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THE BRITISH FLORA IN THE ARCTIC

I should like to preface a discussion of the flora with a few words about British botanists in the Arctic. It is necessarily few since British botanists, like romantics and artists, gourmets, hedonists and political Europhiles have long been seduced by the lure of the south, Goethes land where the orange trees bloom. In the nineteenth century the only arctic territory in the former British Empire was northern Canada and thanks to largely Admiralty inspired initiatives there was a succession of expeditions seeking to find a vital safe route, the north-west passage, to the Indies. Besides the crew, the expeditions usually included a number of variously qualified scientific members and during the course of these expeditions botanical collections were brought back to Britain to be identified and, not infrequently, written up. Two famous botanists who had a part in this were Robert Brown and William Hooker. Neither were especially interested in the Arctic, or at least not sufficiently motivated to visit it, but both made important contributions in describing species: Hooker, chiefly during the period of his professorship at Glasgow University, prior to his southwards move to Kew. The most important collections processed by Brown were those made by Ross and Sabine on the former's 1818 expedition (Ross 1819) to Baffin Bay, during which they explored both the Greenland and Canadian shores, and one made by the members of Parry's expedition of 1819–1820, chiefly during their long overwintering on Melville Island. The collectors included Parry himself, Sabine, Edwards and Ross, all of whom had taxa, both genera and species, named after them by Brown in his botanical supplement to Parry's *Narrative* (1821). About the same time, Hooker published a similar appendix in Scoresby's *A Journal of a Voyage to the Northern Whale-fishery* (1822), an account of the first visit by Europeans to the coast of north-east Greenland. He listed 35 vascular plants, many of which were already familiar to him in Scotland. However, Hooker was mainly interested in the Canadian arctic flora and it was he who wrote up the botanical collections in Richardson's scientific appendices to Franklin's narrative (1823) of the first of his two amazing expeditions (1819–22, 1825–27), again in search of the elusive Passage. Richardson, a naturalist and surgeon, covered thousands of miles on both expeditions on foot and canoe, mostly in conditions of extreme hardship, around Great Bear Lake, down the Mackenzie and Coppermine Rivers, the coast between these rivers and for more than 500 miles eastwards. The extensive collections from these expeditions formed the basis of Hooker's subsequent *Flora boreali-Americana* (1829–40). The hazardous Passage was finally completed in the 1850s.

I can think of no other British botanist of note who took an interest in the Arctic other than Nicholas Polunin, sometime Curator of the Fielding Herbarium at Oxford and a man with wide-ranging interests. During the 1930s he spent a considerable amount of time carrying out floristic and ecological work in the Canadian Arctic, publishing a number of important papers under the auspices of the National Museum of Canada. He also made a number of visits to the west coast of Greenland. He is, however, best remembered for his *Circumpolar Arctic Flora* (1959), which is still the only Flora to cover the whole area although, of necessity at that time, it features an unduly wide species concept.

The importance of Brown and Hooker is demonstrated by the fact that 10% of the vascular plants in Svalbard were first named by them, and to these we can add Smith's *Alopecurus alpinus* and Polunin's *Festuca baffinensis*.

Before proceeding to consider the flora we need to remind ourselves of the limits of the Arctic and its subdivision (Fig.1). The southern limit is now generally taken to be the latitudinal tree-line and as is very evident from the map this follows a very different path in the western and eastern Arctic. In the Hudson Bay area it plunges south to 55° N (the latitude of Carlisle) whereas in Russia and Siberia it follows the Arctic Circle, more or less, for most of its length. Within the Arctic it is helpful to distinguish between the High Arctic and Low Arctic. The latter has an oceanic climate with a relatively small annual temperature range, a mean July temperature above 5° C and a moderate to high precipitation. Conversely the High Arctic has a wide temperature range, a mean July temperature below 5° C and low precipitation.



FIGURE 1. Delimitation of the Arctic and its division into Low Arctic (stippled) and High Arctic (between Low Arctic and the Pole) (from Freuchen & Salomonsen (1960)).

In the following discussion I shall be concentrating on east Greenland, partly because this is the area that I am most familiar with but also because it has the advantage of a continuous land surface taking us from the latitude of the Shetlands to within 700 km of the Pole.

It was a surprise to me to discover just how well the British flora is represented in the Arctic. Using his wide species concept Polunin (1954) estimated that native British species account for 32% of the total arctic vascular flora of 833 species. Table 1 shows the percentage representation in four sectors of the Arctic; the critical genera *Hieracium* and *Taraxacum* are excluded from these and subsequent calculations. Not surprisingly the percentage decreases westwards, and eastwards

TABLE 1. BRITISH SPECIES IN THE ARCTIC
(excluding Russia)

		Total
Alaskan Arctic Slope	26%	438
Canadian Arctic Archipelago	31%	318
Greenland	45%	452
Svalbard	40%	158
Total Arctic flora (Polunin 1954)	32%	833

also if the data for the Russian Arctic were readily available, but 26% for the Alaskan Arctic Slope, on the opposite side of the world, is, I think, quite impressive. The north American figures, likewise the Russian, would be appreciably higher but for the major role played by certain genera such as *Ranunculus*, *Draba*, *Astragalus*, *Oxytropis*, *Pedicularis*, *Antennaria*, *Artemisia* and *Puccinellia*, which have virtually no British arctic representatives. On the other hand, ericaceous shrubs are well represented, three quarters of the Alaskan species occurring in Britain; a third of Alaskan sedges are British and nearly half of the 47 Greenland species. The Alaskan Arctic Slope includes two British montane species which we never consider as arctic, namely *Potentilla fruticosa* and *Myosotis alpestris*, the national flower of Alaska. Both these species have a limited distribution in the Arctic from the Yukon to western Siberia.

