by ice.

Birkeland (1930), who published temperature data from Green Harbour (78°02′N, 14°14′E) covering a 15-year period from 1912, reported a marked increase in the annual mean temperature from 1920.

The same phenomenon was shown by Ahlman (1953). The mean temperature on Spitsbergen expressed in overlapping 10-year anomalies from the mean value during the period 1901-30 is below the mean value for the period 1894/1903 to 1914/23. Particularly large negative divergences occur from 1906/15 onwards. After the change in temperature in 1914/23 the values remain continuously above the mean.

The first meteorological station on Hopen was established by German soldiers in November 1944 at 76°24′N, 25°E and operated until July 1945. In October 1945 the station was re-established at 76°30′N, 25°04′E and has operated continuously since then (Steffensen, 1982).

Isfjord Radio (78°04′N, 13°38′E) has the longest observation period on Svalbard. It operated from September 1934 but was destroyed during the war in September 1941. In August 1946 it was reopened and operated until June 1976 (Steffensen, 1982). A comparison between the temperature values for Hopen and Isfjord Radio show considerable agreement (Steffensen, 1982: Fig. 5). If the development was

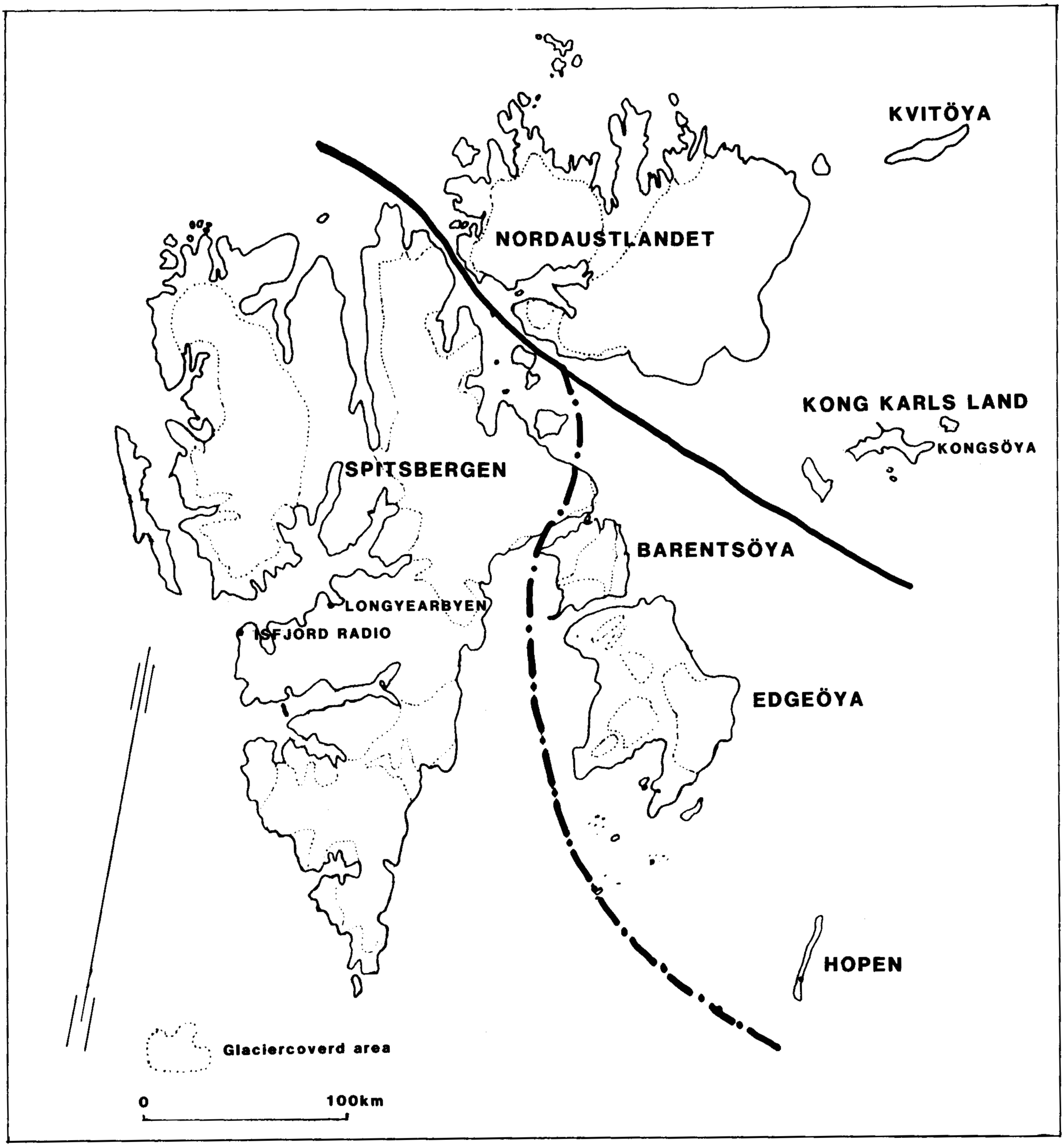

FIG. 2. The limit between the arctic tundra and the polar desert region within the Svalbard Archipelago. ———— according to Aleksandrova, 1980; — — — — — — according to the present author.

similar at both places, then the temperature development on Hopen from 1912 could be estimated.

The annual mean temperature at Isfjord Radio during the 1910s was −7.8°C. After a clear increase in about 1920, annual mean temperatures averaged −4.2°C up to and including 1961, when they again started to decrease. The mean value for 1960-68 was −6.0°C. After a brief period of warmer weather in the early 1970s the downward trend started again towards the end of the decade. The curve for the annual mean temperature on Hopen may be estimated to be about 1°C lower than for Isfjord Radio (Fig. 3c).

In comparison with the annual mean temperature, the summer temperature (June-August) shows considerably smaller variations (Fig. 3a). From the 1910s until 1923/24,

