

# Theories on migration and history of the North-Atlantic flora: a review

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**Abstract** — *Two theories on migration and the history of the North Atlantic flora have been the subject of a popular debate for over a century. In late 19<sup>th</sup> century when signs of glaciations had been recognized in Scandinavia, it was concluded that the entire flora and fauna had been destroyed during glacial periods and that all plants immigrated after the last glacial period. This so called tabula rasa theory was soon opposed by the glacial survival theory which stated that plants survived the last or several of the Pleistocene glaciations in ice-free refugia within North Europe. The glacial survival theory was very popular, in the mid-20<sup>th</sup> century, notably because of three botanical arguments that were forwarded in its support: 1) it alone could explain the distribution of the so-called west arctic element e.g. species found in Scandinavia, Iceland and North America but missing in the Alps, Ural Mountains and Asia, 2) the alpine endemic element e.g. the relatively higher proportion of endemic species in the alpine flora of Scandinavia compared to the lowland, and 3) the special disjunction of the alpine flora. Later, those arguments were reconsidered for the Scandinavian flora and it was concluded that they could be explained without glacial survival. In the last decade, new techniques e.g. molecular methods, results from ice core projects and pollen analyses have offered fascinating possibilities to re-formulate the questions asked by research pioneers. The debate on the plant migration and origin of the flora in the North Atlantic region thus continues.*

## INTRODUCTION

It is generally believed that the present-day distribution of plants and animals in the North Atlantic regions is largely a product of Quaternary climate and environmental change (e.g. Bennike, 1999; Tremblay and Schoen, 1999; Tiffney and Manchester, 2001). Contrasting ideas on plant migration and the origin of the flora in the North Atlantic regions have been the subject of popular debate for over a century, with two contrasting theories emerging by the close of the 19<sup>th</sup> century: a) The *tabula rasa* (clean slate) theory, according to which all plants immigrated after the last glacial period (Nathorst, 1892; Nordal, 1987) and b) The glacial survival theory of plant survival during the last or several of the Pleistocene glaciations in ice-free refugia (e.g. Dahl, 1963; Löve and Löve, 1963).

## The first ideas

### *The Tabula rasa Theory*

It was not until the mid-19<sup>th</sup> century that scientists first began accepting the fact that major parts of northern Europe, North America and Siberia had once been covered with ice. Besides striated and polished rocks, European scientists found extensive unsorted sediments that could only be explained by the existence of a large ice sheet (Dahl, 1946; 1955).

Before the end of the 19<sup>th</sup> century, signs of glaciation were recognized on the outermost islands along the coast of Scandinavia. This led to the conclusion that the entire Scandinavian peninsula had been covered with ice during the “ice age” with the consequent destruction of the flora and fauna. This argument sub-

sequently became the foundation of the theory of *tabula rasa* i.e. that as a result the entire Scandinavian biota had been erased and must have immigrated after the “ice age” from parts of central Europe, British Isles, and Siberia where plants and animals had been able to survive (Dahl, 1955).

The *tabula rasa* theory was already supported with strong arguments. When the biota of Scandinavia was compared with biota from unglaciated areas, the former had remarkably few endemics. The *tabula rasa* theory could explain this by the youth of the flora and fauna. The time span from the “ice age” was not sufficient for the development of new species (Dahl, 1955). Nathorst (1892) and Anderson (1906) were the first to report fossils of arctic and alpine plants in southern Scandinavia (e.g. *Betula nana*, *Dryas octopetala*, *Diapensia lapponica*, *Saxifraga oppositifolia* and *Thalictrum alpinum*). These fossils were found in deposits formed under glacial conditions after the retreat of the inland ice of the last glacial age (Dahl, 1955). By this time, the *tabula rasa* theory was firmly established. Migrations along the borders of the waning ice could explain the presence of alpine and arctic plant species in Scandinavia (Dahl, 1955). In Iceland the main supporters of the *tabula rasa* theory were the geologist Thorvaldur Thoroddsen (1911; 1914) and the botanist Stefán Stefánsson (1913). Later Sturla Friðriksson (1962) also supported the theory.

#### *The Glacial Survival Theory*

In Scandinavia, Blytt (1882) was the first to oppose the *tabula rasa* theory and come up with the idea of glacial survival e.g. plants surviving the last or several of the Pleistocene glaciations in ice-free refugia. Blytt concluded that most of the Norwegian mountain flora consisted of plant species with their main centre of distribution in Greenland and North America. To explain the occurrence of the Greenlandic/American element in the mountain flora of Norway, which he called the west-arctic element, he proposed that a land bridge had connected Greenland to western Norway via Iceland and the Faeroes during the Quaternary. This land bridge would have been glaciated only in part and never simultaneously throughout, thus facilitating dispersal of plants in both directions (Blytt,

1893; Nordhagen, 1963).

The Swedish botanist Rutger Sernander further formulated the glacial survival theory in 1896. He pointed out that in some of the Norwegian (Dovre, Nordland and Finnmark) and Swedish (Jamtland and Harjedalen) mountains, remnants from the interglacial flora of Scandinavia, which had not been overrun by the second inland ice, had been preserved. Sernander’s theory received almost unanimous support from biogeographers dealing with the distribution and history of plant species in the North Atlantic regions at that time e.g. Hansen (1904), Fries (1913) and others (Dahl, 1955).

The idea of glacial survival also became popular in Iceland. The possibility of plants surviving glacial periods in Iceland was first mentioned in the works of Lindroth (1931) and Gelting (1934). As early as 1879, Kornerup had proposed the existence of un-glaciated areas in western Greenland during the last glacial period. Warming (1888) and many others agreed with Kornerup, and other ice-free areas in Greenland were suggested (see e.g. Gelting, 1934). It was even proposed that the most northerly part of Greenland (northernmost Peary Land) had never been glaciated (Koch, 1928).