If we look at the representation of Preston & Hill's (1997) British phytogeographical elements in the Greenland flora (Fig. 2) we find, as one would expect, that their Arctic-Montane and Boreal-Arctic-Montane species feature prominently but not overwhelmingly, accounting for 44% of the total British component. The Boreal-Temperate element even exceeds the Boreal-Montane and there is a not insubstantial tail of 12 Temperate zone species. However, these include two

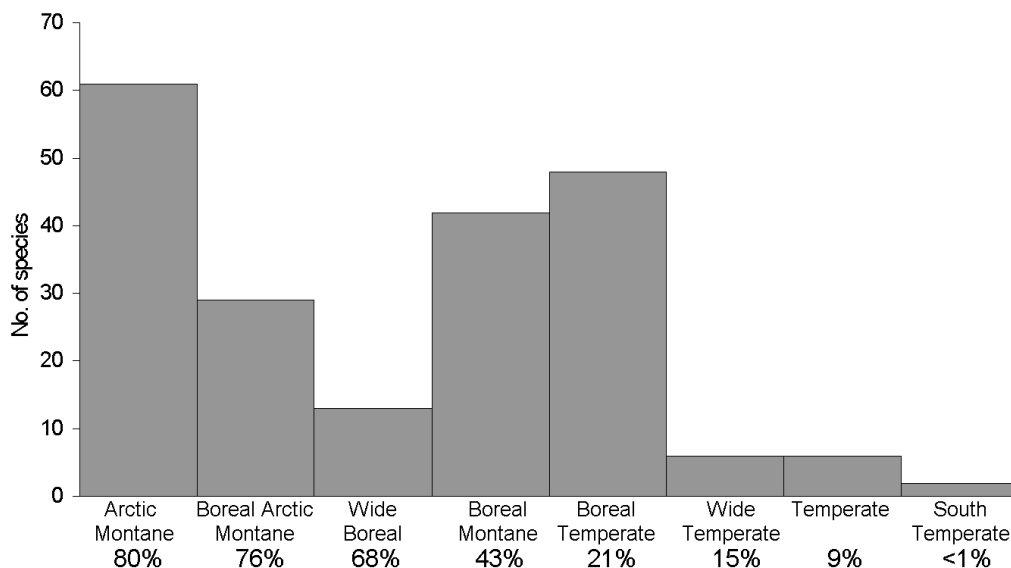


FIGURE 2. Number of species and percentage representation within each British phytogeographical element of British species occurring in Greenland.

Wide Temperate: *Agrostis stolonifera*, *Anthoxanthum odoratum*, *Eleocharis palustris*, *Juncus gerardii*, *Poa pratensis**

Temperate: *Eleocharis uniglumis*, *Juncus squarrosus*, *Myriophyllum spicatum*, *Polygala serpyllifolia*, *Rumex acetosella**

South Temperate: *Juncus ambiguus*, *Potentilla pusillus*

* aggregate species replaced, to varying extent, in the Arctic by northern segregates.

aggregate taxa, *Rumex acetosella* and *Poa pratensis*, both of which are increasingly replaced northwards by arctic segregates. In the case of *Poa pratensis* this is subsp. *alpigena*, a strongly stoloniferous plant with a narrow panicle. Interestingly, Hultén (1964), in his atlas of *The Circumpolar Plants*, shows it as occurring in the Scottish Highlands. I do not know the basis of this but it is a plant worth searching for.

The British Arctic-Montane and Boreal-Arctic-Montane species which occur in Greenland are shown in the Table 2a. It reads like E. S. Marshall's Highland shopping list, positively bristling with *Red Data Book* and *Scarce Plant* species. Notice again the large numbers of sedges. Although *Luzula arcuata* is absent from Greenland, I have included it since it is generally subsumed in the ubiquitous *L. confusa*. I have also included *Deschampsia alpina* as a species, since it is treated as such in all the Arctic Floras. The remaining species in Preston & Hill's two lists are shown in the Table 2b under their respective geographical ranges in the eastern Arctic. Note the appearance of our 'Alpine' species *Gentiana verna*, *Lloydia* and *Pinguicula alpina* in the Russian Arctic, together with *Myosotis alpestris*. Notice also the surprising absence of *Salix reticulata* from Iceland and Greenland although this willow is otherwise circumpolar. These two lists do not include three species in Preston & Hill's Arctic-Montane list: *Cochlearia pyrenaica*, *Minuartia recurva* and *M. sedoides*. These fail to reach the Arctic but were included on the grounds that they occur above the tree-line in the Boreal zone.

TABLE 2A. BRITISH ARCTIC-MONTANE* AND BOREAL-ARCTIC-MONTANE SPECIES OCCURRING IN GREENLAND

<i>Alchemilla alpina</i>	<i>Diphasiastrum alpinum</i>	<i>Oxyria digyna</i>
<i>A. glomerulans</i>	<i>Draba norvegica</i>	<i>Phyllodoce caerulea</i>
<i>Arabis alpina</i>	<i>Dryas octopetala</i>	<i>Pericaria vivipara</i>
<i>Arenaria ciliata</i>	<i>Empetrum nigrum</i>	<i>Phleum alpinum</i>
<i>Athyrium distentifolium</i>	<i>E. anagallidifolium</i>	<i>Poa alpina</i>
<i>Alopecurus borealis</i>	<i>Equisetum variegatum</i>	<i>P. glauca</i>
<i>Arctostaphylos alpinus</i>	<i>Erigeron borealis</i>	<i>Potentilla crantzii</i>
<i>Bartsia alpina</i>	<i>Euphrasia frigida</i>	<i>Sagina nivalis</i>
<i>Betula nana</i>	<i>Festuca vivipara</i>	<i>S. saginoides</i>
<i>Calamagrostis stricta</i>	<i>Gentiana nivalis</i>	<i>Salix herbacea</i>
<i>Carex atrata</i>	<i>Gnaphalium norvegicum</i>	<i>Saxifraga aizoides</i>
<i>C. atrofusca</i>	<i>G. supinum</i>	<i>S. cernua</i>
<i>C. bigelowii</i>	<i>Huperzia selago</i>	<i>S. cespitosa</i>
<i>C. capillaris</i>	<i>Juncus biglumis</i>	<i>S. hirculus</i>
<i>C. chordorrhiza</i>	<i>J. castaneus</i>	<i>S. nivalis</i>
<i>C. lachenalii</i>	<i>J. trifidus</i>	<i>S. oppositifolia</i>
<i>C. maritima</i>	<i>J. triglumis</i>	<i>S. rivularis</i>
<i>C. microglochin</i>	<i>Kobresia simpliciuscula</i>	<i>S. stellaris</i>
<i>C. norvegica</i>	<i>Koenigia islandica</i>	<i>Sedum rosea</i>
<i>C. rariflora</i>	<i>Lathyrus japonicus</i>	<i>S. villosum</i>
<i>C. rupestris</i>	<i>Leymus arenarius</i>	<i>Sibbaldia procumbens</i>
<i>C. saxatilis</i>	<i>Ligusticum scoticum</i>	<i>Silene acaulis</i>
<i>C. vaginata</i>	<i>Loiseleuria procumbens</i>	<i>Thalictrum alpinum</i>
<i>Cerastium alpinum</i>	<i>Luzula arcuata</i>	<i>Tofieldia pusilla</i>
<i>C. arcticum</i>	<i>L. spicata</i>	<i>Vaccinium uliginosum</i>
<i>C. cerastoides</i>	<i>Lychnis alpina</i>	<i>V. vitis-idaea</i>
<i>Cornus suecica</i>	<i>Lycopodium annotinum</i>	<i>Veronica alpina</i>
<i>Deschampsia alpina</i>	<i>Mertensia maritima</i>	<i>V. fruticans</i>
<i>Diapensia lapponica</i>	<i>Minuartia rubella</i>	<i>Woodsia alpina</i>
<i>Draba incana</i>	<i>M. stricta</i>	<i>W. ilvensis</i>

* bold type

TABLE 2B. BRITISH ARCTIC-MONTANE* AND BOREAL-ARCTIC-MONTANE SPECIES ABSENT FROM GREENLAND BUT OCCURRING ELSEWHERE IN THE GREENLAND-RUSSIAN SECTOR OF THE ARCTIC

ICELAND <i>Euphrasia ostenfeldii</i> <i>Poa flexuosa</i>	NORWAY, RUSSIA <i>Allium schoenoprasum</i> <i>Artemisia norvegica</i> <i>Carex aquatilis</i> <i>Eriophorum vaginatum</i> <i>Oxytropis campestris</i> <i>Salix arbuscula</i>
ICELAND, NORWAY <i>Arenaria norvegica</i> <i>Juncus balticus</i>	<i>S. lapponum</i> <i>S. myrsinites</i> <i>S. phyllicifolia</i>
ICELAND, NORWAY, RUSSIA <i>Arabis petraea</i> <i>Carex dioica</i> <i>Epilobium alsinifolium</i> <i>Salix lanata</i>	RUSSIA <i>Astragalus alpinus</i> <i>Gentiana verna</i> <i>Lloydia serotina</i> <i>Myosotis alpestris</i> <i>Pinguicula alpina</i>
NORWAY <i>Euphrasia salisburgensis</i> s.l.	
NORWAY, RUSSIA, SVALBARD <i>S. reticulata</i> <i>Saussurea alpina</i>	

* bold type

The progressive northern limits of certain British species up the east coast of Greenland, a range of 2670 km and 24° of latitude, are shown in Fig. 3. The boundary of the High and Low Arctic lies just south of Scoresby Sund at c. 70° N. It has to be remembered that there is very little ice-free land along some 350 km of inhospitable coast, the Blossville Kyst, to the south of this. By contrast, immediately to the north is a series of fjord complexes which extend inland by up to 300 km and northwards to 77° N. These provide relatively benign conditions for many species, with mean summer temperatures actually rising locally in the interior above 5° C. These mean temperatures are shown in the figure for a number of mainly outer coastal stations.

Notice the presence in the extreme south of such common British upland species as *Drosera rotundifolia*, *Isoetes lacustris*, *Juncus squarrosus* and *Viola palustris*, as well as, surprisingly, *Achillea millefolium*. Further north, *Sedum acre* has its only Greenland station. *Juniperus communis*, *Alchemilla alpina*, *Sedum villosum* and *Armeria maritima* all fail to pass the Blossville Kyst and reach the fjords. A cluster of warm springs at 69° 30' N and 50–60° C provides outlying stations and northern limits for *Epilobium palustre*, *Sagina saginoides*, *S. procumbens*, *Selaginella selaginoides* and *Subularia aquatica*, as well as the only Greenland localities for *Geum rivale* and *Ophioglossum azoricum*. The decrease in species proceeds apace in the fjord region, *Veronica fruticans* disappears before *V. alpina*, and the dwarf shrubs disappear in the order *Phyllodoce caerulea*, *Arctostaphylos alpinus*, *Betula nana*, *Empetrum nigrum*, *Salix herbacea* and, finally, *Vaccinium uliginosum*. Some of the species shown on this map have southern limits. The significance of some of these will be discussed later. There are also a number of species (Table 3) which occur in northernmost Greenland, the nearest land to the pole, and therefore have no northern limit; most occur throughout Greenland.

TABLE 3. BRITISH SPECIES OCCURRING IN NORTHERNMOST GREENLAND

<i>Alopecurus borealis</i>	<i>Juncus biglumis</i>	<i>Sagina nivalis</i>
<i>Carex maritima</i>	<i>J. triglumis</i>	<i>Saxifraga cernua</i>
<i>Cerastium arcticum</i>	<i>Minuartia rubella</i>	<i>S. cespitosa</i>
<i>Cystopteris fragilis</i>	<i>Oxyria digyna</i>	<i>S. nivalis</i>
<i>Equisetum arvense</i>	<i>Persicaria vivipara</i>	<i>S. oppositifolia</i>
<i>E. variegatum</i>	<i>Poa glauca</i>	<i>Silene acaulis</i>

All, apart from *Alopecurus borealis*, occur throughout Greenland and all are circumpolar with the exception of *Silene acaulis* which has a large gap in arctic Russia.

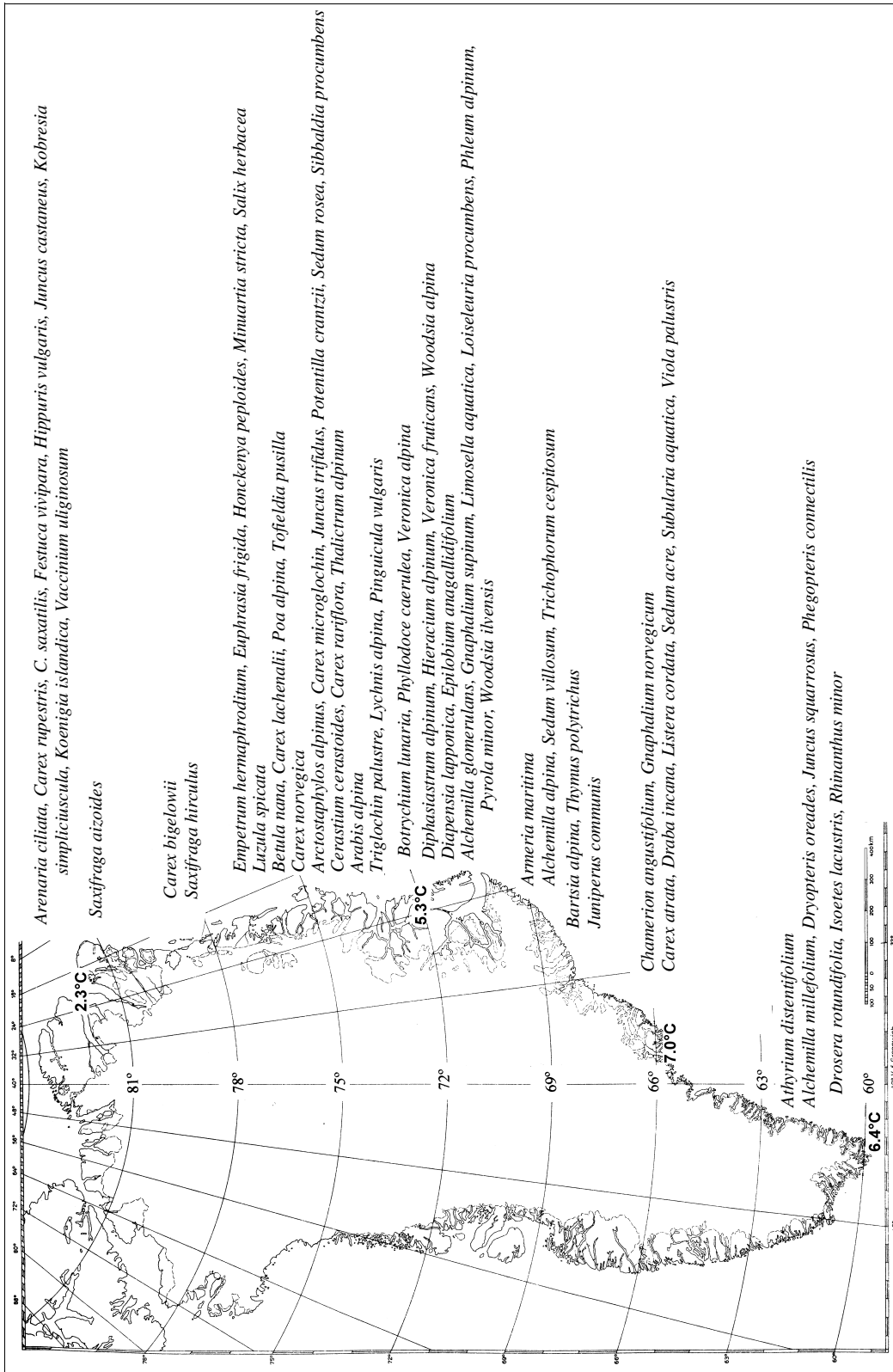


Figure 3. Northern limits of British species in east Greenland. The temperatures are the July means of coastal stations.

A number of British arctic taxa are largely replaced northwards in the Arctic by related taxa (Table 4). About half of these pairs are diploid, or more or less so. *Huperzia selago* subsp. *arctica* and *Empetrum hermaphroditum* are the only northern taxa reported so far from Britain.

TABLE 4. BRITISH TAXA WHICH ARE REPLACED IN THE ARCTIC WHOLLY OR PARTLY BY RELATED SPECIES

a) with little or no difference in chromosome number

<i>Huperzia selago</i>	<i>Eriophorum angustifolium</i>
<i>H. selago</i> subsp. <i>arctica</i>	<i>E. triste</i>
<i>Lycopodium annotinum</i>	<i>Eriophorum vaginatum</i>
<i>L. pungens</i>	<i>E. spissum</i>
<i>Armeria maritima</i>	<i>Juncus balticus</i>
<i>A. scabra</i>	<i>J. arcticus</i>
<i>Erigeron borealis</i>	<i>Carex aquatilis</i>
<i>E. uniflorus</i>	<i>C. stans</i>
<i>Luzula arcuata</i>	
<i>L. confusa</i>	

b) with different ploidy

<i>Rumex tenuifolius</i> 2x	<i>Chrysosplenium alternifolium</i> 2x
<i>R. acetosella</i> s.s. 4x	<i>C. tetrandrum</i> 4x
<i>R. graminifolius</i> 6x	<i>Vaccinium uliginosum</i>
<i>Draba norvegica</i> 3x	subsp. <i>uliginosum</i> 4x
<i>D. glabella</i> 4x	subsp. <i>microphyllum</i> 2x
<i>Primula farinosa</i> 2x	<i>Empetrum nigrum</i> 2x
<i>P. scotica</i> 6x	<i>E. hermaphroditum</i> 4x
<i>P. stricta</i> 14x	<i>Campanula rotundifolia</i> 4x
<i>Saxifraga stellaris</i> 2x	<i>C. gieseckiana</i> 2x
<i>S. foliolosa</i> 4x	<i>Puccinellia maritima</i> 5x
<i>Saxifraga nivalis</i> 4x	<i>P. phryganodes</i> 2x
<i>S. tenuis</i> 2x	
<i>Saxifraga rivularis</i> 4x	
<i>S. hyperborea</i> 2x	

Probable allopolyploids

<i>Saxifraga aizoides</i> 2x	×	<i>S. oppositifolia</i> 2x	×	<i>Woodsia glabella</i> 2x	×	<i>W. ilvensis</i> 2x
		<i>S. nathorstii</i> 4x		<i>W. alpina</i> 4x		

It has long been known that the frequency of polyploids increases dramatically with latitude. In Iceland, for example, it reaches 55%, and in Svalbard 77%. It is also commoner in monocotyledons than in dicotyledons. The reasons for this have been argued at length. It has been suggested that polyploids, *per se*, are hardier. Others argue that the ebb and flow of the ice cover during the Pleistocene allowed scope for extensive mixing of floras with the potential for hybridisation and possible chromosome doubling to produce species with a wider ecological tolerance. Another suggestion is that monocotyledon families, such as Juncaceae, Cyperaceae and Poaceae, with their propensity for vegetative reproduction, were pre-adapted to take advantage of the newly-exposed, demanding habitats uncovered by the retreating ice.

However, it has to be said that the diploid-polyploid pairs listed here show almost as many instances of diploid northern and southern polyploid pairs as vice-versa. The only diploid-tetraploid pair to occur in Britain are the *Empetrum nigrum* subspecies, or species, although *Vaccinium uliginosum* subsp. *microphyllum* could perhaps turn up. The table also shows two examples of allopolyploid species believed to have originated by hybridisation involving arctic species and subsequent chromosome doubling.

While on the subject of hybridisation, I should like to mention *Cerastium* and *Dryas*. *Cerastium alpinum* is a low-Arctic species which appears to have undergone extensive hybridisation and introgression throughout the Arctic with related species, including *C. arcticum*, the high-Arctic *C. regelii*, *C. jenisejense* and *C. beeringianum*, in the process forming some very stable taxa, such as *C. arcticum* subsp. *vestitum*, the prevailing taxon over much of Greenland and Svalbard. *Dryas octopetala* occurs alone throughout most of the eastern Arctic and east Greenland, as does *D. integrifolia* in western Greenland and Canada. Hybrids probably occur wherever the two species overlap, namely in eastern Siberia, Alaska, the Rockies and Greenland. The complex pattern of hybridisation and introgression in Greenland is shown in Fig. 4.



Figure 4. Leaf variation in *Dryas* in Greenland demonstrating regional introgression between *D. octopetala* (equilateral triangles) and *D. integrifolia* (narrow triangles) (from Elkington (1965)).

I mentioned earlier that a number of British species in east Greenland are restricted to the high Arctic, mostly north of 70°. These include *Alopecurus borealis*, *Kobresia simpliciuscula*, *Minuartia stricta* and *Saxifraga hirculus*, all of which, as it happens, occur in and around upper Teesdale. It seems to me highly probable that the British populations of these species, together with those of the *Minuartia* and saxifrage in Iceland, differ significantly in their physiology from those luxuriating in the Arctic Riviera climate of the east Greenland fjord region. Physiological differences in populations of wide-ranging species are of course well known. Scandinavian populations of *Solidago virgaurea*, for example, from lowland woodlands have lower optimum light requirements and higher temperature optima than montane populations, and arctic populations of *Oxyria digyna* and *Thalictrum alpinum* have lower temperature optima than those from mountains to the south. Some evidence for this in the case of *Kobresia* is provided by T. W. Böcher's observation, frequently impressed on visiting botanists, that Greenland plants grown at Copenhagen could only be overwintered in the Arctic Greenhouse and not outdoors with the Teesdale plants.

Two examples of ecological behaviour in the Arctic which differ substantially from what we might expect are provided by *Lychnis alpina* and *Carex maritima*. The former occurs in Britain on serpentine in Clova and at one locality on pyritic rocks in the Lake District. It is often assumed that the plant has a requirement for heavy metals, although analyses have revealed little unusual about the soil at the Lake District site, other than a slightly higher than expected manganese level, and the plants are readily grown in ordinary soil. However, the plant is widespread in the Scandinavian mountains and over the southern half of Greenland on soils with or without a substantial heavy metal content. It seems likely that, as in *Minuartia verna*, heavy metal tolerant populations of *Lychnis* are readily selected for. The other example, *Carex maritima*, is exclusively maritime in Britain but in Iceland, Scandinavia and Greenland it occurs far inland and, in Greenland, at altitudes up to 1200 m.

British botanists visiting the Arctic are often surprised by the wider ecological range of familiar British basicolous species, examples include *Dryas octopetala*, *Saxifraga oppositifolia* and *Silene acaulis*. Exceptions include most plants of base-rich mires, such as *Carex atrofusca*, *C. microglochis*, *Juncus castaneus* and *Kobresia simpliciuscula*, which behave much as in Britain. It is worth noting that limestone exposures are rare in the southern half of Greenland but common in the north and in the western Canadian arctic archipelago where, because of the relatively arid climate, they present a distinctly hostile environment.

In any discussion of the arctic flora one subject guaranteed to raise the emotional temperature is the question of where the component species survived the Holocene ice ages, or, more particularly, the last one, the Weichsel. In Scandinavia the debate still continues with Gjaerevoll upholding the views of Nordhagen and the late Eilif Dahl that many species survived on ice-free refugia, nunataks, near their present sites. Dahl in particular was impressed by the very weak dispersal ability of many relict mountain populations and also by the very local occurrence of certain western Arctic species. However, the discovery of substantial and extensive sub-fossil remains to the south of the ice sheets, including Britain, demonstrates that invasion following the ice retreat was an alternative and more likely possibility. Furthermore, as Birks (1993) has shown, using a powerful correlation technique, there is a high correlation between the present day distribution and topographic, climatic and edaphic factors, but only a low correlation with ice-free areas. As he says, the subfossil evidence renders any nunatak hypothesis superfluous. These opposing arguments are essentially the same as those used by British periglacial survivalists, particularly in relation to Teesdale, and by Quaternary botanists, with their impressive lists of full and late-glacial plant remains.

However the situation regarding Greenland, and Svalbard, is radically different since there was no post-glacial land bridge to facilitate dispersal and, if the nunatak hypothesis is rejected, one is thrown back on long-distance dispersal by various agencies. Gelting, and later Böcher, favoured survival, and Nathorst and later Sørensen long-distance dispersal.

The last glaciation in Greenland is known to have lasted c.130,000 years and to have finished relatively abruptly some 11,500 years ago. There is now strong geological evidence that some relatively extensive areas in east Greenland were ice-free during the whole of this glaciation (Funder 1979). Estimates from Europe of the drop in mean temperatures during this period suggest a figure of about 6° C. The summer temperatures shown in Fig. 3 suggest that the corresponding

TABLE 5. RECORDS OF TAXA FROM SITES IN THE EAST GREENLAND FJORD REGION UNGLACIATED DURING THE LAST ICE AGE

MACROFOSSILS FROM DEPOSITS 11,900 - 11,000 YEARS BP (Bennike *et al.* 1999)

<i>Carex</i> sp.	<i>Oxyria digyna</i>
<i>Cerastium</i> sp.	<i>Minuartia</i> sp.
<i>Draba</i> sp.	<i>Papaver radicum</i>
<i>Eriophorum</i> sp.	<i>Poaceae</i>
<i>Juncus</i> sp.	<i>Potentilla</i> sp.
<i>Luzula</i> sp.	<i>Saxifraga oppositifolia</i>
<i>Melandrium apetalum</i>	
<i>Empetrum nigrum</i> 10,400	
<i>Saxifraga cespitosa</i> 10,400	
<i>Salix herbacea</i> (pollen) 10,000	
<i>Dryas</i> sp. (pollen) 10,000	

sea-level summer temperature in central east Greenland would therefore be close to zero. This would seem to preclude the vast bulk of the flora from the list of potential survivors. Table 5 shows a list of species with macrofossil remains from the period 11,900 to 11,000 BP and Table 6 of species found at the present day at over 2000 m on nunataks in south-east Greenland. 2000 m is equivalent to a drop in temperature of c. 12° C below that at sea-level, indicating that these plants probably survive a mean summer temperature of c. -6° C. Incidentally, studies of photosynthesis in *Ranunculus glacialis* and *Oxyria digyna* from the Tyrol showed that they still achieved net photosynthesis at this temperature. Furthermore, some 58 species are now known to occur at altitudes in excess of 1200m on nunataks in south-east Greenland. This is equivalent to a temperature decrease of at least 7° C, which would correspond to a mean summer sea-level temperature of c. -2° C. I think, therefore, we can assume that many of these species were capable of withstanding such temperatures at sea-level during the last glaciation, although of course they are likely to have been restricted to favourable south-facing microclimates. Some species may have survived since before the last ice-age, others may have invaded during the 130,000 years of the glaciation. I think, however, that one has to accept that the 'thermophilous' bulk of the flora has invaded Greenland subsequently, probably via Iceland (Bennike 1999). In this context I would remind you of the existence of *Ophioglossum azoricum* and *Geum rivale* around warm springs on the Blossville Kyst, on the migration route of barnacle geese from Iceland.

TABLE 6. SPECIES RECORDED ABOVE 2200 M ON A NUNATAK IN SOUTH-EAST GREENLAND

Species	Height
<i>Minuartia rubella</i>	2480 m
<i>Papaver radicum</i>	2450 m
<i>Saxifraga cernua</i>	"
<i>S. oppositifolia</i>	2400 m
<i>S. cespitosa</i>	"
<i>Carex nardina</i>	2330 m
<i>Poa glauca</i>	"
<i>Phippsia algida</i>	"
<i>Antennaria canescens</i>	2300 m
<i>Cerastium arcticum</i>	"
<i>Draba nivalis</i>	"
<i>Oxyria digyna</i>	2280 m
<i>Silene acaulis</i>	2200 m
<i>Erigeron uniflorus</i>	"
<i>Luzula spicata</i>	"

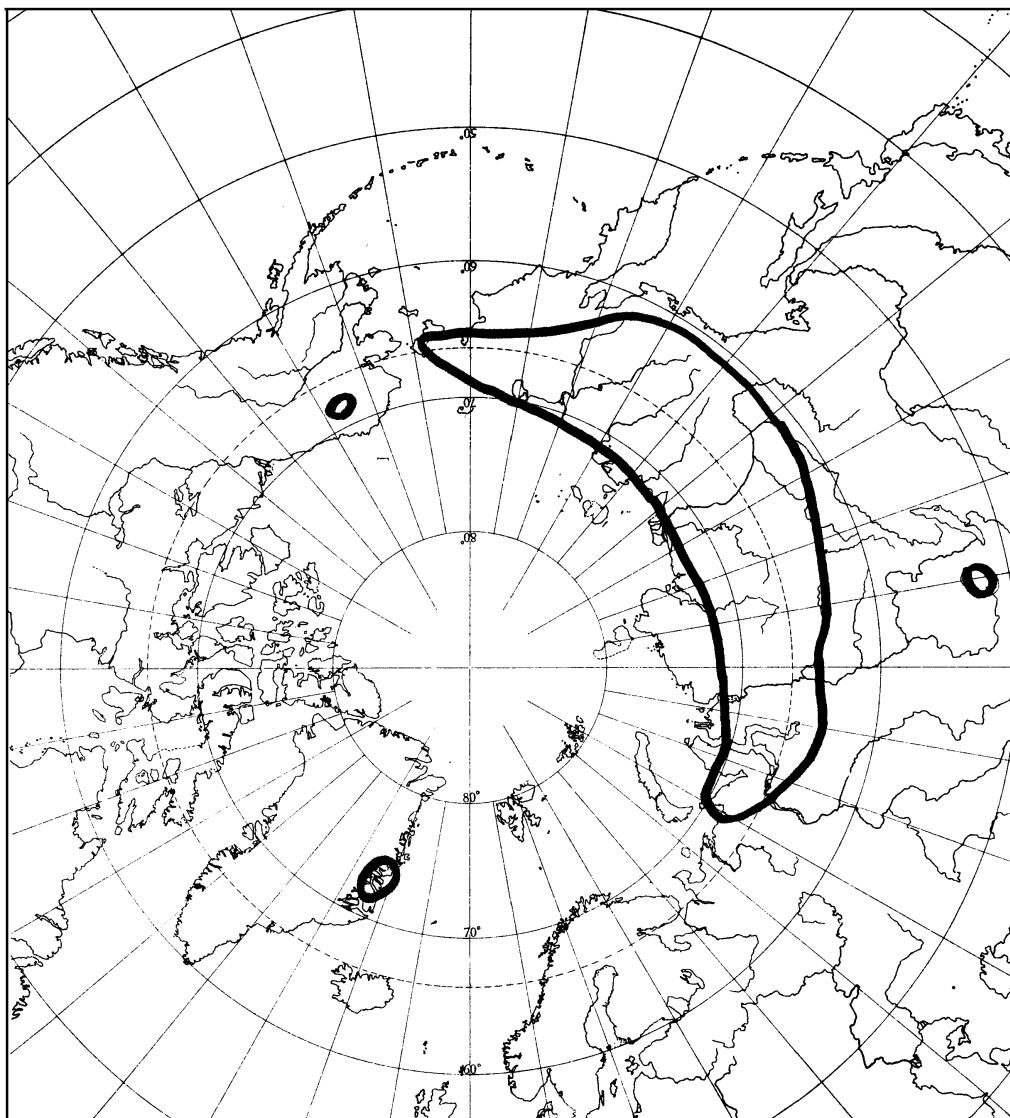


Figure 5. Distribution of *Potentilla stipularis*.

Nevertheless there are certain high-arctic Greenland species which raise doubts, in my mind at least, about the uncritical acceptance of long distance dispersal. Outside the high Arctic *Alopecurus borealis* is known only from Britain. It seems a highly likely survivor. And what of *Kobresia simpliciuscula*, likewise absent from Iceland? Did this invade from Scandinavia or get blown over the inland ice from central west Greenland? What of *Saxifraga hirculus*? The strong probability that the southern and northern populations of these three species – possibly also of *Minuartia stricta* – are physiologically distinct, supports the idea that they have had a similar history during the last glaciation. Then there are the remarkable relict east Greenland populations of certain other non-British species. Prominent in discussion of perglacial survival is the small, creeping, yellow-flowered *Draba sibirica*. This occurs in a very limited, unglaciated area of east Greenland, but is otherwise known only from Siberia. Similarly, *Potentilla stipularis* is known from a few scattered sites in central east Greenland, far distant from its main range from the Urals to Alaska (Fig. 5). Must we really accept that these two species have succeeded in establishing

themselves by long-distance dispersal over 3000 km? There are also a very few relict populations in east Greenland of the Siberian - American *Dryopteris fragrans*, which also has an outlying site in northern Finland and others in the north Urals, and of the western arctic *Saxifraga tricuspidata*. I mentioned earlier the occurrence in Norway of certain western arctic species. One such is *Carex scirpoidea*, known from two localities in northern Norway, but otherwise restricted to North America and west and east Greenland. I find it difficult to credit such distributions to the vagaries and uncertainties of long-distance dispersal but the alternative is to accept that the list of possible periglacial survivors must be appreciably longer than previously thought.

In conclusion I hope I have said enough to convince you of the importance and significance of the British flora in the Arctic and I should like to think there are, in the audience, young spirits prepared to fan the flickering flame of British interest in the Arctic.

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