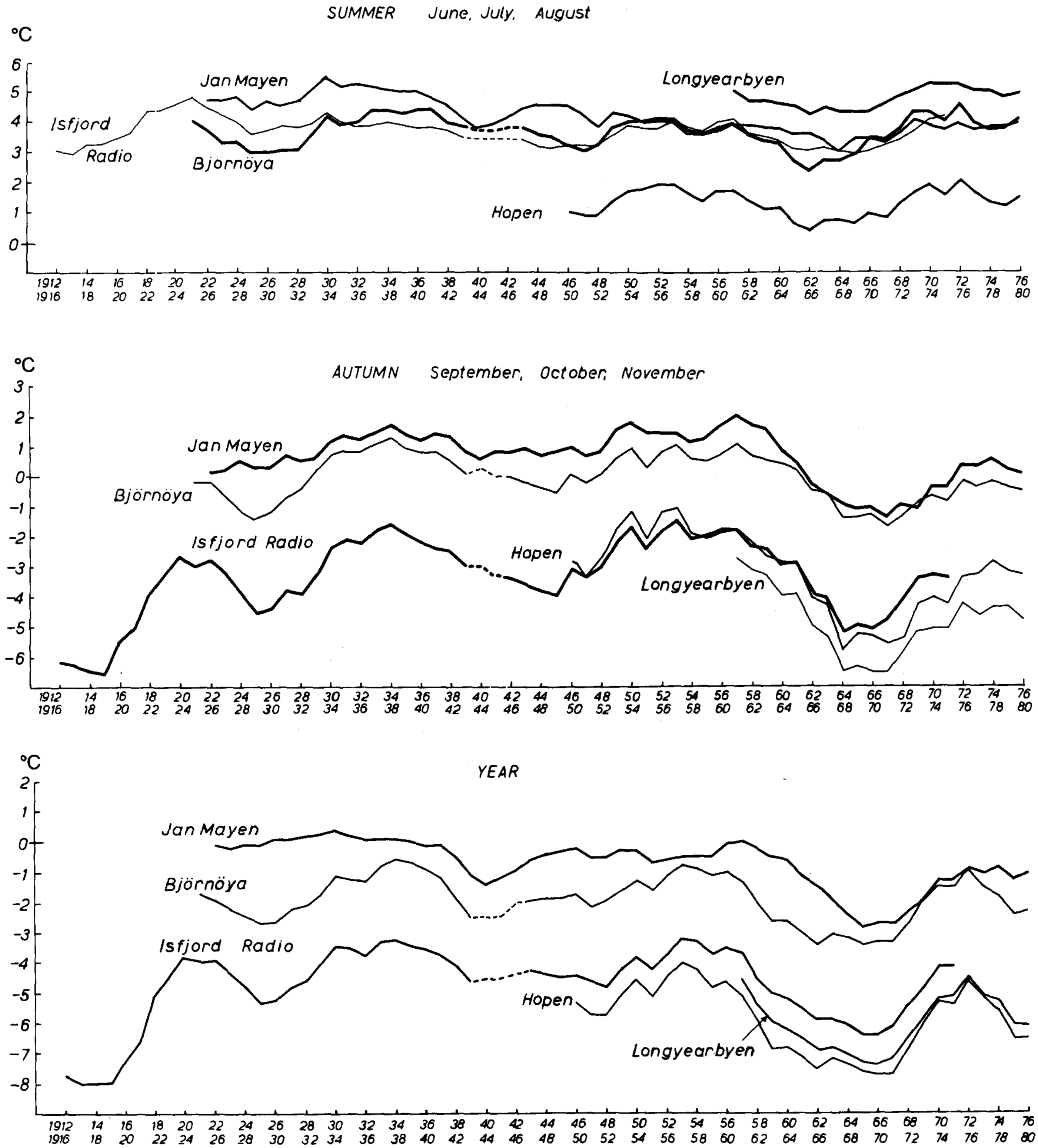

FIG. 3. Summer, autumn and annual mean temperatures at Hopen, Longyearbyen, Jan Mayen, Isfjord Radio and Bjørnøya expressed in overlapping 5-year mean values (Steffensen, 1982).

when a peak was reached, the summer temperature increased by more than 1.5°C at Isfjord Radio. Since then the summer temperature has fluctuated, with increases and decreases similar to the variations in the annual mean temperatures. The average summer temperature for 1925-75 was about 0.5° higher than during the 1910s. It should be noted that a difference of 0.5° may be of considerable importance for the melting of snow and ice.

The summer period (June-August) is quite consistently 2°C colder on Hopen than at Isfjord Radio. The spring (March-

May) is also colder, by about 1°C. The autumn (September-November) curves at Hopen and Isfjord Radio are very similar (Fig. 3b), whereas the winter (December-February) is colder on Hopen.

The July temperature at Isfjord Radio during the period 1945-75 (Steffensen, 1982) was about 3° higher than on Hopen. If a corresponding difference existed between the two stations during the 1912-19 period, then Hopen would have had a July mean temperature slightly above +1°C. Between 1951 and 1980 Hopen had a July temperature of +2°C and an August temperature of 2.3°C.

The temperature curves for September and October are almost identical at the two stations, with mean temperatures mainly above freezing in September and below, sometimes considerably below, in October.

The daily maximum values on Hopen during 1951-80 were +1.3, +3.9, +4.0 and +2.1°C for June, July, August and September respectively. Corresponding values for the period 1951-75 at Isfjord Radio are +3.4, +6.6, +5.9 and +2.5°C.