The macro-lichen flora of south Greenland has a strong resemblance to the Scandinavian arctic/alpine macro-lichen flora (Dahl, 1946). Dahl maintained that post-glacial migration could not explain this affinity, thus the flora must have survived the last glacial period in south Greenland or in areas nearby.

In Svalbard, various areas have been proposed as ice-free Pleistocene islands and candidates for refugia for different plant groups (Dahl, 1946). Lichen studies in Spitsbergen convinced Lynge (1938) that the northernmost part of Spitsbergen had remained unglaciated. King Karl’s Land (in eastern Svalbard) (Nathorst, 1901; 1910) and Björnoya (Hadač, 1941) were also considered to have escaped glaciation (Dahl, 1946).

#### **The Geologists’ Point of View**

##### *Iceland*

Were ice-free refugia geologically possible in Iceland during the ice age? At the beginning of the

last century, Thoroddsen (1905–1906) introduced the idea that the highest parts of the coastal mountains in Iceland had remained ice-free during the maximum extent of the one major glaciation that he recognized. Nearly three decades later, Lindroth also supported the idea, based on entomological studies in southeast Iceland (Norðdahl, 1991 and references therein). Based on geomorphological evidence, the Icelandic geologist Sigurdur Thorarinsson (1937) argued that large parts of northwest and north Iceland were unglaciated during the last glacial period.

#### *Scandinavia*

The Norwegian geologist Hansen (1904) proposed a theory of a broad ice-free margin along the Norwegian Atlantic coast, where a large number of plant species could have survived the last glacial period. Hansen also believed that he could trace a more or less continuous line of moraines in the fjord-districts of Norway, which marked the outer border of the last large ice-sheet along the Norwegian Atlantic coast (Dahl, 1955). Later it was shown that this line marks a certain stage during the deglaciation of Norway and not the outer boundary of the last ice-sheet (Nordhagen, 1963). In 1912, the geologist Vogt claimed that the outermost Norwegian islands of Lofoten, Værö and Röst, had been ice-free during the last glacial period (Nordhagen, 1963). Although some early geologists believed that ice-free areas existed during the last glacial period, the glacial survival theory also received strong criticism from several Norwegian and Swedish Quaternary geologists who demanded proof for the existence of ice-free areas. Other geologists did not totally denounce the “refugium theory” but preferred to remain uncommitted (Nordhagen, 1963).

### A MATURATION OF IDEAS - IS GLACIAL SURVIVAL THE ANSWER?

*The North Atlantic Biota and their History* was the title of a symposium held at the University of Iceland, Reykjavík in 1962 (Löve and Löve, 1963). Biologists participating in the symposium almost unanimously agreed that the observed distribution of certain Scandinavian plant species could not be explained unless they had survived in ice-free refugia at least during the

last glacial period. The *tabula rasa* theory, claiming that all plants immigrated after the last glacial period, had few proponents.

Three botanical arguments were primarily forwarded in support of the glacial survival theory:

1. The west-arctic element,
2. The alpine endemic element and
3. The special disjunction of the alpine flora.

#### *1. The West-Arctic Element*

Dahl (1955) discussed some plant/geographic patterns which were difficult to reconcile with the *tabula rasa* theory. The west-arctic element is of special interest. This comprises plant species found in Iceland, Scandinavia, Greenland and North America (a few occurring also in Novaya Zemlya and Svalbard) but missing in the Alps, Ural Mountains, and Asia. Dahl felt it was difficult to explain the west-arctic element in the Scandinavian mountain flora by migration from the south or east after the last glacial age. No similar west-arctic elements have been found in the Alps, but why did these plants not migrate to the Alps if they lived along the margins of the ice in central Europe through the ice age (Dahl, 1955)? As Blytt (1881) and others pointed out, the plant/geographic connections within Greenland, Iceland, Scotland and Scandinavia are so close that direct migration across the Atlantic Ocean was very likely (Dahl, 1955).

In Scandinavia, the west-arctic element includes about 30 species. About half of these species are represented in Iceland and about 40% in Spitzbergen (Dahl, 1955). They show several distinct distribution patterns, e.g. species which have their western limits in Greenland (e.g. *Arenaria pseudofrigida*) and in eastern North America (e.g. *Pedicularis flammea*). Other species reach as far as the Alaska/Beringia region (e.g. *Campanula uniflora*) and some have a high arctic distribution, connecting Svalbard with northern Greenland (e.g. *Minuartia rossii*) (Dahl, 1955, 1998).

#### *2. The Alpine Endemic Element*

According to Dahl (1955), the glacial survival theory is important to explain endemism in the Scandinavian

flora. Although Scandinavia only has a very small endemic element, there is a difference between the lowland and the alpine flora, the latter having more endemic species. If the *tabula rasa* theory is correct, the arctic-alpine plant species and the lowland plant species are approximately of the same age in Scandinavia, assuming that their ancestors migrated from the south and east to Scandinavia in late-glacial and early postglacial times. If so, the relatively large number of endemic taxa in the mountain flora was considered to be a problem. However, their relatively large number can be explained if the mountain flora survived the last glacial age in refuges along the Scandinavian coast (Dahl, 1955).

### 3. Disjunction and Centricity in the Alpine Flora of Scandinavia

The Swedish botanist Fries (1913) was the first to divide the Scandinavian mountain flora into groups according to distribution patterns. Fries showed that many species in the Scandinavian mountain flora had a centric distribution. About 25 species showed a bi-centric distribution, occupying an area in the mountains of southern Norway and another in northern Scandinavia. The uni-centric plant species were only found in one of these areas (Gjærevoll, 1963). The fact that 80% of the west-arctic element are “centric” (Nordal, 1987) was explained by e.g. Nordhagen (1936, 1963) by the glacial survival theory. The species must have survived in two separate refugia in Scandinavia; one in the Dovre/Jotunheimen mountains in south Scandinavia and the other in north Scandinavia from the Arctic Circle northward to Troms and Finmark (Dahl, 1955).

