Birch hybridization in Thistilfjördur, North-east Iceland during the Holocene

LILJA KARLSDÓTTIR[1], MARGRÉT HALLSDÓTTIR[2], ÓLAFUR EGGERTSSON[3], ÆGIR TH. THÓRSSON[1,4] AND KESARA ANAMTHAWAT-JÓNSSON[1]

[1] *Institute of Life and Environmental Sciences, University of Iceland, Sturlugata 7, IS-101 Reykjavik, Iceland, liljaka@hi.is (corresponding author*), kesara@hi.is*

[2] *Icelandic Institute of Natural History, Urridaholtsstræti 6–8, Gardabær, IS-212 Iceland, m.hallsd@gmail.com*

[3] *Icelandic Forest Research, Mógilsá, IS-116 Reykjavik, Iceland, olie@skogur.is*

[4] *The Farmers Association of Iceland, Bændahöllinni by Hagatorg, IS-107 Reykjavík, Iceland, aegir@bondi.is*

ABSTRACT
Past episodes of birch hybridization in Iceland were studied by pollen analysis. The low stature and polycormic form of downy birch *Betula pubescens* in the subarctic probably results from such hybridization with the dwarf birch *Betula nana.* Two previous studies in different regions in Iceland revealed events of hybridization connected to early *B. pubescens* expansion. The present study examined a peat monolith from Thistilfjördur, North-east Iceland, covering the last ten thousand years. *Betula* pollen was measured, proportions of *B. nana* and *B. pubescens* calculated and the presence of hybrids estimated. *Betula pubescens* expansion started around 7.2 cal ka BP with a peak in non-triporate pollen, indicating hybrids. Low *Betula* pollen concentrations followed. A second period of considerable hybridization is indicated around 3.3 cal ka BP. Both peaks were associated with *B. pubescens* expansion.

Keywords: *Betula nana, Betula pubescens*, birch hybrid, Holocene climate, Iceland, pollen

YFIRLIT
Kynblöndun ilmbjarkar og fjalldrapa í Þistilfirði á Nútíma
Tegundablöndun ilmbjarkar og fjalldrapa var rannsökuð í frjókornum. Lágar og margstofna ilmbjarkir á norðlægum slóðum eru líklega afleiðing slíkrar blöndunar. Tvær eldri rannsóknir frá mismunandi landshlutum sýndu hrinur blöndunar snemma á Nútíma sem tengdust framrás ilmbjarkar. Í þessari rannsókn voru sýni tekin úr mósniði í Þistilfirði, sem spannar síðustu tíu þúsund ár. Birkifrjókorn voru mæld, hlutföll tegundanna reiknuð og leitað ummerkja um blöndunina. Ilmbjörk tók að breiðast út fyrir um 7200 árum og fram kom toppur afbrigðilegra frjókorna sem gefa til kynna fjölda blendingstrjáa. Tímabil með litlu birki fylgdi í kjölfarið en önnur hrina erfðablöndunar varð fyrir um 3300 árum. Báðar hrinurnar tengdust aukinni útbreiðslu ilmbjarkar.

INTRODUCTION
Downy birch (*Betula pubescens* Ehrh.) is the most important native tree in Iceland as it is the only tree species forming continuous natural woodlands. Birch woodland is an integral component of the subarctic ecosystem. In Iceland as well as in the higher parts of northern Scandinavia, downy birch has lower stature and more frequently displays polycormic growth than in most other parts of Europe. This growth form, often referred to as mountain birch, may be the result of introgressive

hybridization with dwarf birch (*B. nana* L.), facilitated by downy birch's adaption to harsh climatic conditions. Theories attributing the growth form of the mountain birch to introgressive hybridization began to evolve in the mid-twentieth century (Elkington 1968) and were confirmed around the turn of the century (Anamthawat-Jónsson & Thórsson 2003). However, the extent of the hybridization, its frequency through time and circumstances promoting it were still unclear. It is therefore our objective to investigate past hybridization events in Iceland through the Holocene period.

For several years now, we have been studying birch hybridization and introgression, both past and present. This paper is the third in a series on past hybridization in Iceland based on subfossil pollen records spanning the period from the early Holocene to the present. In our studies, we have relied on the previously established fact that hybrids of the two *Betula* species present in Iceland, downy birch and dwarf birch, produce a considerable quantity of easily recognisable abnormal pollen (Karlsdóttir et al. 2008). As the dwarf birch *B. nana* is diploid with chromosome number 2n=2x=28 and the downy birch *B. pubescens* is tetraploid with 2n=4x=56, their hybrids are triploid with 2n=3x=42 (Anamthawat-Jónsson & Tómasson 1990). Triploid plants are viable although their fertility is drastically reduced as meiosis cannot proceed in the normal fashion. A considerable proportion of the gametes will be aneuploid (Ramsey & Schemske 1998) and may suffer from genetic imbalance (Birchler & Veitia 2007) or from disturbances in gene expression during the process of microsporogenesis and pollen development (McCormick 1993). The consequences may include morphological variation in the pollen produced by triploids, the most common anomaly being four or more pores instead of the normal three (non-triporate vs. triporate). Triploids in natural woodlands in Iceland were found to be relatively common (Thórsson et al. 2007). In a further study (Karlsdóttir et al. 2008), pollen from several triploid trees/shrubs was compared to pollen from diploid and tetraploid individuals and the results revealed a high frequency of non-triporate pollen from the triploids, around 12% compared with 1 or 2% among tetraploid and diploid individuals.