No data are available on the ice conditions at Isfjord Radio. The fjord and the sea to the west of the station have very variable ice conditions during the winter, ranging from total ice cover to open water. The outer part of Isfjorden is, however, frequently open, even though the sea to the west and the inner part of the fjord are ice covered. During the summer the ice map for 1971-80 suggests that only negligible amounts of ice occur (Steffensen, 1982). Hopen, on the other hand, is surrounded by ice for 9-10 months of the year, from November to July. This explains the late spring on the island. In addition, cold sea currents from the northeast sweep along the eastern coast of Svalbard, whereas the western coast receives warmer Atlantic water from northerly flowing currents (Zenkevitch, 1963: Fig. 22).

The large cyclonic activity causes considerable variations in wind conditions. During the winter season the distribution of air pressure is such that northeasterly winds prevail on Hopen. At this time the strongest winds also occur. During the summer the winds are more variable, but even then there are many occasions with northeasterly winds (Steffensen, 1969, 1982).

The annual precipitation for Hopen during 1951-80 was 400 mm. Precipitation is lowest in May (20 mm) and highest in September and October (44 mm). The precipitation usually accompanies winds from the northeast and falls as light snow, rain or drizzle. Frequently the daily values measured are only in the 0.1-1.0 mm range. Bjørn Aune, at the Norwegian Meteorological Institute in Oslo (pers. comm. 1983), has emphasized the uncertainty and the difficulties involved in the precipitation measurements during certain types of weather.

Rain may also occur during the winter and snow may fall during the summer (Steffensen, 1969, 1982). Steffensen reported that the precipitation at Isfjord Radio, Bjørnøya and Hopen does not differ to any great extent. Both amounts and the distribution during the year are similar. Although older reports from Isfjord Radio appear to show lower values than the more recent observations, whether the precipitation has actually increased is difficult to determine, since the annual fluctuations are large and the measuring periods are short.

The air humidity on Hopen during each month from June to September is above 90%; at Isfjord Radio it is about 5% lower and at Longyearbyen it is 20% lower. The frequency of mists is remarkably high at Hopen during the summer, with a maximum of almost 25% in July.

The development of glaciers and permanent snow fields is influenced both by temperature and precipitation. Koryakin (1967) showed that of a total of 163 glaciers on Spitsbergen, 34 appear to have advanced and 33 appear to be stationary, whereas the remaining 96 have retreated during the present century. Holmgren *et al.* (1984) pointed out the difference in development of glaciers on Spitsbergen and Nordaustlandet in comparison with small arctic islands such as Kong Karls Land and Hopen. On the latter it is not primarily a high accumulation during the winter that explains the occurrence of ice fields at or close to sea level. The reason must be sought in the low summer temperature, which, in turn, depends on the proximity to the melting sea ice. On the western side of Hopen there are large snowdrifts extending from the crest down towards sea level, which may be compared with Rektangelisen on Kongsøya (Fig. 4, top figure).

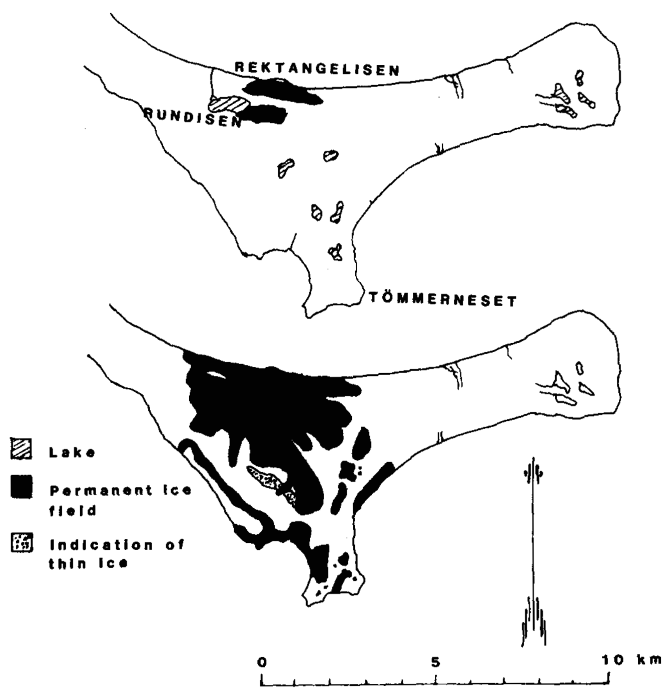

FIG. 4. Eastern part of Kongsøya, Kong Karls Land. Comparison between the maximum extent of the ice within the marked area as indicated by lichen vegetation (bottom figure) and the present extent (top figure).

All ice fields on Kongsøya lost not only the winter snow but also a considerable amount of old ice during the year 1979/80. Holmgren *et al.* (1984) were also able to show that the crest of Rundisen had decreased in height from 133 to 103 m a.s.l. between 1898 and 1980. This gives a mean value of 0.33 m per year. The area of the ice field has also decreased strongly during the same period (Fig. 4).

The observations on Kongsøya and my own observations of lichen vegetation on Nordaustlandet and Hopen support the assumption that the glaciers and permanent snow fields had a considerably greater extent during the Little Ice Age than today, and that consequently also smaller areas were available to vegetation. It does not appear unreasonable to consider that the melt accelerated around 1920, when the summer temperatures increased markedly.

After 1920 the melt probably was at a relatively high level apart from a period during the 1940s and 1960s, according to Steffensen's temperature curves. It may be noted that an increase in the summer temperature of 1°C above an ice field according to the measurements at Kongsøya led to an increase in the melt, which corresponded to 300-400 mm water value, i.e., more than the average total snow precipitation during the year.

The present improvement of the climate causes not only a decrease in the permanent ice and snow fields, so that new ground becomes available for plants, but also results in longer vegetation periods. Some habitats get drier and more suitable for vegetation. How large a part of Hopen will be influenced by these changes is, however, hard to estimate.

CHANGES TO THE VASCULAR FLORA

The hypothesis that the number of species would increase on Hopen owing to larger areas being offered to the plants as a result of the climate improvement has been found to be untenable. Eaton noted 17 species during a period with cool summers and cold springs and autumns. The fields of snow and ice were large and the growing period short. When Iversen visited the area the summer climate was better, but more important, the spring and autumn temperatures had increased considerably. This resulted in a longer growing period and an increased melting of snow and ice. Kofoed found 16 species, about the same as found by Eaton 51 years earlier. After the improvement during the 1920s, the temperature curve fluctuated about a slightly lower mean. In particular, the summer temperature showed very small fluctuations. The 1970s presented a new improvement, and the length of the growing period should have increased. Schweitzer found 18 species during his short visit to Hopen. When compared with the 16 found by Kofoed during walks of several days over large parts of the island, it must be realized that this is a small increase in the number of species. The melting of ice and snow has continued throughout the period, and new areas that can be colonized have appeared.

Within the area inventoried by Schweitzer, I found in 1982 the same number of species as he did, despite several changes in climate having occurred. During the late 1970s the springs were colder and autumns warmer than average. The summer curve remained unchanged. It is difficult to know how these conditions influenced the length of the growing period. Probably it is now slightly longer, even though growth starts later. Consequently, no increase in the number of species has been found, but there is a certain change in the species composition.

The changes in the flora on Hopen during the past century suggest that the island does not demonstrate island biogeography equilibrium as postulated by MacArthur and Wilson (1967). According to this theory, a new equilibrium should occur following the increase in exposed area.

Rannie (1986) asserted that the number of vascular species in different parts of arctic Canada can be correlated with summer temperature. Among the variables tested, the mean temperature in July gave the best correlation with the number of species.

He found a high correlation despite the fact that his lists of species were not related to area. This indicates that the current species-area relationships are not suitable for arctic systems and consequently the change in temperature may be assumed to be of decisive importance.

During the past 110 years changes have not only occurred in the number of species but also in reproduction strategies (Table 2). Among the 26 species noted from Hopen, 15 have only sexual reproduction, 5 have both sexual and asexual reproduction and 6 have only vegetative reproduction.

TABLE 2. Reproduction strategies among vascular plants on Hopen Island

	Σ Species	Only sexual No.	Only sexual %	Only vegetative No.	Only vegetative %	Both sexual and vegetative No.	Both sexual and vegetative %	Note
Eaton	17	9	53	3	18	5	29	
Iversen	17*	10	58	2*	12	5	29	Lid*
Schweitzer	18	10	55	3	17	5	28	Engelskjøn *et al.*
Skye	19	11	58	3	16	5	26	
Total	26	15	57	6	23	5	19	

*Lid (in Iversen, 1926) mentions a sterile *Poa*, which here has been included among species with only vegetative reproduction.

The number of species with seed dispersal increased proportionally up to 1982. No fewer than 6 of Eaton's 9 species are found in all inventories. Two seed-dispersed species in Iversen's material are found in subsequent investigations. One new species in Schweitzer's list appeared in my material, and in addition, I also have 2 new species (Table 1) with seed dispersal.

The number of species with only vegetative reproduction — the group contains only grasses — is nearly constant, even though the turnover is large. Nonetheless, the relative proportion is decreasing. Table 1 shows that only one of Eaton's species was reported by Iversen. Schweitzer reported none of Eaton's species but one has returned in my material. On the other hand, there are 3 new species in Schweitzer's listing, of which 2 are included in my material. Three species that have appeared in the last two investigations are viviparous.

In the entire material 5 species have the ability of both sexual and vegetative reproduction. They are represented in all inventories. Apart from the fact that seed-dispersed species have fewer problems in spreading to Hopen than, for example, those growing as clones, they should also have better opportunities to create a population rapidly and to disperse over the island during a few favourable years. In this way they should be less exposed to random factors that otherwise might result in extinction (cf. MacArthur and Wilson, 1967). Two such examples are *Cerastium regelii* and *Cochlearia officinalis*, which belong to the most common species on the island (Skye, 1986). The shift in species distribution on Hopen implies a shift towards species with more r-selected characteristics (Fig. 5). Theories on the history of life predict that successful colonizers should have a close relationship between birth and death rates (MacArthur and Wilson, 1967). The newcomers on Hopen are at least species with potentially high "birth" rates, but the mortality circumstances are not

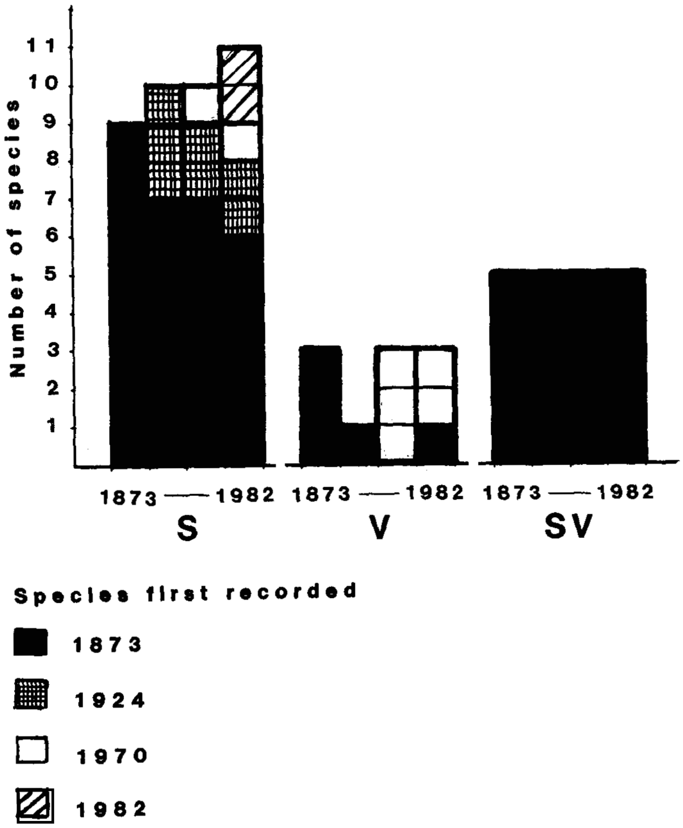

FIG. 5. The turnover in vascular plants divided into three categories based on reproduction strategy. S = Seed dispersel only. V = Vegetative reproduction only. SV = both sexual and vegetative reproduction.

known. Sexual reproduction is nonetheless unreliable, depending, for example, on the frequently miserable weather and thus lack of pollinating insects. Consequently, it is not surprising that the turnover is as large as it is within the group. One form of adaptation to the uncertain conditions is that a number of species, for example, *Papaver dahlianum*, are more or less self-fertile.

The sparse vegetation disfavours wind-pollinated species. Consequently, vegetative reproduction among the grasses can be seen as an adaptation to the lack of reproductive success. However, the ability to survive changes will decrease. *Puccinellia phryganodes* is an example of this. According to Rønning (1972), it flowers frequently, but ripe seeds have never been reported from Svalbard and thus Rønning assumes that they cannot be produced. The species has difficulty in reinvading lost ground. Vivipary is interpreted as an adaptation to prevailing climatic conditions (Ulbrich, 1928; Schwarzenbach, 1956), which makes it possible for a species to increase population size and to disperse over larger areas than if the plant is relying only on formation of stolons. A comparison may be made of *Alopecurus alpinus* with *Poa arctica, P. alpigena* and *P. alpina* in Skye (1986).

IMMIGRATION AND DISPERSAL

Hopen has an isolated position in the Barents Sea to the southeast of the main body of the Svalbard Archipelago and about 100 km from the closest island, Edgeøya. The closest land to the northeast is the island group Frans Josefs Land, at a distance of more than 600 km (Fig. 1). The isolated position of the island makes immigration and dispersal conditions of interest.

Wind dispersal of diaspores may occur over open fields of ice and snow. Many species have small and light fruits or seeds, which facilitate dispersal by wind (cf. Porsild, 1951). However, the distance to the source of the dispersal is very long, making immigration by means of wind transport less probable.

Use of the ice as a means of transporting diaspores is discussed, for example, by Nordal (1985b). Since the strand zone on Hopen is extremely inhospitable to vegetation, it is necessary to have further means of transport to the actual place of growth. During the Ymer 80 Expedition, I noticed on several occasions the snow buntings (*Plectrophenax nivalis*) visit icebergs while seeking food; consequently, transport by birds in the last stage is not out of the question, possibly aided by wind dispersal.

When visiting Nordaustlandet during the same expedition we occasionally found fairly large amounts of soil among remnants of roots on driftwood that had floated ashore. However, we never saw any seeds, seedlings, etc., nor did I see anything of that kind on Hopen. *Puccinellia phryganodes* grows on Svalbard right down to the belt of seaweed on shores of clay and gravel (Rønning, 1979). It may be expected that plants are spread with currents and drift ice, but whether or not plant transports can reach Hopen by this means is uncertain.

It would appear that birds are the most important vector. Among the 19 species of birds noted on Hopen (Løvenskiold, 1964), 4 may be regarded as plant eaters. The snow bunting nests on Hopen, whereas the pink-footed goose (*Anser brachyrhynchus*) and the brent goose (*Branta bernicia*) visit the island temporarily, mainly during migration. The ptarmigan (*Lagopus mutus hyperboreus*) visits Hopen occasionally but mainly during the winter (Løvenskiold, 1964).

The snow bunting eats both insects and seeds. During the autumn before the start of migration seeds are the main food. I have observed the snow bunting eating seeds from capsules of *Papaver dahlianum*. Løvenskiold (1964:15) observed the same behaviour. Also the geese eat poppy capsules. Finds of *Papaver dahlianum* in north Norway and possibly also on northeastern Greenland may be suspected to have been spread by birds from Svalbard. Long-distance dispersal of grasses by means of geese cannot be excluded. The ptarmigan may also be considered capable of carrying diaspores to Hopen from other parts of the Svalbard Archipelago.

Among the species noted on Hopen, all are more or less common on Svalbard. It is probable that most of the vascular plants on Hopen have come from the west and northwest, but it is possible that immigration has also come from the northeast. Birds are probably the most important means of transportation. Local dispersal on Hopen takes place by wind, water and birds.

The question of where the vascular plants on Svalbard originated is difficult to answer, particularly if it is considered that the entire archipelago was under ice during the Weichsel glaciation. Three of Hopen's vascular plant species are not found in Scandinavia and some of them have isolated occurrences on the mainland to the south of Novaya Zemlya.

Among other species, eight are those found in Scandinavia with so-called centric dispersal, i.e., found within very restricted areas in the Scandes and assumed to have an important role in the interpretation of events during and after the latest glaciation.

Neither is the situation clear as to the conditions under which the immigration has occurred. Aleksandrova (1980) considers that the paucity of endemics suggests that the entire Svalbard Archipelago was covered by ice during the Weichsel glaciation. Today, however, it is thought that the origin of new species is considerably faster than previously believed possible (Nordal, 1985a). Thus, the presence or absence of endemics is of no consequence in this connection.

The glaciation in the Barents Sea is occasionally revived as a subject of discussion. An opinion stated during recent years is that the main centre of the glaciation was in the area of Kong Karls Land. With regard to the wind and precipitation conditions it is possible that the area in the northern part of the archipelago was ice free. Large parts of the Barents Sea have depths of less than 100 m. It may therefore be assumed that fairly extensive areas now submerged were then above sea level. It is difficult to believe that the amphi-atlantic species (Hultén, 1958) survived the latest glaciation completely outside their present range of dispersal.

Among these 159 species that can be associated with Svalbard — excluding Bjørnøya — 64.8% may be regarded as circumpolar (Hultén, 1962, 1971) and 30.8% as amphi-atlantic (Hultén, 1958). Despite the large changes in species composition, the relationship between these types of species has remained nearly constant (2:1) on Hopen throughout the entire past century. Somewhere around the North Atlantic there should have been ice-free land of sufficient extent to host a fairly species-rich flora. Investigations on Greenland (Funder, 1982) and Iceland (Hjort *et al.*, 1985) show that refugia are not just a figment of the imagination (cf. also Rudberg, 1986).

More penetrating plant geographical studies using modern genetic analytical methods should contribute to tracing the origin and roots of migration of these species.

ACKNOWLEDGEMENTS

Lars Brydsten and Rolf Zale, University of Umeå, accompanied me during my visit to Hopen in 1982. During the work in preparing the manuscript, I have been given valuable comments by Håkan Rydin and Hugo Sjörs, Department of Plant Ecology, and by Björn Holmgren, Department of Meteorology, Uppsala University. The Norwegian Meteorological Institute, Oslo, has placed basic data at my disposal that has greatly facilitated my work. Nigel Rollison helped me with the translation, Ulla Johansson and Märta Ekdahl with the typing. To all above I extend my warmest gratitude.

The research presented here was financed by grants from Swedish Natural Science Research Council and from Stiftelsen Ymer -80.

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