### Land bridge or Long-Distance Dispersal

The close phytogeographic relationship within the flora of Scandinavia, the Scottish mountains, the Faeroes, Iceland and Greenland, made scientists wonder how the species originally dispersed. Dahl (1958; 1961; 1963) proposed the following alternatives:

1. Beringian land bridge,
2. Land bridge connecting North America with Europe and,
3. Long-distance dispersal.

#### 1. Beringian land bridge:

The flora was originally circumpolar through migration across the Bering Strait. Subsequently, some species became extinct in Siberia and western North America but survived in areas on both sides of the Atlantic Ocean (Dahl, 1958).

#### 2. North American – European land bridge:

Plants dispersed from northeast America/Greenland to northwest Europe via an earlier land bridge connecting Europe and North America.

According to Lindroth (1963), R. F. Scharff was the most ardent early supporter of the land bridge idea and he introduced it in papers from the beginning of the 20<sup>th</sup> century. The Norwegian botanist Dahl (1958) later supported the idea. Several others (e.g. Löve and Löve, 1956; Einarsson, 1961) assumed that the land bridge remained into Late Tertiary with subsequent survival of the biota through all Pleistocene glaciations.

#### 3. Long distance dispersal:

Plants dispersed from northeast America/Greenland to northwest Europe by long distance transport. They were classified according to their mode of transport into: 1) Wind dispersed, 2) Dispersed with animals, 3) Dispersed by the sea, 4) Limnic species and 5) Species with no adaptation to long-distance dispersal (Dahl, 1958).

Dahl (1963) concluded that the second alternative, dispersal via an earlier North Atlantic land bridge, was the most probable one. Dahl rejected alternative 1 (original circumpolar distribution becoming extinct) as a general explanation, because several polymorphic taxa on both sides of the Atlantic are closer to each other than to related forms in the Bering region. Dahl also considered long distance dispersal unlikely, due to lack of special adaptations in the west-arctic element. Steindórsson (1963) agreed with Dahl when he discussed the likelihood of plant species immigrating to Iceland. Steindórsson (1963) considered three possibilities for immigration; ocean currents, air, and migrating birds, and found them all unlikely.

## DID THE ICELANDIC FLORA SURVIVE THE ICE AGE?

Lindroth's and Gelting's suggestion that plants survived in Iceland in ice-free refugia, as mentioned earlier, inspired the Icelandic botanist Steindór Steindórsson to make further studies to test this theory. Already in 1949, Steindórsson pointed out five areas (which he called districts) in Iceland, which he considered possible refugia. Later the districts became six (Steindórsson, 1963). Their definition was based on the distribution of about 100 vascular plant species that seemed to be concentrated in them. Some had highly discontinuous distributions in Iceland with no obvious natural obstacles to explain the gaps (Steindórsson, 1963). Steindórsson compared these six districts with the areas that Thórarinnson (1937) had earlier suggested had been ice-free during the glacial ages and they appeared to match well. These plant centres pointed out by Steindórsson (1963) were: (1) The Breiðafjörður district, (2) Vestfirðir district, (3) Eyjafjörður district, (4) Austfirðir district, (5) Mýrdalur district and (6) Hvalfjörður district.

According to Steindórsson (1963) at least 13 plant species, classified as west-arctic in Scandinavia, are also found in Iceland: *Campanula uniflora*, *Carex macloviana*, *C. nardina*, *C. rufina*, *Cerastium articum*, *Draba norvegica*, *Epilobium lactifolium*, *Erigeron humilis*, *Euphrasia frigida*, *Festuca vivipara*, *Pedicularis flammea*, *Sagina caespitosa* and *Stellaria calycantha*. Five (*C. uniflora*, *C. macloviana*, *C. nardina*, *E. humilis* and *S. caespitosa*) have a distinct centre in the Eyjafjörður district (Steindórsson, 1963). Eight are found at more than 300 m a.s.l. in Iceland and some even up to 1000 m.

Steindórsson (1963) not only proposed the west-arctic species as ice-age candidates, he also considered the so-called North Atlantic species, a group closely affiliated with the west-arctic group, to be ice age survivors. The five plant species, which Steindórsson sorted under this group, were *Alchemilla faeroensis*, *Arenaria norvegica*, *Poa flexuosa*, *Saxifraga aizoon* and *Carex bicolor*. Of these 18 (west-arctic and North Atlantic) species, 11 have a distinct centric distribution in Iceland. Two more species

showed the same kind of tendencies but the rest displayed no centricity at all (Steindórsson, 1963). Other centric species in Iceland were e.g. classified as alpine (>200 m) or lowland (<200 m) plants. The alpine group contains 18 species and the lowland group 37 species (Steindórsson, 1963).

Altogether, Steindórsson (1963) pointed out that the six districts contained 100 species almost exclusively limited to them or to other places with possible nunatak landscape. However, some of these districts are now considered very unlikely to have been ice-free areas, notably the Mýrdalur district (Einarsson, 1963) (Figure 1).

Steindórsson (1963) himself pointed out that "the Mýrdalur district may be considered a dubious refugium area". Mýrdalur enjoys the mildest climate in Iceland and most of its exclusive species e.g. *Plantago lanceolata*, *Succisa pratensis* and *Vicia sepium*, are thermophilic with their present distribution in Iceland most likely limited by temperature, as Steindórsson (1964) himself recognized.

Steindórsson (1963) asked if the plant species mentioned above immigrated in postglacial time, should they not just as easily have taken root in other parts of Iceland? Glacial survival was therefore the most probable explanation for their distribution.

In 1964, Steindórsson suggested that not only had the 100 species already mentioned survived, but that up to 214 species, 48% of the present vascular flora, may have survived the Pleistocene in Iceland. He divided the Icelandic flora into three groups:

- 1) 214 species (48%) that survived in ice-free refugia,
- 2) 92 species brought in by humans (21%) and
- 3) 136 of uncertain origin (31%).