The frequency of abnormal birch pollen in relation to hybridization had been noted before without being studied further. Fredskild (1991) studied birch in Greenland, especially downy birch (*B. pubescens*) and the local dwarf birch (*B. glandulosa* Michx.), which is a relative of *B. nana* and is also diploid. He compared pollen retrieved from several individuals of each species and their hybrids, identified by morphology. The results showed non-triporate pollen, around 7% within species and 13% from hybrids. Since then it has been shown that triploid birch hybrids cannot be identified by plant morphology alone (Thórsson et al. 2007) and this probably explains the difference in the results from Greenland and Iceland. From our results (Karlsdóttir et al. 2008), it is clear that significant occurrence of non-triporate pollen indicates the presence of triploid birch hybrids.

We have published findings of periods of intensive hybridization in the vegetation succession following the glacial retreat of the Weichselian ice sheet in North Iceland (Karlsdóttir et al. 2009) and South-west Iceland (Karlsdóttir et al. 2012). These hybridization periods were attributed to climate warming, when *B. pubescens* expanded over areas previously covered with heath, including *B. nana*. To complete the picture of birch hybridization in Iceland during the Holocene a further study was needed. The most urgent question was if the hybridization was limited to the original establishment of tree birch in Iceland or occurred also in the latter half of the Holocene. The interpretation of the current frequency of triploid hybrids in present-day woodlands (Thórsson et al. 2007) depends on the answer to this question. A study from a third region within Iceland was also needed to confirm that the trends observed are general and not reflecting only local conditions. Based on the established picture of Holocene vegetation development in Iceland (e.g. Hallsdóttir and Caseldine 2005), a progression of birch woodland establishment occurred first in the northern valleys and inner fjords, but in South Iceland the development was delayed. Very little is known about palaeovegetation in the eastern and north-eastern part of Iceland. Therefore, we decided to investigate vegetation history in Thistilfjördur, and aimed for a peat monolith covering the entire Holocene history of birch. This was necessary, not only to gather new information about birch woodland/forest establishment and development in this part of Iceland, but also to gain a better insight into changes in birch species composition and possible hybridization through time. Our previous studies provided us with the methods to differentiate *Betula* pollen at the species level and to recognize the presence of hybrids (Karlsdóttir et al. 2007, 2008) and based on these, we were able to calculate the proportions of *B. nana* and *B. pubescens* in total *Betula* pollen in palynological samples (Karlsdóttir et al. 2009, 2012).

MATERIALS AND METHODS

Study area

Peat samples were taken from a drainage ditch in a pasture at the farm Ytra-Áland in Thistilfjördur, North-east Iceland (Figure 1), at the co-ordinates of 66.2076 °N/15.556 °W and the altitude of 34 m. Coastal areas in Thistilfjördur were deglaciated and transgressed by sea in the early Bölling and shorelines, presumably formed at that time, are now at an altitude of around 65 m (Norddahl & Pétursson 2005). The Younger Dryas glaciation covered the area again around 12 cal ka, but lowland areas became ice-free in the Preboreal around 11.2 cal ka (Norddahl et al. 2008).

The area of Thistilfjördur was settled by Ketill Thistill during the Icelandic period of settlement in 874-930 AD. The earliest written source of information about the farm Áland is a document from the year 1378 (Óbyggdanefnd 2005).

The site is approximately 600 m from the shoreline and is surrounded by sparsely vegetated hills and pasture land. The nearest hill is 92 m a.s.l. though there are higher mountains to the west; the nearest, Flautafell, is approximately 13 km from the site. The weather station at Thorvaldsstadir, located 30 km south-east of Ytra-Áland, shows a 30 year (1961-1990) annual mean temperature of 2.8°C, a mean July temperature of 8.5°C, an average maximum July temperature of 11.2 °C and a four month average maximum temperature in June-September of 10.1°C.

Sampling and stratigraphic description

A section from the northern bank of the drainage ditch was cut and scraped clean. Samples were taken by hammering 5×5×20 cm metal boxes into the peat and cutting them free without disturbing their contents. The monolith consisted of six boxes, more or less in a single column but the third and sixth boxes were shifted a few centimetres to one side horizontally with a vertical overlap of adjacent boxes. This was necessary to obtain undisturbed peat (Figure 1c). The unbroken monolith measured 108 cm, spanning the depth interval of 17-125 cm, mostly consisting of peat with several bands of tephra. At the bottom of the monolith, the Saksunarvatn tephra (Gudrún Larsen, personal communication) was 17-20 cm thick and underlying it was a light coloured silted soil, which was sampled separately.

Loss on ignition (LOI) was tested to ascertain an estimate of the proportion of soil organic matter. Parallel to each pollen sample, approximately 3 g of (wet) peat were sampled for this purpose. The samples were dried overnight at 110°C and weighed to the nearest mg. They were then heated to 550°C for 4 hours, cooled down to 110°C and weighing repeated.

The stratigraphy of the section was described based on field observation, peat samples in boxes and sieve residues with regard to the Troel-Smith (1955) system as described by Faegri and Iversen (1989) and Kershaw (1997).

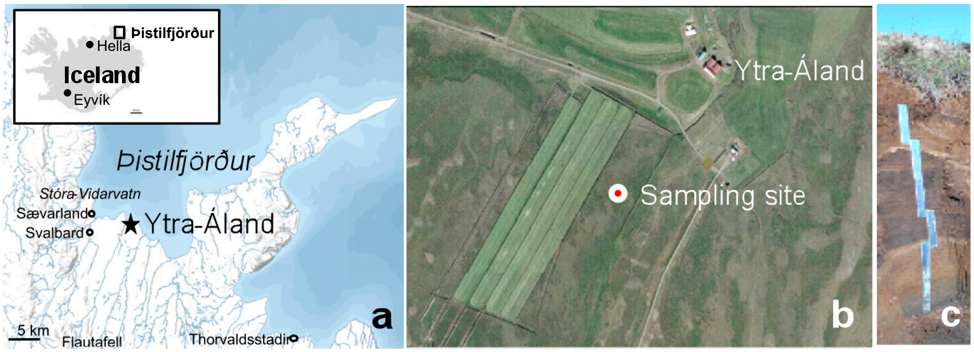

Figure 1. Sampling site. a) Map, sample site indicated by star. b) Aerial photo showing farmhouses and draining ditches. c) Photo showing sampling in process.

Chronology

Ten distinct tephra layers were noted in the peat monolith and more were suspected. Five previously dated tephra layers, recognized in the sampled peat section, were used for the age-depth model. Four samples were extracted from the peat and sent for AMS radiocarbon dating to the Lund University Radiocarbon Dating Laboratory. From the upper half of the monolith, twigs and bark were used. No good material for dating was found in the lower half, so *Carex* rootlets were used and this produced inadequate results. The carbon dates of the rootlets were lower than from the samples above, presumably because roots had grown down through the peat into the samples. Therefore, only two radiocarbon datings, i.e. at depths of 43 and 70 cm, were used for the chronology (Table 1). Radiocarbon ages were calibrated using the Intcal09 calibration dataset (Reimer et al. 2009). The age model was based on linear interpolation between the midpoints of calibrated age ranges.

Five tephra layers and two radiocarbon datings were used for the chronology of the Ytra-Áland peat section (Table 1). On average, each pollen sample represented approximately 50 years, varying from 25 to 74 years. The mean peat deposition rate was 0.11 mm year^{-1}, varying from 0.07 to 0.20 mm year^{-1}.

Throughout the paper cal ka and cal years refer to calibrated time before present (BP), "present" meaning 1950 AD.

Pollen preparation

From the monolith, 47 samples were taken for pollen preparation. Forty-six were from the peat in the boxes and one sample from the soil underneath the Saksunarvatn tephra. All samples were 1 ml, 5 mm thick and taken at approximately 25 mm intervals. One tablet of *Lycopodium* spores (Lund University, Department of Quaternary Geology, batch 1031, with 20848 ± 1546 spores per tablet) was added to each sample to enable estimation of pollen accumulation rates (PAR). The sample preparation was adapted from Fægri and Iversen (1989), including 10% NaOH, sieving, 10% HCl, 46% HF and acetolysis.

Pollen analysis

Counting was performed under a Leica DM 2500 light microscope using x400 or x630 magnification. A minimum of 300 land pollen grains per sample were counted except for seven samples at depths 106-121 cm, where pollen concentration was very low (149-439 grains ml^{-1}). In those samples, only 15-60 land pollen grains were counted. Pollen was identified to family or genus, seldom to species (Nilsson 1961, Fægri & Iversen 1989, Kapp et al. 2000). The number of land pollen taxa recovered was 29.

Betula pollen measurements

Slides were scanned separately for *Betula* pollen and every grain found was digitally photographed. About 90% of the pollen images

Table 1. Chronological data from tephras and ^{14}C datings in the Ytra-Áland peat sequence.

Tephras:

Depth (cm)	Name	Cal yr BP	Source
22.5-22.7	Veidivötn 1477AD	473	Larsen (1984)
39.0-40.5	Hekla 3	~3000	Dugmore et al. (1995).
57.0-58.0	Hekla 4	~4200	Dugmore et al. (1995)
85.0-86.0	Hekla 5	~7050	Thorarinsson (1971)
123-139 cm	Saksunarvatn	~10300	Rasmussen et al. (2007)

^{14}C datings:

Depth (cm)	Lab no	Code	Material	Dry weight (mg)	^{14}C age ± 1σ (^{14}C yr BP)	Calibrated age interval (cal yr BP)
43	LuS 10601	YA-43	twig and bark	4	3270 ± 50	3445-3560
70	LuS 10602	YA-70	twig and bark	12	5120 ± 50	5885-5920
89*	LuS 10603	YA-89	rootlets	8	4555 ± 55	not used
104*	LuS 10604	YA-104	rootlets	5	4515 ± 50	not used

* These samples consisted of *Carex* roots which probably had grown deep down through the peat.

showed measurable pollen grains. The pollen diameter was measured as in Karlsdóttir et al. (2007) as the distance from the outside tip of pore to the outer margin of the facing wall. Non-triporate pollen grains (identified as in Karlsdóttir et al. 2008) were noted and counted but not measured for size.

Data analysis and presentation

Analysis of size distribution of *Betula* pollen diameters within samples was performed as described in Karlsdóttir et al. (2009), using Bhattacharya's method (Bhattacharya 1967, Pauly & Caddy 1985). For successful calculation of species proportions, an effort was made to include 100-200 grains per sample. Due to varying *Betula* pollen concentrations, this was only possible in 38 out of 47 samples.

Means and standard deviations of subsets within samples (presumably *B. nana* vs. *B. pubescens*) were calculated from three or more points when the correlation coefficient was below -0.95. Results were refined with the Bmod program (Morgan 2005) and the best-fitted proportions calculated using Járai-Komlódi's formula (Prentice 1981).

Pollen stratigraphic, lithostratigraphic (including LOI) and chronological data were plotted using the PSIMPOLL 4.27 software (Bennett 2009). Pollen data is presented as percentage of total terrestrial pollen (TLP), while zonation of the pollen diagram (Table 2; Figure 2) using optimal splitting, implemented in PSIMPOLL, was based on all pollen and spore taxa.

RESULTS

Lithological description

The whole monolith consisted of brown herbaceous peat and *Carex* rootlets were abundant in sieve residues from all samples (Table 2). Fragments of wood were found in the upper half of the monolith. Ten layers of tephra were noted but grains of tephra were found in variable quantities throughout the monolith (Fig-ure 2). On the whole, loss on ignition was around 34% but varied from 6 to 71% (Figure 2), with the lowest values near the Saksunarvatn tephra layer.

In Table 2, zones from the pollen diagram (Figure 2) are shown. The Preboreal light silt (YA-1) was buried under the thick Saksunar-

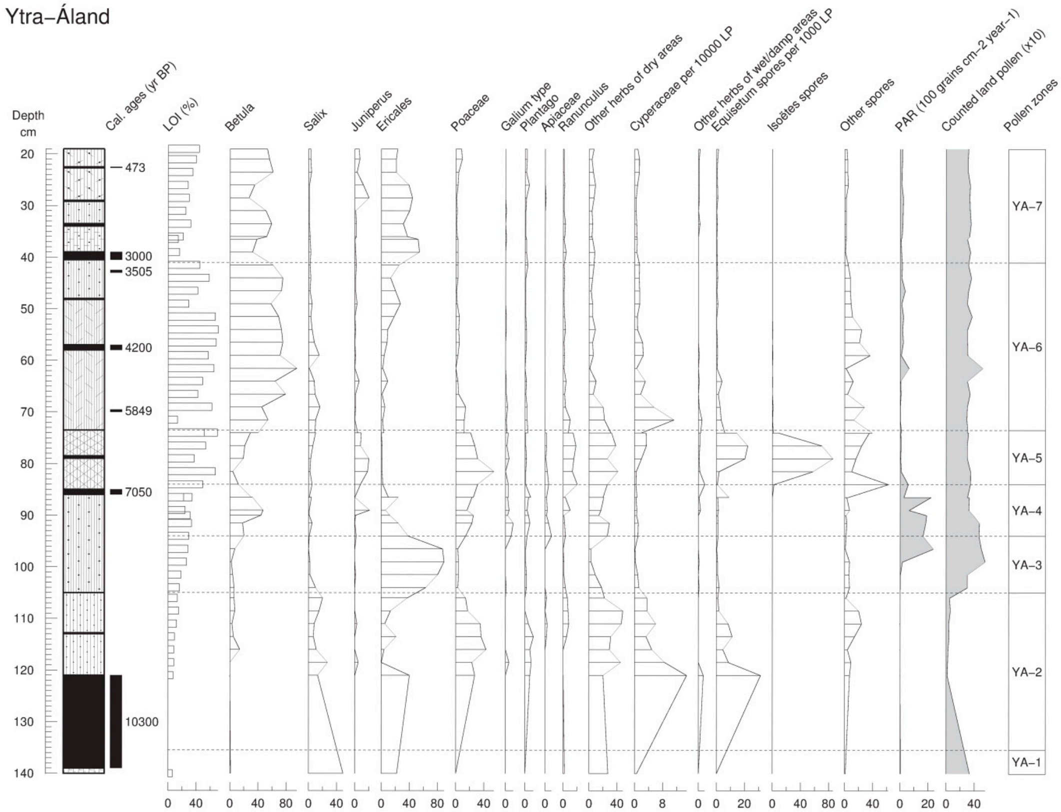

Figure 2. Pollen and spore diagram for the peat monolith from Ytra-Áland, Thistilfjördur, North-east Iceland. Lithostratigraphy, loss-on-ignition (LOI) data and chronological data on the left. Pollen percentages are based on total land pollen (TLP), Cyperaceae and spores excluded. Pollen accumulation rates, number of counted land pollen and local pollen zones on the right. Note different scales on Cyperaceae, Equisetum, pollen accumulation rate (PAR), LOI and counted land pollen. Calibrated ages of carbon dated samples at 43 and 74 cm are 3445-3560 and 5885-5920 cal years respectively.

vatn tephra at 10.3 cal ka (Rasmussen et al. 2007). The amount of organic matter was low, and sand in the soil indicates frequent wind deposition of loose tephra (YA-2). Gradually, the soil stabilized and the organic part of the soil increased while soil at the sampling site remained wet. This phase (YA-3) ended around 7.7 cal ka BP. In the earlier part of the next phase (YA-4), the organic content increased. Wetter conditions were detected in the later part of the zone by the increased presence of mud. The H5 tephra, deposited at 7050 cal years, marked a colour shift in the peat from light to much darker brown (Figure 1c), possibly as a result of increased degradation of organic matter. A period of very wet conditions followed (YA-5), when the sampling site was practically under water, as indicated by the presence of algae and quantities of presumed *Isoetes* spores. The amount of organic matter and mud in the peat increased. Ponds dried out and became fens (YA-6) and small woody fragments were found in the peat. The H4 tephra (4.2 cal ka) occurred within this section. Near 3.5 cal ka, wood remains became slightly less common. The H3 tephra (3 cal ka) was found at the bottom of the zone YA-7 and the Veidivötn AD 1477 was in its upper part.

Table 2. Lithostratigraphy and pollen stratigraphy for the Ytra-Áland peat sequence and inferred site development.

Depth (cm)	Age (cal ka)	Pollen zones	Samples (n)	PAR TLP	PAR *Betula*	Main components of sieve residue	Implied site conditions	Implied conditions of pollen source area
17-41	~0-3.1	YA-7	10	72-230	27-113	Brown herbaceous peat with grains of fine sand and small woody fragments	Mire with sedges	Shrub heath with stands of downy birch
41-73	~3.1-6.1	YA-6	13	19-633	10-604	Brown herbaceous peat with grains of fine sand and small woody fragments	Mire with sedges	Woodlands and shrub heath. Birch hybrids at 3.3 cal ka
73-84	~6.1-6.8	YA-5	5	45-277	8-39	Brown herbaceous peat and mud with algae	Shallow pond	Woodlands and shrub heath
84-94	~6.8-7.7	YA-4	6	78-2204	9-964	Light brown herbaceous peat and mud with algae	Mire with sedges and ponds	Tree birch advancing. Birch hybrids
94-105	~7.7-8.8	YA-3	5	17-2368	1-326	Light brown herbaceous peat and mud with algae	Mire with sedges and ponds	Shrub heath with Ericales and dwarf birch
105-121	~8.8-10.3	YA-2	7	2-5	0	Light brown herbaceous peat, sand and mud	Mire with sedges and seasonal ponds	Sparsely vegetated land with willows, grasses and herbs
121-139	10.3	-	-	-	-	Saksunarvatn tephra		
140	~10.4	YA-1	1	-	-	Coarse silt with light herbaceous soil	Wetland with sedges	Tundra/Arctic heath with *Salix*

Pollen record and birch vegetation

The Holocene pollen record of Ytra-Áland, Thistilfjördur, was divided into seven zones (Figure 2). In this diagram, *Betula* pollen was not differentiated in the pollen count.

In Figure 2, the first zone YA-1 at the depth of 140 cm, containing a single sample taken just below the Saksunarvatn tephra where *Salix* pollen was the most abundant, together with *Silene* type of Caryophyllaceae and *Empetrum*, indicated arctic heath vegetation. Pollen of *Koenigia*; a hardy annual arctic plant was present, pointing to a tundra-like ecosystem. Pollen concentration was 4500 land pollen grains cm^{-3}. Two *Betula* pollen grains were found, which is too few to draw a conclusion as to species or the distance to the source.

Zone YA-2 covered 10.3~8.8 cal ka and included seven samples taken above the thick Saksunarvatn tephra. Pollen concentrations were extremely low, or 149-439 land pollen grains cm^{-3}, and the pollen accumulation rate (PAR) was approximately 2-5 grains year^{-1} cm^{-2}. The total number of land pollen counted in all seven samples was only 253. The pollen taxa indicated sparsely vegetated land with shrubs, Ericales and grasses. *Betula* pollen accounted for 6% of land pollen, while calculations of species proportions from combined samples suggested only *B. nana* was present.

Zone YA-3, ~ 8.8-7.7 cal ka, was marked by a peak in Ericales pollen, together with high pollen concentration, the highest being more than 200,000 grains cm^{-3} with PAR values of nearly 2400 land pollen grains cm^{-2} year^{-1}. *Betula* pollen concentrations were rising at the end of the period, from 100 to 30,000 grains cm^{-3}. A few grains from aquatic plants, i.e. *Isoetes* spores and *Myriophyllum* pollen, were found.

Zone YA-4, ~ 7.7-6.8 cal ka, showed a peak in the *Betula* pollen percentage and an increasing number of *Juniperus* pollen towards the end and a decline in Ericales. Pollen concentrations were still high or 50-200 thousand grains cm^{-3}. *Betula* pollen concentrations were high but falling sharply by the end of the period. According to size, the *Betula* pollen was mostly *B. nana* but with a fair amount of *B. pubescens*, suggesting arctic-alpine heath with stands of downy birch.

Zone YA-5, ~ 6.8-6.1 cal ka, revealed a wet period with birch almost absent but an increase in grasses, *Ranunculus* and Apiaceae. The *Ranunculus* was probably mostly *Ranunculus aquatilis* L., an aquatic plant, although counted as terrestrial, as the pollen could not be identified to species. The Apiaceae were probably *Angelica*. There was also a marked peak in *Isoestes* spores. Land pollen concentrations were 3-20 thousand cm^{-3}.

In zone YA-6, which covers the long period of ~ 6.1-3.1 cal ka, mixed birch wood- and shrublands were re-established and became dominant. Land pollen concentration increased from 1500 to 18000 grains cm^{-3}, of which approximately two-thirds were *Betula* pollen and in turn half of the *Betula* pollen was *B. pubescens*.

Zone YA-7 covers the last 3000 years of the Holocene. No changes in vegetation connected to the human settlement in the area 1100 years ago were obvious, although sampling at a higher resolution might have detected small-scale changes. Birch continued to decline and there was a slight increase in Poaceae; however, neither change was drastic. Land pollen concentrations came to 10-30 thousand grains cm^{-3}, about half of them *Betula*.

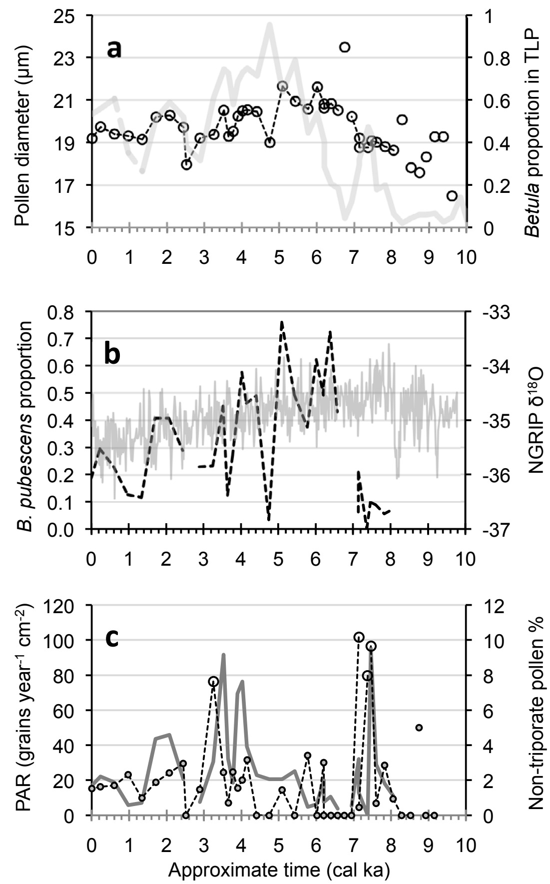

Figure 3. a) Mean *Betula* pollen diameter (circles and dashed line, data points with n less than 20 not connected) and proportion of *Betula* pollen in total land pollen (grey line). b) Calculated proportion of *B. pubescens* pollen in all *Betula* pollen (dashed line) and stable oxygen isotope ($\delta^{18}O$) data from the NGRIP Greenland ice core project (fine grey line) primarily indicating temperature changes during the Holocene (Vinther et al., 2006). c) Calculated PAR values of *B. pubescens* (grey line) and proportion of abnormal *Betula* pollen (circles and black dotted line, data points over 5% large circles, data points with n < 20 not connected).

Betula pollen size and species balance

The average size of all measured *Betula* pollen was 19.6 µm. Average sizes within samples increased between 10 cal ka and 5 cal ka but decreased slightly from 5 cal ka to the present (Figure 3a). Correlation between mean size of *Betula* pollen and the proportion of *Betula* pollen in TLP within each sample was weak but statistically significant ($r = 0.30$; $P_{one\text{-}tailed} = 0.027$; Figure 3a). Calculated proportions of

Betula species within each sample revealed mean *B. nana* pollen sizes around 19 µm, ranging from 18.7 to 19.5 µm and *B. pubescens* mean pollen size around 23 µm, ranging from 22.6 to 23.2 µm. The results from calculations, which were possible for 35 of the 47 samples, showed great fluctuations in species balance, suggesting an unstable climate (Figure 3b). Calculated PAR values for *B. pubescens* pollen in particular never reached 100 grains year^{-1} cm^{-2} but peaked at 95 grains year^{-1} cm^{-2} at ~ 7.5 cal ka and again at 92 grains year-1 cm^{-2} at ~ 3.5 cal ka (Figure 3c).

Abnormal Betula pollen

Non-triporate *Betula* pollen grains are indicative of the presence of triploid *Betula* hybrids when they occur in a significant amount (Karlsdóttir et al. 2008). A total of 156 non-triporate *Betula* pollen grains from the Ytra-Áland monolith were noted (examples shown in Figure 4). Of these, 82 were found in just 4 samples at depths of 90, 89, 86.5 and 41.5 cm, corresponding to two peak periods, ~ 7.5-7.1 cal ka and ~ 3.3 cal ka (Figure 3c). The percentage of non-triporate pollen in these samples was 8-10%. To confirm that these samples were indeed statistically different from other samples, Tukey's boxplot method was used, confirming the data points as suspected outliers. The abnormal pollen is unlikely to be normally distributed (KS-test P<0.01). Two additional samples with a raised percentage of non-triporate *Betula* pollen, at depths of 111 (out of scale in Figure 3c) and 104 cm (~8.8 cal ka), had too few *Betula* pollen grains to be regarded as evidence of hybridization (Figure 3c).

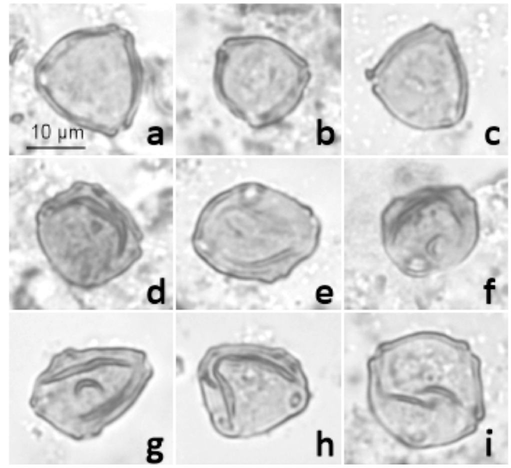

Figure 4. Examples of *Betula* pollen from Ytra-Áland samples. a-c) Normal triporate pollen. d-i) Non-triporate pollen.

DISCUSSION

Characteristics of the research area in comparison to previous sites investigated

The present study on the relative abundance and hybridization of the two *Betula* species in Iceland, based on subfossil pollen, spans the period from the first Holocene colonization of birch to the present. We have previously used the same approach on samples from two other sites; Hella in Eyjafjördur, North Iceland (Karlsdóttir et al. 2009) and Eyvík in Grímsnes, South-west Iceland (Karlsdóttir et al. 2012), but both studies only cover a few thousand years in the early Holocene from ~10.3 cal ka and onwards. Because of the extended time span, the present study not only strengthens our previous results from the earlier half of the Holocene, but it also reveals for the first time birch hybridization in the late Holocene. Furthermore, the addition of Thistilfjördur makes it reasonable to consider Holocene birch hybridization to be applicable to Iceland as a whole.

Besides being situated in different regions of Iceland, the three sites differ in other respects. The Hella site in Eyjafjördur lies on the western side of a major fjord with steep mountain slopes to the west. In Akureyri, the site of a nearby weather station, the mean annual temperature from 1961-1990 was 3.2 °C and the mean July temperature was 10.5 °C. The Eyvík site in Grímsnes lies in a relatively flat landscape. It is now around 65 m a.s.l. and 30 km inland but was close to the shoreline during the early Holocene. At Hæll, a nearby weather station, the mean annual temperature from

1961-1990 was 3.6 °C and the mean July temperature was 10.6 °C. Ytra-Áland is neither far from the shore nor is it sheltered by steep mountain slopes. In comparison to the two other sites Ytra-Áland has the least favourable climate for downy birch. At the weather station Thorvaldsstadir, the mean annual temperature from 1961-1990 was only 2.8 °C and the mean July temperature was 8.5 °C. the mean wind velocity is also a little higher near Ytra-Áland or approximately 4.4 m sec^{-1} compared to 4.0 and 4.1 m sec^{-1} near Hella and Eyvík, respectively (The Icelandic Meteorological Office 2013).

Soil development

The parent materials of Icelandic soils are mixtures of tephra layers and aeolian sediments consisting mostly of volcanic glass (Arnalds 2004). In Icelandic soils, there are more than 800 Holocene tephra layers (Larsen & Eiríksson 2008). They were generated by various volcanoes and the distribution of each tephra depends mainly on the size of the eruption and wind directions during the first fierce eruption days. Gudmundsdóttir et al. (2012) listed 85 tephras aged 10,300-70 cal years, recognized from the core MD99-2275 on the North Icelandic shelf 100 km north-west from the sampling site at Ytra-Áland. Five of the most easily recognized of these tephras have been used to date the samples in this study but most of the others are likely to have been present too, adding bulk material to the sequence and depressing LOI values.

The low pollen concentration and LOI values of the samples just above the Saksunarvatn tephra indicate frequent sandstorms but the duration of this period is unknown as we did not find suitable material for radiocarbon dating in the lower part of the monolith. Hallsdóttir and Caseldine (2005) inferred several decades or even centuries of unstable environment as a consequence of the huge eruption that produced the Saksunarvatn tephra. After this period, LOI values increased slowly until around 7 cal ka, near the boundaries of zones YA-4 and YA-5. At first, the low values were probably due to erosion in the sparsely vegetated environment where tephra was abundant, but later a warmer and dryer climate may have kept the rate of organic matter accumulation low through faster decomposition. The peak of *Betula* pollen in zone YA-4 (around 7.5-7.0 cal ka), with its high values of *B. pubescens* PAR, may well represent the Holocene thermal maximum in the area. In zone YA-5 (from 7 cal ka) the LOI values increased rapidly as the conditions became wetter. Even though the ponds gave way to fens in zone YA-6 (from ~6.2 cal ka), LOI values remained high for the most part until around 3 cal ka, when the great eruption of Hekla deposited the H3 tephra. After that, LOI values were low for a while, but then started to grow slowly again and kept growing in spite of human settlement from around 900 AD. Volcanic eruptions thus seem to have been a major factor in determining the carbon content of the soil at Ytra-Áland, although ground-water level, controlled by climate, also played a part.

In general the main changes in Icelandic soils related to human settlement have been a decrease in woodlands mostly caused by winter grazing and wood cutting for iron processing (Hallsdóttir 1987), followed by a marked increase in the deposition rate caused by wind erosion (Thorarinsson 1961). Climate cooling has doubtless enhanced these effects. In remote areas without birch woodlands, these changes are less conspicuous. Zutter (1997) studied the anthropogenic impact on vegetation in Thistilfjördur and published two pollen records for the period ~7.3 cal ka to the present, obtained at the Svalbard and Sævarland farms, 7-8 km from Ytra-Áland. She found a marked increase in deposition rates at the Svalbard site but not at Sævarland, showing that these effects can be very local.

Birch in Thistilfjördur through the Holocene
Changing equilibrium of Betula species
– the rise and fall of tree-birch

The size of the pollen differs between *Betula* species but is also affected by conditions during development and continues to change as a response to environmental factors after being shed (Dunbar & Rowley 1984, Edwards et al. 1991). Chemical treatment has been shown to alter pollen sizes (e.g. Reitsma 1969) and there are reasons to suspect size differences in relation to soil conditions of subfossil pollen (Karlsdóttir et al. 2009). We therefore do not put any emphasis on absolute difference in pollen size between samples, but concentrate on size distribution within each sample when calculating the relative number of different species. When these data were used to calculate PAR values for *B. pubescens* pollen we obtained the maximum value of 95 grains cm^{-2} $year^{-1}$ at around 7.5 cal ka. This is far below the PAR values seen in birch woodlands in other studies including Eyvík, South-west Iceland (Karlsdóttir et al. 2012) and in Scandinavian forests (Seppa & Hicks 2006, Hättestrand et al. 2008). Based on this, birch woodlands in the Thistilfjördur region were never dense during the Holocene, but rather a shrubland with dwarf birch and scattered birch trees. This conclusion was strengthened by the observation of birch remains, up to 10 cm in diameter, protruding from the peat in a nearby ditch. No such wood remains were found at the sampling site.

Dwarf birch seems to have found its way to North-east Iceland sometime around 9 cal ka. The pollen concentration was still low, however, until after ~8.2 cal ka when rapid colonization took place. Downy birch became established in Thistilfjördur around that time, 8.2-7.6 cal ka. That is later than seen in some other parts of Iceland where the first birch woodlands appeared ca. 9.5-8.2 cal ka (Vasari & Vasari 1990, Hallsdóttir 1995, Hallsdóttir & Caseldine 2005), but may be comparable to data from Lake Efstadalsvatn in North-west Iceland at 123 m a.s.l., where conditions for tree birch were also limited (Caseldine et al. 2003). Where tree birch had been established early, a decline in birch vegetation is seen during the cold event of 8.2 cal ka (Thomas et al. 2007), followed by a rapid recovery and a new expansion when conditions improved. The peak of the birch period, both in North and South Iceland, was between 8.0 and 6.8 cal ka (Vasari & Vasari 1990, Hallsdóttir 1995, Hallsdóttir & Caseldine 2005). At Ytra-Áland the peak in *B. pubescens* at ~7.5-7.1 cal ka was short-lived (Figure 3c). Both *Betula* species retreated, probably in response to cold and wet conditions. The dwarf birch recovered faster but the downy birch took a thousand years to begin its recovery and did not reach another peak until around 4 cal ka. The peak in combined *Betula* pollen around 4.7 cal ka (Figure 2) mainly reflects *B. nana* pollen. This is consistent with Zutter´s (1997) results on birch woodlands in Thistilfjördur where periods of birch expansion and decline with wetter conditions were found at similar times. Our results show that from 4 cal ka until the present, birch has been declining. Downy birch almost disappeared from the area around 3 cal ka, recovered for a while in the Roman warm period, but was retreating even before settlement at 1.1 cal ka. The dwarf birch, on the other hand, prevailed and seems to have expanded rather than decreased. The human settlement in the area had little or limited effect on the already declining tree birch vegetation.

Holocene climate in Thistilfjördur

A temperature of 10°C in the warmest month has usually been considered a minimum for birch forest limits in the northern temperate belt (Odland 1996). Attempts to define the climatic requirements for the mountain birch have proved difficult. Other figures for the July temperature have been suggested (reviewed by Odland 1996; in Iceland measured by Wöll 2008), and the temperature during the entire growing season, either air (Odland 1996) or soil (Körner & Paulsen 2004), has been found to predict tree line altitudes somewhat better, but the results are never far from the 10 °C July mean temperature. Using this conventional figure, we see that in the Thistilfjördur area a climate warmer than in the late twentieth century would have been needed for tree-birch to thrive there. A minimum July temperature for *B. nana*, on the other hand, is estimated closer to 6°C (De Groot et al. 1997), which is well below the present-day conditions in the area. Therefore we would expect *B. nana* to be the dominant source of *Betula* pollen except during the Holocene Thermal Maximum (HTM) when temperatures may have been around 1.5 °C higher than present (Kaufman et al. 2004). Even at that time, the downy birch would have been struggling near the lower limits of its temperature requirements. If some local meteorological condition reduced or delayed the HTM, it would have further limited downy birch to scattered stands of trees in favourable places rather than continuous woodlands.

Zutter (1997) concluded, mostly from *Betula* pollen, that conditions in Thistilfjördur had been warmer and drier than present in the period 5.1-2.1 cal ka. Later Axford et al. (2007) studied subfossil midges in Thistilfjördur throughout the entire Holocene and came to the conclusion that in North-east Iceland the HTM occurred several thousand years later than expected or around 5.0-2.5 cal ka, compared with the HTM between 10.3-5.6 cal ka, as reflected by five studies on terrestrial sites in Iceland (Kaufman et al. 2004). The reasons for this are far from clear as summer insolation peaked in the early Holocene. The authors suggest modulation by sea ice, enhanced by salinity stratification of sea waters. Our records of *Betula* pollen proportion and *Betula* species balance suggest a period of warmer climate than present between 8 and 7 cal ka, followed by a cold and wet period 7.0-5.5 cal ka. It is therefore debatable if the peak in *B. pubescens* PAR at 7.5-7.1 cal ka represents the HTM in the area or if the HTM was delayed until 5.4-3.5 cal ka when *Betula* in TLP was highest. Anomalies in pollen concentrations in the earlier half of the Holocene and variation in the *Betula* species balance support theories of an unstable climate in far north-eastern Iceland during the early and mid-Holocene; something that might be attributed to variations in drift ice or periods of persisting northerly winds.

Holocene birch hybridization

In the present study, we detected two significant peaks of non-triporate *Betula* pollen indicating the presence of hybrids in the Ytra-Áland peat; an earlier peak at 7.5-7.1 cal ka and a later one around 3.3 cal ka. