

Plant survival in Iceland during periods of glaciation?

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Abstract

Aim The paper addresses the classical question of possible plant survival in Iceland during the last glacial period in the light of a palaeobotanical record from northern Iceland, spanning the period 11,300–9000 BP, including the Younger Dryas stadial. We review the Late Cenozoic fossil plant record, the past debate on glacial plant refugia in Iceland, and the evidence for ice-free areas during the Weichselian.

Location The investigated lake sediment record comes from Lake Torfadalsvatn, which is situated in the northwestern part of the Skagi peninsula in northern Iceland.

Methods The sediment chronology was constructed from the occurrence of the Vedde Ash and the Saksunarvatn ash, two well-dated Icelandic tephros, together with the results from five AMS and conventional radiocarbon dates performed on bulk sediment samples. The vegetational reconstruction was based on detailed pollen analysis of the sediment sequence.

Results The pollen analysis revealed that many of the taxa present in the area prior to the Younger Dryas stadial continued to produce pollen during that cold event. The more or less immediate reappearance of a few other pollen taxa at the Younger Dryas-Preboreal boundary suggests that these plants also survived, even if they did not produce sufficient pollen to be recorded during the Younger Dryas stadial.

Main conclusions We conclude that the relatively high plant diversity found in high Arctic areas and present-day nunataks in Iceland and Greenland, together with the fact that many plant species were able to survive the Younger Dryas stadial on the Skagi peninsula, suggest that species with high tolerance for climate fluctuations also survived the whole Weichselian in Iceland. This conclusion is supported by recent palaeoclimatic data from ice-cores and deep-sea sediments, indicating that Icelandic climate during the last glacial was only occasionally slightly colder than during the Younger Dryas stadial.

Keywords

Iceland, vegetation, glaciation, refugia, palaeobotany.

INTRODUCTION

This paper addresses the classical question of possible survival of vascular plants in Iceland during the last glacial period, in the light of palaeobotanical data from Lake Torfadalsvatn on northern Iceland. The Lake Torfadalsvatn pollen record from the Skagi peninsula (Fig. 1) extends farther back into the Late Weichselian than any other Icelandic palaeobotanical record (Rundgren, 1995). Thereby it provides data that are relevant for the question of possible Weichselian plant refugia in Iceland. It shows, for example, that a diverse Icelandic flora existed already in the period 11,300–10 600 BP, considerably earlier than previously believed (Hallsdóttir, 1990, 1995; Björck *et al.*, 1992). Here, we assess the impact of the cold climate during the

Younger Dryas stadial on this flora and discuss its implications for possible plant survival in Iceland during the entire Weichselian and earlier glacials. Throughout this paper, BP refers to uncalibrated ¹⁴C years, and plant nomenclature follows Kristinsson (1987).

The fossil plant record

The geological record implies that local ice-caps appeared in Iceland already in the Miocene, but full-scale glacial–interglacial cyclicality with regional ice cover was not initiated until ≈2.6 my. ago (Geirsdóttir & Eiríksson, 1993). Progressive cooling is indicated by increasingly extensive

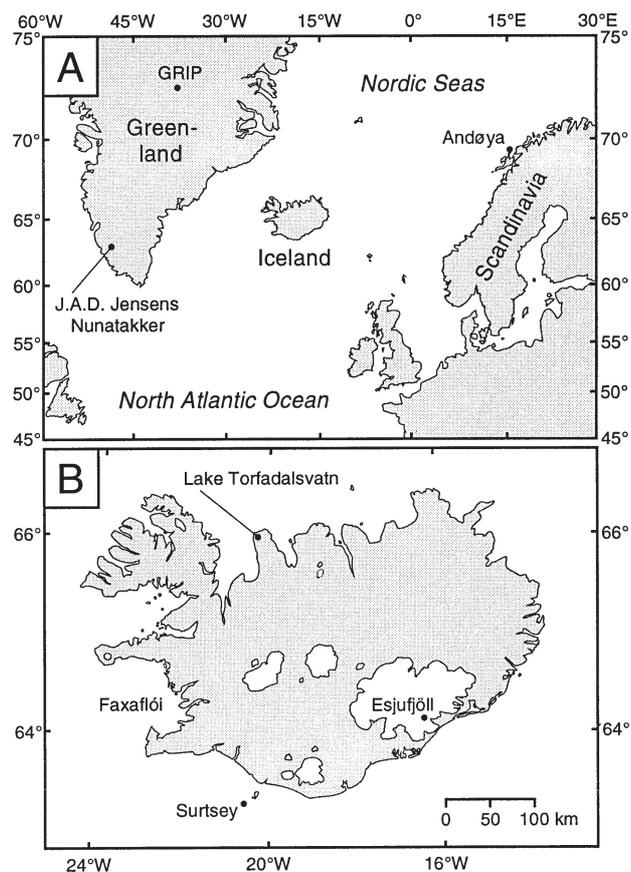


Figure 1 Maps of (A) the North Atlantic region and (B) Iceland showing location of sites mentioned in text.

glaciations through the Pliocene and Pleistocene. Late Cenozoic cooling is also suggested by the fossil plant record (Simonarson, 1979; Th. Einarsson, 1994). The oldest known flora (≥ 14 my) is characterized by mixed warm-temperate forest taxa such as *Sequoia*, *Pinus*, *Juglans*, *Alnus*, *Fagus*, *Ulmus*, *Tilia* and *Vitis*. Lower and middle Pliocene forests were dominated by *Pinus*, *Abies* and *Larix*, but *Quercus*, *Fagus*, *Corylus*, *Ilex*, *Betula*, *Alnus* and *Salix* were also present. Lower and middle Pleistocene interglacials were characterized by *Alnus*, *Betula*, *Salix* and Poaceae, and *Alnus* seems to have become extinct three glacial periods ago. These fossil floras imply a progressive elimination of warmth-demanding species during late Tertiary cold periods and Pleistocene glacials, and they suggest that these species were unable to re-immigrate during subsequent warm intervals and interglacials. This is explained by the fact that all land connections with adjacent continents were lost in the lower Miocene (Nilsen, 1978).

In addition to an overall cooling, the fossil records reflect a transition from a flora dominated by American elements during the Miocene to one with more European affinities (Simonarson, 1979; Th. Einarsson 1994). It is interesting to note that many of the taxa that are important in the present vegetation, e.g. *Betula nana*, *Salix*, *Empetrum nigrum*, Ericaceae (e.g. *Calluna vulgaris*), Poaceae, Cyperaceae, *Dryas octopetala*, Caryophyllaceae, *Plantago* and *Lycopodium*, are recorded by

their pollen or as leaf imprints already in the early Pleistocene (Áskelsson, 1938; LINDAL, 1939; Th. Einarsson, 1994).

Biological evidence

Possible survival of vascular plants within glaciated areas was first discussed for Scandinavia by Blytt (1876) and Sernander (1896). The absence of some Norwegian mountain species in alpine areas further south and east in Europe suggested to them that the present distribution of these species cannot be the result of glacial survival outside the limit of the Scandinavian ice sheet and subsequent immigration. They therefore introduced the so-called nunatak hypothesis, which proposes that plants survived the last glaciation on mountain tops protruding above the inland ice sheet, or in other unglaciated areas within or adjacent to it. Up to that time, the idea of total elimination of terrestrial biota, the so-called *tabula rasa* hypothesis, prevailed universally. The formulation of the nunatak hypothesis was the beginning of a long debate among biologists and geologists concerning the possible existence of Weichselian plant refugia in both Scandinavia and other glaciated areas in the northern hemisphere.

Glacial survival of terrestrial biota in Iceland was first proposed by Lindroth (1931). He suggested, mainly with reference to the distribution of flightless Coleoptera species, that coastal refugia with boreo-temperate conditions existed in southern and south-eastern Iceland during at least the Weichselian glacial. Later, Steindórsson (1937, 1962, 1963) pointed out some mountainous areas as refugia, based on the present centric distribution of some plant species. As their absence in intermediate areas cannot be explained by absence of suitable habitats, or unfavourable climatic conditions, he claimed that the patchy distribution of these species reflects their inability to disperse from glacial refugia. Glacial plant survival was, according to Th. Einarsson (1961, 1963), further supported by palaeobotanical data. The concept of centric distribution as an indicator of nunatak survival had earlier been applied in Scandinavia by Nordhagen (1936), and it has become one of the major botanical arguments for glacial plant survival in Scandinavia (e.g. Dahl, 1955) and other glaciated areas. An interesting contribution to the discussion on the relevance of centric distribution patterns for the existence of nunatak refugia was made by H.J.B. Birks (1993), who tested the statistical significance of unglaciated areas in explaining present-day alpine plant distributions in the Norwegian mountains. His conclusion was that the nunatak hypothesis is unnecessary to explain these distribution patterns, and that the observed centricity may be predicted from modern topography, geology and climate. This does not, however, imply that plants were unable to survive the Weichselian glaciation in Norwegian nunatak areas. Strong evidence against glacial survival on Norwegian nunataks was put forward by H.H. Birks (1994). Her compilation of pleniglacial and late-glacial plant macrofossil data shows that many of the present mountain plants grew close to the last ice-sheet margin and that they rapidly migrated into new habitats as the ice retreated.

The latest contribution to the debate on the history of Icelandic biota was made by Buckland & Dugmore (1991).

They concluded that the low number of endemic plants and animals, together with the cool temperate rather than arctic character of the Icelandic biota, is incompatible with glacial survival. In their opinion, these characteristics are best explained by a dispersal model earlier proposed by Coope (1979, 1986) and Buckland *et al.* (1986). This model ascribes the immigration of the bulk of the present Icelandic biota to a short-lived episode of ice-rafting at the Late Weichselian–Holocene transition around 10,000 BP. South-western Scandinavia, south of the decaying ice sheet, is suggested to be the source area for these plants and animals. After this event, some species may have arrived as aerial plankton, but a much larger number has been introduced by Man since the ninth century. This ice-rafting model is based on the assumption that ocean circulation at the Late Weichselian–Holocene transition was different from today, allowing more direct drift-ice transport from Scandinavia to Iceland on a sea with low salinity. Recent palaeoceanographic research has shown, however, that Late Weichselian surface circulation in the Nordic Seas differed little from the present one (Koç *et al.*, 1993; Sarnthein *et al.*, 1995). Summers were ice-free, even during the Younger Dryas stadial, and relatively saline waters flowed north along the Norwegian coast. These palaeoceanographic conditions are incompatible with the concept of exceptional conditions for drift-ice dispersal from Scandinavia to Iceland at the Late Weichselian–Holocene transition and, consequently, this dispersal model has to be reconsidered.

Geomorphological indications of ice-free areas

There are strong indications in the form of alpine landscapes, glacial trim lines, felsenmeers and deep-weathering on high plateaux that ice-free areas existed in coastal mountain areas during the last glacial maximum (Thorarinsson, 1937; Hoppe, 1982; Norddahl, 1983; Sigbjarnarson, 1983; Sigurvinsson, 1983; Hjort *et al.*, 1985; Ingólfsson, 1988; Norðdahl, 1991; Guðmundsson, 1995), but it has not yet been demonstrated that plants survived there. Our reconstruction of ice-thickness at the maximum glacial situation (Fig. 2) indicates relatively large nunatak areas in northern, eastern and north-western Iceland.

Hjort *et al.* (1985) suggested that shallow shelf areas off the present coast, transformed to land due to eustatic lowering of sea level, could have acted as refugia during maximum glacial situations. During the earliest part of the Holocene, when the rapid isostatic rebound was completed and relative sea level was lower than present, peat bogs formed off the present coast in Faxaflói Bay at levels as low as 18–30 m below present sea level (Thors & Helgadóttir, 1991; Ingólfsson *et al.*, 1995). This shows that vegetation can quickly invade a recently emerged seafloor.

MATERIALS AND METHODS

Lake Torfadalsvatn is situated in the north-western part of the Skagi peninsula on northern Iceland (66°04'N, 20°23'W; Fig. 1), at 47 m a.s.l. Its catchment (0.37 km²) consists mostly of rocky plateaux, and dwarf shrubs (*Betula nana* L., *Salix herbacea* L.

and *Empetrum nigrum* L.) dominate the surrounding vegetation. A detailed description of the lake and its surroundings was given by Rundgren (1995).

The investigated lake sequence (core B1), which is identical to that used by Rundgren (1995), was collected with Russian samplers of 5 and 10 cm width at a water depth of 5.1 m in the centre of the basin. The basal sediments are dominated by clay, with some silt, sand and gravel, followed by gyttja clays and clay gyttjas further up in the sequence (Fig. 3). A major tephra horizon, the Saksunarvatn ash, is present at 7.00 m. This black and silty deposit, dated to c. 9000 BP (e.g. Björck *et al.*, 1992; H.H. Birks *et al.*, 1996), was chosen as the upper boundary for the present investigation. Another tephra, the Vedde Ash, dated to ≈ 10,300 BP (e.g. H.H. Birks *et al.*, 1996), is present at 7.425–7.400 m. Our core chronology is based on the occurrence of these tephras and on five AMS and conventional radiocarbon dates performed on bulk sediment samples (Björck *et al.*, 1992; Rundgren, 1995). The same chronology was used by Rundgren *et al.* (1997). Too few terrestrial plant macrofossils were recorded to allow for AMS radiocarbon dating.

Rundgren (1995) defined seven local pollen-assemblage zones (LPAZs) for the period 11,300–9000 BP in Lake Torfadalsvatn (Fig. 3). One of these zones (T-4) was regarded as redeposited, and this was later confirmed by its absence in another Skagi lake (Rundgren *et al.*, 1997). The pollen spectra of LPAZ T-4 are therefore ignored in the following discussion of past vegetation.

Pollen preparations followed standard techniques, and *Lycopodium*-tablets were added in order to estimate pollen concentration values. Identifications were made using the key of Moore *et al.* (1991) and the reference pollen collection at the Department of Quaternary Geology, Lund University. Pollen nomenclature follows Moore *et al.* (1991) except for the following taxa: *Betula* pollen were separated into *Betula nana* and *Betula pubescens* ssp. *tortuosa* using size and morphological criteria as described by Rundgren (1995), and *Juniperus communis* was used instead of *Juniperus* type since this is the only Icelandic species included in this pollen type. The pollen-taxon name *Empetrum nigrum* was preferred to the *Empetrum nigrum* ssp. *nigrum* type of Moore *et al.* (1991), and *Capsella bursa-pastoris* type was used as equivalent to *Hornungia* type since *Hornungia* is absent from Iceland and *Capsella bursa-pastoris* is the only Icelandic species known to belong to this pollen type. Furthermore, *Caltha palustris*, *Thalictrum alpinum*, *Plantago maritima* and *Armeria maritima* were used instead of the pollen types *Caltha* type, *Thalictrum*, *Plantago maritima* type and *Armeria maritima* type (A and B) of Moore *et al.* (1991), assuming an Icelandic origin for the recorded pollen grains. *Oxyria* type, *Rumex acetosa* type and *R. acetosella* type, which include the Icelandic species *Oxyria digyna*, *R. acetosa*, *R. acetosella* and *R. crispus* (a rare alien), were combined to form *Oxyria* + *Rumex*. The great majority of determinable grains was found to be derived from *Oxyria digyna*.

RESULTS

The pollen record (Fig. 3) shows that most of the taxa present in the surroundings of Lake Torfadalsvatn prior to the Younger Dryas stadial (LPAZ T-1 and T-2) also could continue to flower

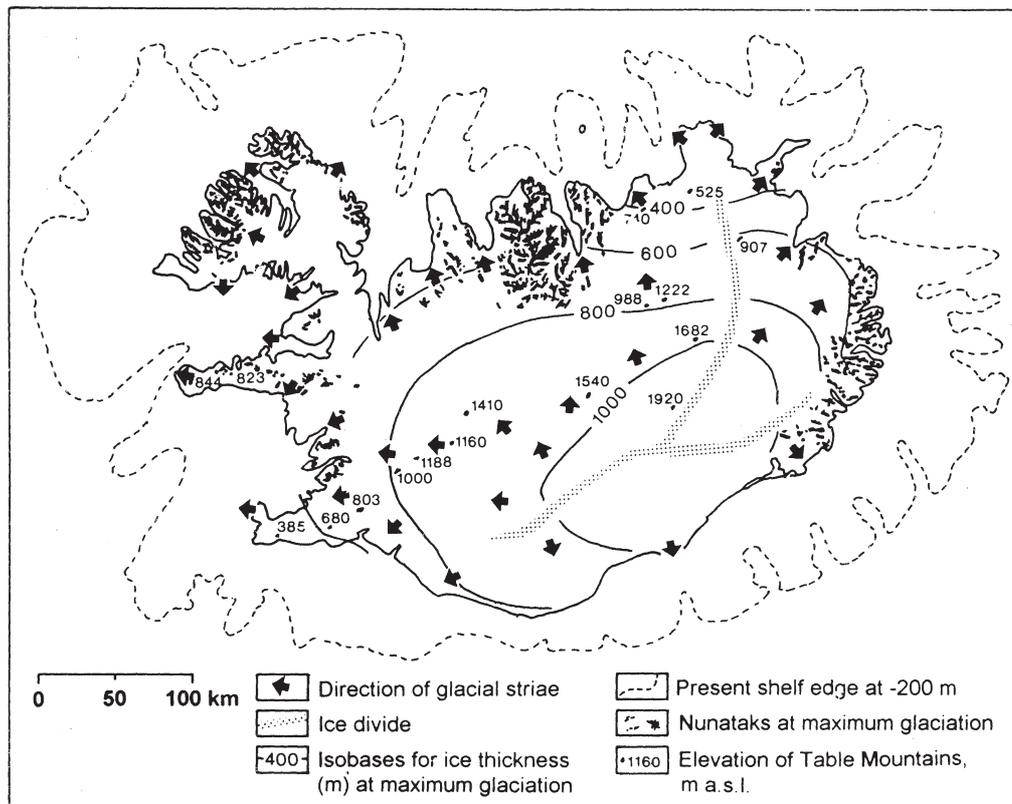


Figure 2 Ice thickness and nunataks at the last maximum glaciation. Isobases for ice thickness are primarily approximations based on the height of Table Mountains above their surroundings, checked against field data on nunataks in the coastal regions. Compilation based on Walker (1965), Th. Einarsson (1963, 1994), Hoppe (1982), Hjort *et al.* (1985), Ingólfsson (1988), Norðdahl (1991), Guðmundsson (1995) and Norðdahl & Hjort (1993). Ice-free areas could also have existed on the shallow shelf during periods of low global sea levels, in sheltered coastal positions between ice-streams draining out from the fjords.

and produce pollen during that event (LPAZ T-3 and T-5). More than ten pollen taxa are continuously recorded or encountered in such numbers in the Younger Dryas sediments that they indicate local presence. Even woody plants like *Betula nana*, *Salix*, and possibly also *Juniperus communis*, endured the Younger Dryas stadial on northernmost Skagi. Some Younger Dryas taxa, e.g. *Betula nana*, Caryophyllaceae and *Oxyria* + *Rumex*, show an immediate response to the Preboreal warming. At the same time, some pollen taxa present in LPAZ T-2, but not recorded during the Younger Dryas stadial, reappear in the sediments of Lake Torfadalsvatn. This applies to, among others, *Empetrum nigrum*, *Plantago maritima*, *Armeria maritima* and *Koenigia islandica*. The reappearance of these taxa at the

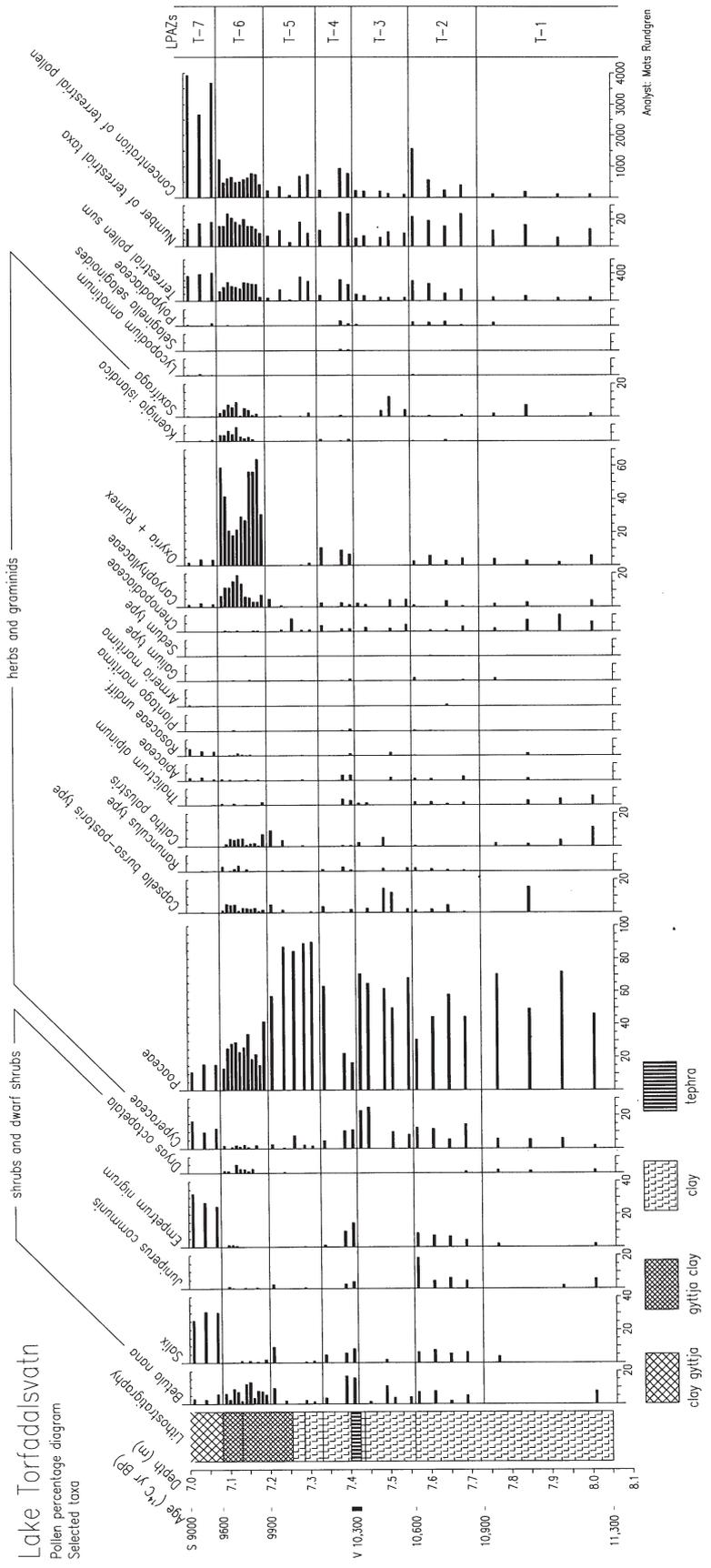
Younger Dryas–Preboreal transition suggests that also they were present in the area during the Younger Dryas stadial, but their pollen production was insufficient to be recorded.

DISCUSSION

Plant survival under harsh conditions

The relatively low pollen concentration values and the low number of recorded pollen taxa during the Younger Dryas stadial do not necessarily imply reduced populations or the elimination of species. They may just reflect reduced flowering, which in many species could be compensated for by an increased

Figure 3 Pollen percentage diagram from Lake Torfadalsvatn showing the most abundant pollen types. Only locally derived pollen taxa have been included (*Artemisia* and all tree-pollen taxa excluded; cf. Rundgren (1995)). *Saxifraga* includes *S. undiff.*, *S. oppositifolia* type, *S. cernua* type and *S. granulata* type. Polypodiaceae includes Polypodiaceae undiff., *Woodsia* type and *Cystopteris fragilis*. Caryophyllaceae includes Caryophyllaceae undiff. and *Cerastium* type. Pollen percentages are based on the sum of terrestrial pollen grains. Frequencies of pteridophytes are expressed as percentages of the terrestrial pollen sum plus the sum of the corresponding taxon. Number of terrestrial taxa and concentration values for terrestrial pollen are indicated. The ^{14}C ages given are local pollen assemblage zone (LPAZ) boundaries according to Rundgren *et al.* (1997). Note that LPAZ T-4 is redeposited (Rundgren, 1995; Rundgren *et al.*, 1997). S=Saksunarvatn ash, V= Vedde Ash.



importance of vegetative reproduction. This is a common adaptive response to adverse conditions in many Arctic plants (Billings & Mooney, 1968; Savile, 1972; Callaghan & Emanuelsson, 1985). Flowering is highly variable in arctic vascular plant populations today and may be at extremely low levels or completely absent in some years (Sørensen, 1941; Carlsson & Callaghan, 1994; Jónsdóttir, 1995). It has been shown on Iceland that gene transfer probably occurs between *Betula pubescens* Ehrh. and *Betula nana* via hybrid introgression, increasing the climatic and topographical tolerance of birch (Elkington, 1968; Anamthawat-Jónsson, 1994).

Botanical data from the high Arctic (e.g. Aleksandrova, 1980; Edlund & Alt, 1989; Bay, 1992) show that, even in areas with extreme climatic conditions, there are very few places where the number of vascular plant species falls below 20. Plant survival in ice-free refugia is basically a question of how these organisms respond to climate-controlled changes in their physical environment. It has been shown by, e.g. Bliss *et al.* (1984) and Bliss (1988) that, although temperature is the regional control for vegetational and floristic zonation in the Arctic, locally the pattern of vegetation is a product of topography, temperature, soil water balance and geological substrate. Although the structure of arctic vegetation and floristics changes from the low arctic to the high arctic environment, the latter, with its harsher environment, can be as diverse in its vegetation as the former (Bliss & Matveyeva, 1992). The changes include a shift from the predominance of low-shrub, dwarf-shrub (heath-species) and grass-dwarf-shrub tundras to landscapes dominated by cushion plants, prostrate shrubs and rosette species (Bliss & Matveyeva, 1992). Fredskild (1973) reported extremely low pollen influx values from pollen traps in Peary Land, northernmost Greenland, at the border between high arctic tundra and polar desert. This is in accordance with the sparse vegetation cover (2–3%) in that area. Still, Peary Land hosts a relatively diverse flora with 106 species of higher plants, which shows that a poor pollen record does not necessarily imply a poor flora.

The ability of plants to survive under climatically very harsh conditions can be illustrated by the situation in two high Arctic areas: In spite of July temperatures $\leq 2^\circ\text{C}$ and 85% glacial cover, the Franz Josef Land Archipelago in the north-eastern Barents Sea supports fifty-seven species of vascular plants and 272 species of cryptogams, and plant cover at fifteen observation sites varied between 3 and 46% (Aleksandrova, 1988). On the Queen Elisabeth Islands in the Canadian Arctic Archipelago, classified as a barren polar desert with July temperatures of $\leq 2^\circ\text{C}$ and precipitation less than 50 mm year^{-1} , a total of seventeen vascular species and fourteen species of lichen and mosses were found, although the total plant cover did not exceed 2% (Bliss *et al.*, 1984; Bliss & Svoboda, 1984). The relative species richness found at high northern latitudes implies that a large number of vascular plants could survive a glacial in Iceland if climatic conditions resembled those of the present high Arctic, and given that ice-free areas existed.

Diverse floras are also reported from present-day nunatak areas. A total of sixty-two vascular plant species have, for example, been reported from J.A.D. Jensens Nunatak within

the south-western part of the Greenland ice sheet (Gjærevoll & Ryvarden, 1977; Fig. 1), and the flora reported from Esjufjöll, an Icelandic nunatak area (Fig. 1), comprises ninety-six vascular plant species, including shrubs and dwarf-shrubs like *Juniperus communis* L., *Empetrum nigrum*, *Salix callicarpea* Trautv., *S. lanata* L., *S. herbacea* and *Vaccinium uliginosum* L. (E. Einarsson, 1970).

Palaeobotanical investigations on Andøya in northern Norway (Fig. 1), have shown that several vascular plant species survived there during a series of climatic oscillations in the period 22,000–10,000 BP, many of them which lead to local readvances of the Scandinavian ice-sheet margin (e.g. Vorren *et al.*, 1988; Alm & Birks, 1991; Alm, 1993). More than twenty terrestrial pollen taxa were recorded in this interval, and the presence of plant macrofossils in sediments dating from the last glacial maximum, around 20,000 BP, suggests that a few hardy species survived the entire Weichselian glacial on Andøya.

Younger Dryas vs. last glacial maximum survival

If a large part of the flora could survive the Younger Dryas stadial in Iceland, as suggested by the Lake Torfadalsvatn pollen record, could plants also have survived the entire Weichselian glaciation there? To assess the possibility of this scenario, it is necessary to evaluate the climatic situation in Iceland during both the Younger Dryas stadial and the last glacial maximum (LGM). Calculations of air temperature variations over the Greenland ice sheet from $\delta^{18}\text{O}$ in the GRIP ice core (Johnsen *et al.*, 1995; Fig. 1) show that the coldest events of the last glacial were of about the same duration as the Younger Dryas stadial, but associated with 5–10 °C lower temperatures. Recent studies by Dokken & Hald (1996) have shown that during the Weichselian glaciation there were at least six incursions of relatively warm North Atlantic surface water into the Arctic basin, which led to seasonally ice-free surface waters. These relatively warm episodes lasted from 2000 to > 10,000 years, and they constitute $\approx 50\%$ of the duration of the Weichsel. These data fit very well with the Greenland ice-core record, which also indicates rapid climatic shifts and large temperature fluctuations in the polar North Atlantic during the Weichselian.

A palaeoceanographic reconstruction based on a compilation of marine records from the Nordic Seas and the North-east Atlantic (Sarnthein *et al.*, 1995) suggests that summer sea-surface temperatures north of Iceland were no more than 3 °C lower during the LGM (3–4 °C) than during the Younger Dryas stadial (3–7 °C), while winter temperatures were almost identical (0 to -1 °C and 3 to -1 °C, respectively). The Nordic Seas were seasonally ice-free in both periods, which implies that precipitation should not have been a limiting factor for plant growth in Iceland. The main difference was in surface circulation patterns. During the LGM there was no northward transport across the eastern Iceland-Faeroe Ridge at all, while during the Younger Dryas stadial there was a restricted Atlantic inflow in a narrow corridor along the Norwegian coast, but far from the shores of Iceland. Thus, on Iceland the coldest events of the last glacial may have been only slightly more severe than during the Younger Dryas stadial (the 3 °C difference), which implies that a relatively large number of

plant species could have survived the entire Weichselian in favourable locations there.

The significance of long-distance dispersal for the Icelandic flora

As earlier mentioned, very few endemics have been encountered in Iceland. Apart from the apomictic genera *Taraxacum* and *Hieracium*, the only endemic elements in the Icelandic vascular plant flora are of lower rank than species (E. Einarsson, 1963). This is a very unlikely situation if there had been no gene flow from outside Iceland since the Miocene, especially since Icelandic plant populations must have repeatedly been reduced by glacial expansions, i.e. passing through a succession of genetical bottle-necks. The existence of gene flow between Iceland, Svalbard and Norway in the recent past is, however, suggested by the results of an allozyme diversity study of *Silene acaulis* (L.) Jacq. in these areas (Abbott *et al.*, 1995) and by recent studies on genetical relationships between populations of *Betula pubescens* and *Betula nana* on Iceland and in Scandinavia (K. Anamthawat-Jónsson, personal communication 1997).

The importance of different dispersal mechanisms for the Icelandic flora has been extensively discussed (e.g. Dahl, 1963; D. Löve, 1963; Steindórsson, 1963; Glawion, 1985). The latter estimated that around 50% of the present flora cannot be explained by long-distance dispersal, and he concluded that half of the species present in Iceland today must have survived in Weichselian refugia. He further suggested that a maximum of 20% of the present flora was introduced by Man, and that the remaining 30% may have arrived by ocean and air currents or birds.

Although very few Icelandic vascular plant species are believed to be adapted to dispersal by air or sea (D. Löve, 1963), seeds or vegetative parts of thirty-eight taxa have been recorded on the shores of Surtsey, a small island that appeared ≈ 30 km off the southern coast of Iceland during a submarine volcanic eruption in 1963 (Fridriksson, 1975; Fig. 1). Most of these species are found growing on neighbouring islands, but some of them must have been derived from the mainland of Iceland or from beyond. A germination ability test on seeds from six of the recorded species showed 40–70% germination after eight months exposure to sea water. This indicates that successful dispersal to Iceland by ocean currents is not restricted to sea-shore plants, provided that seeds stay buoyant during their journey. However, as Fridriksson (1975) pointed out, seed buoyancy is not crucial as seeds can float long distances attached to ice, driftwood or debris (see below).

Little is known about long-distance dispersal by birds, but seeds can survive both internal and external bird transport, and other plant parts capable of vegetative reproduction may be carried attached to the body of migrating birds (D. Löve, 1963). Savile (1972) emphasized the importance of geese for dispersal of overwintered seeds during spring migration to arctic areas. Snow buntings, *Plectrophenax nivalis nivalis*, known to migrate between the British Isles and Greenland via Iceland, caught in spring on Surtsey were found to carry seeds of several species in their gizzards (Fridriksson, 1975). Some of these

species are not found growing in Iceland, and their closest occurrences are in the British Isles and Greenland, which implies that long-distance dispersal by birds to Iceland is feasible. In addition, seeds of several of the recorded species, albeit not of definite long-distance origin, were found to have retained their germination ability. Since the main routes of migratory birds connect Iceland with north-western Europe, dispersal by birds may account for parts of the present Icelandic flora.

Savile (1972) considered dispersal by wind in winter to be the most important dispersal mechanism in Arctic plants. Seeds and plant fragments may be blown long distances over smooth snow surfaces before they become deposited below a cliff, bluff or high bank. This transport also occurs across sea ice, and Savile (1972) estimated that some seeds may be carried up to 2000 km by this process.

Ice-rafting of seeds and plant material to Iceland is fundamental in the dispersal model of Buckland & Dugmore (1991), but they restricted the action of this process to the Late Weichselian–Holocene transition and the source area to south-western Scandinavia. There are, however, strong indications of present drift-ice transport to Iceland from northern Eurasia via the Transpolar Drift and East Greenland Current. This could be an important plant-dispersal process on a much larger timescale. A dendrochronological study of recent driftwood on the Icelandic shores (Eggertsson, 1993) revealed a northern Russian/Siberian origin for all sampled logs. The buoyancy time of this driftwood (6–17 months) is much shorter than the time needed to reach Iceland (5–10 years), which suggests that the logs are transported by drift ice during some part of their journey (Eggertsson, 1993). The Eurasian origin of Icelandic driftwood indicates that drift-ice transport may partly explain the European affinity of the present Icelandic flora. However, a real Siberian component would also be expected, but does not seem to be there. There is also a total absence of Siberian elements in the flora of Svalbard (Serebryanny & Tishkov, 1996), where driftwood of Siberian origin is abundant (Eggertsson, 1994).

Even if most of the sediment observed in arctic sea ice is fine-grained, which indicates that incorporation of littoral sediments is comparatively rare (Pfirman *et al.*, 1990), plant material has been recorded (Larsen *et al.*, 1987; Reimnitz *et al.*, 1993). Vascular plants have even been found growing on an ice island that later passed north-west Iceland (Hultén, 1962; Fridriksson, 1975). This illustrates the potential of plant dispersal by the drift-ice itself.

CONCLUSIONS

The hypothesis of Icelandic plant survival during previous glacials is supported by the geological record, which shows that many of the taxa dominant in present-day vegetation were present in Iceland already in the early Pleistocene. The fossil plant record reflects both a gradual extinction of warm-demanding species along with the Late Cenozoic cooling, and a transition from a flora dominated by American elements to one with more European affinities. This floral change can be accounted for by gradual changes in the oceanographic patterns in connection with the opening of the North Atlantic, leading

to dominant long-distance dispersal from north-western Europe and northern Eurasia to Iceland in combination with plant survival in Iceland during the glaciations. A continuous long-distance influx of seeds and vegetative parts by ocean currents (in sea water, on drift ice, with driftwood or debris), and by wind or birds, both in the Holocene and earlier epochs, may help explain the lack of endemics.

Recent palaeoceanographic and ice-core studies have shown that climate during the last glacial was far from as cold and stable as previously believed, and Icelandic climate during the last glacial maximum was probably only slightly colder than during the Younger Dryas stadial. The existence of unglaciated areas in Iceland during the last glacial maximum has been suggested from several coastal mountain regions and present shallow shelf areas, although plant survival in these areas has still not been proven. We conclude that the relatively high plant diversity found in high Arctic areas and present-day nunataks in Iceland and Greenland, together with the fact that many plant species were able to survive the Younger Dryas stadial on the Skagi peninsula, suggest that species with high tolerance for climate fluctuations also survived the whole Weichselian in Iceland.

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