Steindórsson was clearly a great supporter of the theory of glacial survival in Iceland.

As mentioned before, Friðriksson (1962) supported the *tabula rasa* theory. By 1978, his views had changed and he had become an adherent to the theory of survival. At that time, Friðriksson was much involved in monitoring the immigration of plants and animals to the new island of Surtsey (Buckland and Dugmore, 1991).

Hallgrímsson (1969, 1970) divided Iceland into five climatic areas and grouped plant species accord-

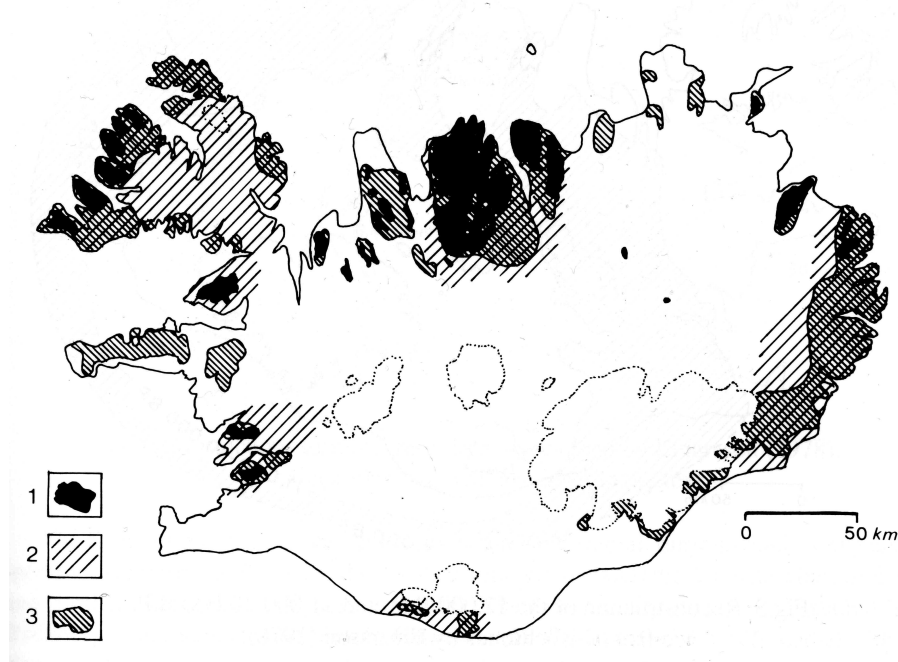


Figure 1. Areas of proposed limited glaciation during the Weichselian period. 1) ice-free areas according to Einarsson (1963); 2) possible plant refugia areas (Steindórsson, 1963) and 3) areas of alpine landscape development, including a relatively limited glaciation (Sigbjarnarson, 1983). Figure reproduced with permission from Ingólfsson, 1991. – Svæði sem líklega höfðu takmarkaða jökulmyndun á síðasta jökulskeiði. 1) líkleg íslaus svæði (Einarsson, 1963); 2) hugsanleg afdrep fyrir plöntur (Steindórsson, 1963) and alpalandslag með fremur lítilli jöklun (Sigbjarnarson, 1983). Myndin er úr grein Ólafs Ingólfssonar, 1991.

ing to habitat and areas. Although he did not reject the idea of glacial survival, he points out that some mountain plants e.g. *Antennaria alpina* and *Carex nardina* are restricted to areas of continental climate.

Geological studies over the last twenty years have suggested that ice-free areas existed in Iceland during the last glacial period. The snowline in the fjords of northern Iceland is believed to have been significantly higher at the northern side of the main ice sheet than on the south side, due to different climate conditions, suggesting that single mountains or peaks were ice-free during the last glacial period (Einarsson, 1991). The Vestfirðir peninsula in northwest Iceland was probably covered by an independent icecap

during the last glacial period. Evidence from Hornstrandir (the northernmost part of the Vestfirðir peninsula) suggests that active glaciers did not cover the high plateaus, as no sign of glacial erosion or deposition were found there. However, it is possible that the plateaus were covered by thin, inactive and/or cold based glaciers or firns (Hjort *et al.*, 1985).

#### Greenland – Survival or not?

Around the middle of the last century, Danish botanists, such as Böcher (1956, 1972) and Gelting (1941) supported the hypothesis of glacial survival in Greenland. Palaeoecologists, on the other hand, argued against this. In 1953, Iversen published the first pollen diagram from a Greenland lake. This in-

licated that only the hardiest plants could have survived. Later, Fredskild (1973) also supported this view. Funder, who published the first pollen diagrams from east Greenland in 1978, also studied the area's geomorphology and glacial geology. The latter studies led him to conclude that some lowland areas in east Greenland were ice-free during the last glaciation. Even though Funder's pollen diagrams indicate that many species were Holocene immigrants, he concluded that some species could have survived the ice age (Funder, 1979; Bennike, 1999). Sediments containing a macroflora of bryophytes and few herbs have recently been studied in NE Greenland. It has been concluded that the woody plants found in these early Holocene sediments did not all survive the last glaciation in nonglaciated areas. However, it is speculated that a few species of vascular plants may have survived (Bennike *et al.*, 1999).

#### TABULA RASA AFTER ALL?

As mentioned earlier, participants at the symposium in Iceland in 1962, on the North Atlantic biota and their history, agreed that glacial survival had replaced the *tabula rasa* theory (Löve and Löve, 1963). However, a different picture has gradually been emerging over the last decades as knowledge about the Pleistocene climate, the ocean floor and tectonic movements has accumulated and become more difficult to reconcile with the refugia theory (Buckland and Dugmore, 1991). For example, putative land connections between North America and Europe have now been pushed back at least 15 million years (Laughton, 1971; Nilsen, 1978; Buckland and Dugmore, 1991).

In 1987, Nordal reconsidered the *tabula rasa* hypothesis in an article titled "*Tabula Rasa After All?*" Nordal queried earlier interpretations of evolutionary rates and went on to consider what she proposed was the most parsimonious hypothesis for the putative endemism in the Scandinavian flora and a reinterpretation of the three main arguments for glacial survival:

- 1) The west-arctic element,
- 2) The alpine endemic element and
- 3) The disjunction and centrality of the alpine flora in Scandinavia.

#### 1) The West-Arctic Element

As Nordal (1987) emphasized, geologists do not agree on the timing of the ultimate disappearance of the Pleistocene North-Atlantic land bridge. Many believe that this happened over two million years ago and some even claimed that the main ridge platform sank below sea level about 15 million years ago (Nordal, 1987). Recent evidence indicates that direct land connection between southern Greenland and Europe was broken in the early Eocene (approx. 50 M yrs ago), allowing Atlantic waters to flow into the Arctic Ocean (Marincovich *et al.*, 1990; Tiffney, 2000; Tiffney and Manchester, 2001).

Reconstruction of glacial limits in Greenland indicates that virtually all of Greenland was covered with inland ice during the penultimate glacial stage. If plant species did immigrate to Greenland via land bridges, then they would have had to survive repeated glacial periods during the last million years and this is hard to reconcile with the above information (Bennike, 1999). But could the Greenlandic flora survive the last glacial period? Then, ice covered much larger areas than it does today. However, fairly extensive land areas and mountain peaks probably remained non-glaciated where plants could have survived the last glacial age in Greenland (Funder 1989; Bennike 1999). Paleoclimatic reconstructions from the Greenland ice cores indicate mean annual temperatures as much as 25°C lower than the present (e.g. Dahl-Jensen *et al.*, 1998; Ganapolski *et al.*, 1998), making survival of most plant species impossible (Philipp and Siegismund, 2003).

Nordal (1987) also challenged Dahl's assertion that the lack of west-arctic species in Siberia and the Alps proved that the west-arctic element did not survive the last glaciation in Europe outside Scandinavia. Fossil remains of *Pedicularis hirsuta* near London have been used as proof that some west arctic species may, after all, have survived the glaciation south of the ice but since become extinct in W-Europe. Today, other amphi-Atlantic species are on the verge of losing their southern area (e.g. *Minuartia stricta*), and others may already have lost it (Nordal, 1987).

## 2) The Alpine Endemic Element

As mentioned earlier, a relatively high proportion of endemic species is found among the Scandinavian arctic-alpine flora compared to the lowland flora. Supporters of the theory of glacial survival believed that these species survived the last glaciation. According to Nordal (1987), glacial survival is not necessary to explain their existence in the Scandinavian flora. Five of these endemic taxa (*Antennaria nordhageniana*, *Arnica alpina*, *Poa stricta*, *Saxifraga opdalensis*, *Taraxacum dovreense* and *T. norvegicum*) belong to apomictic groups within which “speciation” can be rapid, e.g. is a single mutation with phenotypic effect distinct enough to give rise to a new “species”. Five other taxa: *Dactylorhiza pseudocordigera*, *Papaver laestadianum*, *Pyrola norvegica*, *Euphrasia hyperborea* and *E. lapponica* belong to groups with complex and often unresolved taxonomy where justification for specific delimitation may be questioned (Nordal, 1987). Some of the endemics are high polyploids e.g. *Draba cacuminum*, *D. dovreensis* and *Primula scandinavia*. The high polyploids may have been established by hybridization followed by allopolyploidation, but that kind of speciation could certainly occur during postglacial time (Nordal, 1987). She concluded that the endemic species may well be no more than postglacial in age (e.g. no older than about 10,000–15,000 years).

## 3) Disjunction and Centricity

Nordal (1987) pointed out that glacial survival is not necessary to explain the centricity of the alpine flora of Scandinavia. She argued that in the late glacial period, many of the disjunct species may have had a wide and more or less continuous distribution in Scandinavia but later had their range contracted by competition and/or the ice expansion 11,000–10,000 BP (Nordal, 1987).

### Long-Distance Dispersal

Excluding migration along land bridges, could long-distance dispersal explain the present distribution of the west-arctic element? Nordal (1987) questioned whether the lack of special adaptation presented serious obstacles to long-distance dispersal as Dahl (1963) had argued. Nordal’s arguments were

i.a. based on the fact that three of the west-arctic species/species complexes, all of which lack special adaptation to dispersal, are in fact represented in southern South America. If migratory birds brought these species all the way across the American continent, why could they not be brought across the Atlantic Ocean in the same fashion (Nordal, 1987)?

If arctic long distance dispersal actually took place, how did it occur? Most likely, plants were carried by wind across sea-ice in winter, across glaciers and snow in the treeless arctic environment, by icebergs, or by birds. Seeds and fruit lacking hair, wings or other morphological adaptations may occasionally be dispersed by wind over large distances (Bennike, 1999; Brochmann and Steen, 1999). For example, *Cerastium arcticum* has no apparent adaptations for long-distance dispersal. Recent molecular analyses show that populations of *C. arcticum* on both sides of the Atlantic share identical multilocus phenotypes, most probably caused by postglacial dispersal (Hagen *et al.*, 2001).

### Dispersal by Ice and Wood

The idea of biota dispersal by icebergs or drift ice is far from new. Darwin (1859) introduced it in his famous book “The Origin of Species”. A few decades later Blytt suggested this as a possible explanation of the west-arctic element in Scandinavia (Nordal, 1987). Hultén (1962) and Nordal (1987) also considered drift ice or even driftwood as means of long-distance dispersal in the Northern Hemisphere (Johansen and Hytteborn, 2001). Drift ice and driftwood have also been considered important dispersal vectors for the immigration of the Icelandic flora, with the flora transported from northern Eurasia via the Transpolar Drift and East Greenland Current (Rundgren and Ingólfsson, 1999).

During the late Weichselian and early Holocene, both drift ice and driftwood may have been important for the dispersal of diaspores from Siberia and north-west Russia to parts of the North Atlantic region. The basins of the great Siberian rivers, draining areas far to the south, are believed to have been sources of seeds or other biota. Species like *Draba sibirica*, *Oxytropis deflexa* ssp. *norvegica*, *Potentilla stipularis* and *Trisetum subalpestre*, all with highly disjunct distributions



in the North Atlantic regions, may be examples of such long-distance dispersal from Siberia. Moreover, it has been suggested that parts of northern Norway and east Greenland, where extremely disjunct Eurasian vascular plants occur, are linked to coastal areas favourable for accumulation of drift ice and driftwood from Siberia during an initial immigration following the last glaciation (Johansen and Hytteborn, 2001).

### NEW TECHNIQUES – THE DEBATE CONTINUES

Much research has been conducted in the last decade to try to resolve the question of plant migration and history of arctic and alpine plant species. By using molecular methods as well as results from e.g. pollen analyses and statistical models for species richness pattern the debate on the plant migration and the origin of the flora in the North Atlantic region has been revived.

Through molecular techniques, it is now possible to examine genetic similarities between different populations of species and compare them to their geographic distances (Brochmann and Steen, 1999). Biologists have been debating the genetic consequences of survival of isolated plant populations in glacial refugia. Many predict that higher levels of diversity should characterize refugial populations relative to their descendant populations (e.g. Gabrielsen *et al.*, 1997; Comes and Kadereit, 1998). Others assume a massive loss of allelic variability in refugial populations through inbreeding, founder events and population bottlenecks, especially in small refugial areas and populations (Füchter *et al.*, 2001). Even though small and inbred plant populations often show a very small amount of genetic diversity within populations, the genetic distance between different populations is most often large (Nordal *et al.*, 1998).

#### **Tabula Rasa**

Statistical analyses of diversity patterns in the Norwegian mountain flora indicate that contemporary distribution patterns can be explained by climate, geology and topography without recourse to historical variables. The glacial survival theory thus seems to be redundant (Birks 1993, 1996).

RAPD phylogeography has been used to study variation in two arctic/alpine species in Svalbard. Both were interpreted in support of the *tabula rasa* theory (Gabrielsen *et al.*, 1997; Tollefsrud *et al.*, 1998). The results indicate that Svalbard populations of *Saxifraga caespitosa* and *S. oppositifolia* are closely related to Norwegian mainland populations. This close relationship cannot be explained without recent long-distance dispersal across the Barents Sea barrier and it is most likely that this dispersal occurred after the last glaciation (Gabrielsen *et al.*, 1997; Tollefsrud *et al.*, 1998).

Abbot *et al.*, (1995) detected 5 different Cp-haplotypes in a population of *S. oppositifolia* in Svalbard, and interpreted this as an indication of possible survival in high arctic refugia during the last glaciation. A more recent study challenges these conclusions as only two Cp-DNA haplotypes were found in *S. oppositifolia* in Svalbard. This result supports the proposal that there is no molecular evidence for local survival of *S. oppositifolia* within Svalbard or Norway during the last full-glacial period (Abbott *et al.*, 2000).

#### **Glacial Survival**

Pollen records from Iceland have been interpreted in support of the glacial survival theory (Rundgren and Ingólfsson 1999). Pollen records from Lake Torfadalsvatn, N-Iceland spanning 11,300–9,000 BP show that many of the taxa present prior to the Younger Dryas stadial (11,000–10,000 BP) continued to produce pollen during that cold event. Rundgren and Ingólfsson (1999) interpreted this as evidence for glacial survival, e.g. that many plant species with high tolerance for climate fluctuations probably survived the whole Weichselian in Iceland, and cite a high plant diversity in arctic areas and present-day nunataks in Iceland and Greenland as further support for their thesis.

Some recent molecular research also favours glacial survival at high latitudes. Using isozyme analyses, Odasz *et al.* (1991) measured genetic distances between geographically isolated populations of *Pedicularis dasyantha* in Spitsbergen, Svalbard. They found significant variation in allele frequencies and interpreted the pattern of variation, and the evolution of self-compatibility in an otherwise mostly self-

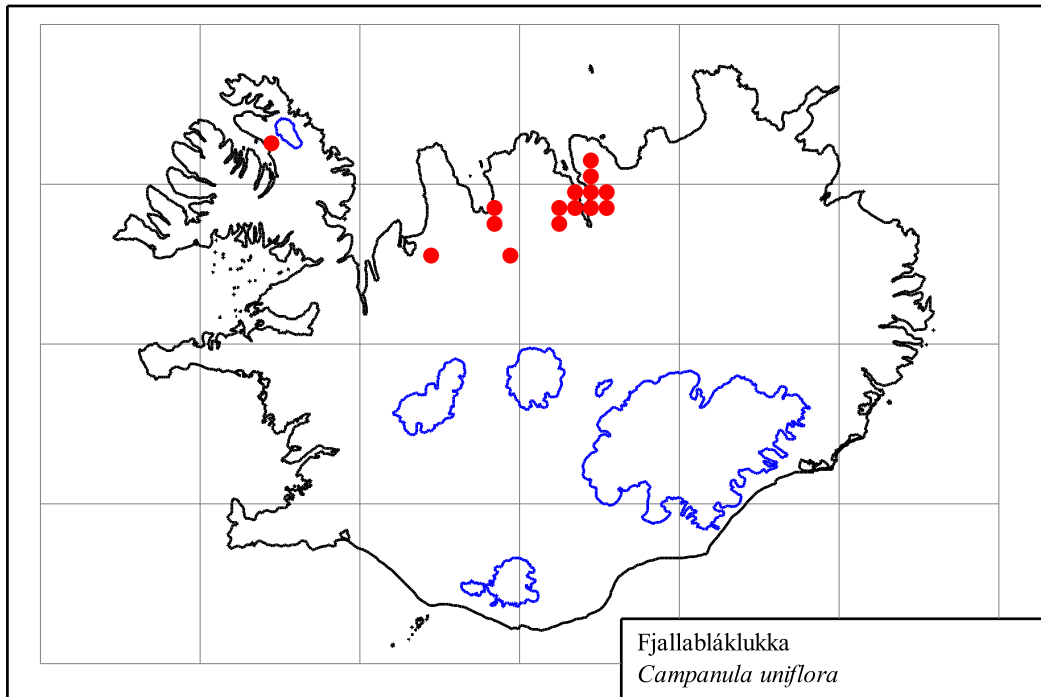


Figure 2. Distribution of *Campanula uniflora* in Iceland. Figure/Mynd: Kristinsson, 2003. – Útbreiðsla fjallabláklukku (*Campanula uniflora*) á Íslandi.

incompatible genus, as consistent with the theory of glacial survival.

#### Tabula Rasa or Glacial Survival?

Where should one look for glacial relicts? A high arctic species with disjunct and isolated populations that are restricted to high mountain habitats is a likely survival candidate. High arctic species are most likely better adapted to in situ survival than species of low-arctic or boreal origin. In terms of environment, high coastal mountains situated close to deep ocean waters are more likely to have been ice-free (Dahl, 1946).

*Campanula uniflora* is a mostly high arctic species with an amphi-Atlantic distribution (Brochmann and Steen, 1999) and can be found as far north as 80°N in Greenland (Böcher *et al.*, 1978) and Svalbard (data provided by Herb. Univers. Osloensis). In Iceland,

*C. uniflora* is rare and its populations are restricted to a few isolated populations in the coastal mountains of the north and northwest (Figure 2) (Kristinsson, 1986), which probably were ice-free during the last glacial period (about 115,000 yrs ago until 10,000 yrs ago) (e.g. Hjort *et al.*, 1985; Einarsson, 1991 and Norðdahl, 1991) (Figure 1). Accordingly, *C. uniflora* is one of the most likely glacial survival candidates in the Icelandic flora (Steindórsson, 1963). A study on the genetic diversity of *Campanula uniflora* in Iceland has recently been completed (Ægisdóttir, 2003). Results from an isozyme study on five different populations in Iceland show no molecular evidence for glacial survival as there was no genetic diversity between geographically isolated populations (Ægisdóttir, 2003).

## INTERPRETING ENDEMISM IN THE ICELANDIC FLORA: A BIOGEOGRAPHICAL COMPARISON

Our present picture of the North Atlantic biota derives from the climatic and glaciation history of the region, species distribution patterns and floristic affinities, apparent speciation patterns and endemisms, with the most recent advances coming from molecular biology. A comparison with the Antarctic has rarely been employed and is mostly of limited value because of the totally different distribution of landmasses in the southern hemisphere. However, for Iceland in particular, a comparative approach may be informative. A survey of the world's oceanic islands soon confirms that there are no comparable islands for all three important criteria, size, degree of isolation and climate (Table 1). Svalbard is most similar in terms of size and isolation but its climate is much harsher. Iceland's closest neighbours, the Faroe Islands, are probably most similar in climate but their area is less than 2% that of Iceland. Some of the subantarctic islands have a comparable climate, although more strongly oceanic. Several have the same degree of isolation, but again they are all much smaller than Iceland.

The most striking pattern to emerge from the table is the difference between the arctic-subarctic, and the subantarctic islands in degree of endemism. Endemism is low (<2% of vascular plant species) in the North Atlantic islands but >10% in all the subantarctic islands. Glaciation history is incompletely known for the subantarctic islands but some appear to have been at least partly glaciated. The difference in endemism between the arctic and subantarctic islands may be a product of the different ages of these floras, or they may reflect much lower probabilities of seed dispersal from the much smaller continental landmasses of the southern hemisphere, even with similar dispersal distances.

Greenland and Svalbard both have some generally acknowledged endemic taxa of vascular plants although the precise number is not agreed upon. Of all the islands, Iceland has the lowest percentage of endemic vascular species, with only one weak claim at present, the apomictic *Alchemilla faeröensis*, also

found in the Faroe Islands. Considering its size, isolation and the presence of endemic taxa both to the east and west, the figure may be lower than expected. However the expectation might be defined and whatever the cause of the lack of endemism, it is at least clear that these data do not support a long and isolated evolutionary history of the Icelandic flora. A similar point was made by Brochmann and colleagues (2003), who remarked on the low degree of endemism in North Atlantic regions compared to areas outside the main ice sheets, and concluded that this did not support the *in situ* Pleistocene survival of the flora.

## CONCLUSIONS

In spite of numerous studies and discussions on the glacial and migratory history of the North Atlantic flora for over a century, conclusive answers have not yet emerged.

Discussion has been limited to the pros and cons of the two contrasting theories. Alternative and less exclusive explanations have been little considered but may be more fruitful. The age, origins and history of the biota of the North Atlantic are likely to vary regionally. While molecular methods have recently opened exciting new avenues for exploring migration history, their power may not suffice to provide a general answer. For example, can we interpret results which indicate a large genetic distance between populations as evidence for glacial survival or should it only be interpreted as an indication of a long time isolation? Will a Pleistocene origin be evident after small relict glacial populations have mixed with perhaps repeated Holocene immigrations? Pollen and macrofossil analyses offer the most direct access to site history. A problem with the interpretation of pollen records is that very high temporal resolution may be needed to distinguish between glacial survival and postglacial immigration, if most immigration took place during unusual conditions prevailing for a short or very short period immediately following deglaciation.

When considering two contrasting hypotheses, the principle of parsimony (Occam's razor) should be employed, e.g. the simplest explanation of a phenomenon (requiring the fewest leaps of logic) should be ex-

Table 1: A comparison of vascular species richness and endemism on selected oceanic islands at latitudes >30°N and >30°S. Greenland is included because of its geographical setting as Iceland's closest neighbour. – *Samanburður á tegundaauði æðplantna og fjölda einlendra tegunda á völdum úthafseyjum á breiddargráðunum >30°N og >30°S. Grænland er tekið með í samanburðinn vegna nálægðar sinnar við Ísland.*

Island or archipelago	ref.	latitude	isolation approx. km to nearest continent	approx. area of island or island group	indigenous vascular species	endemic taxa	% endemism
Greenland	1	59°46'–83°41'N		2,175,600 383,600 <sup>a)</sup>	497	15	3.0
Svalbard	2	74–81°N	930	62,000	164	2–3?	1.2?
Iceland	3	63°23'–66°32'N	810 (Scotl.), 970 (Norw.)	103,000	480	(1) <sup>d)</sup>	(0.3)
Faroe islands	1	62°N	330 (Scotl.), 600 (Norw.)	1,399	250	(1) <sup>d)</sup>	(0.4)
French Southern Territories <sup>b)</sup>	1	37°41'–48°50'S	>2,000	7,829	50	11	22.0
Chatham island	1	43°58'S	800	965	320	40	12.5
subantarctic islands (Auckland, Campbell, Antipodes and Macquarie islands)	1,5	49°42'–54°37'S	200–800 <sup>c)</sup>	949	ca. 250	35	ca. 14
Falkland islands	1	52°S	530–550	12,200	165	14	8.5

<sup>a)</sup> area of ice-free land (Böcher and Petersen, 1997)

<sup>b)</sup> includes the archipelagos of Crozet and Kerguelen and the volcanic islands of Amsterdam and St Paul

<sup>c)</sup> refers to distance to New Zealand

<sup>d)</sup> the bracketed figure of 1 refers to the same species for both Iceland and the Faroe islands, the apomictic *Alchemilla fareoensis*.

References, 1) Davis *et al.*, 1996; 2) Elvebakk, 1997; 3) Válisti 1. Plöntur, 1996; 4) Scott, 1985; 5) McGlone, 2002.

amined and tested first. Here, the hypothesis of a Holocene age for the North Atlantic flora must be regarded as simpler as it requires fewer environmental and biological assumptions. Since the subject was first broached over a century ago, there have been several paradigm shifts, from the early acceptance of *tabula rasa* to glacial survival in the mid 20<sup>th</sup> century. At present, the pendulum seems to be moving towards *tabula rasa* again (Brochmann *et al.*, 2003) but whether that will be the end of the debate is hard to say. Only more studies and discussions in the future will help us further in our search for an answer on the history of the North Atlantic flora.

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### ÁGRIP

#### Kenningar um sögu flórunnar við N-Atlantshaf

Í greininni er fjallað um þróun ördeyðu- og miðsvæðakenninganna frá lokum 19<sup>th</sup>. aldar en þær hafa verið miðpunktur skoðanaskipta um uppruna og sögu flórunnar við Norður Atlantshaf allt fram á okkar daga. Ummerki eftir ísaldarjökulinn í Skandinavíu urðu um miðja 19. öld kveikjan að hugmyndum um að allt lífríki hafi dáið út á jökulskeiðum ísaldar en borist þang-

að úr suðri eftir síðasta kuldaskið (ördeyðukenningin). Í lok 19. aldar var ördeyðukenningunni andmælt og hugmyndin um miðsvæðakenninguna kom fram, þ.e. að plöntutegundir hafi lifað af á íslausum svæðum sem stóðu upp úr meginísbreiðunni. Miðsvæðakenningin átti marga fylgjendur allt til seinni hluta síðustu aldar enda var hún talin geta skýrt útbreiðslu ákveðinna plöntutegunda við N-Atlantshaf, einlendrar tegundir í háfjallaflóru Skandinavíu og tiltekin útbreiðslumynstur í flóru Íslands og Skandinavíu. Síðar voru þessi rök gagnrýnd og t.a.m. sýnt fram á fleiri mögulegar skýringar á útbreiðslu þessara tegunda. Á síðasta áratug hafa verið notaðar nýjar rannsóknaraðferðir s.s. sameindafræðilegar aðferðir, ískjarnaboranir og frjórnagreining til að reyna að svara sömu spurningum og vísindamenn í byrjun 20. aldar höfðu varpað fram. Þessar nýju rannsóknir hafa gefið mikilvægar niðurstöður en gátan um uppruna og sögu flórunnar við N-Atlantshaf er þó enn óleyst.

#### Glossary

**Apomictic groups** reproduce asexually without meiosis or formation of gametes but nevertheless produce seeds that are indistinguishable from normal sexually produced seeds.

**Chloroplast DNA (cpDNA)** is a very useful marker for the analysis of the late Quaternary history of angiosperms because in most angiosperms, cpDNA is transmitted through the ovules, not pollen. This may lead to less swamping through interpopulational gene flow of the initial genetic structure, established during refugial survival and/or at colonization.

**Endemic species** is one that evolved in and has remained restricted to a particular area. In a sense, all plant species are endemic since none has a global distribution but the term is usually reserved for species with a small distributional range.

**Polyploidy** is a mutation like effect that duplicates whole sets of chromosomes in plants. Polyploidy can be divided into autopolyploids, which are composed of multiple sets from within one species, and allopolyploids, which are composed of sets from different but related species.

**Random Amplified Polymorphic DNA (RAPD)** is a molecular method, used to examine phylogeography

and genetic diversity within and among populations.

**Self-compatibility** refers to plants that are capable of self-fertilization.

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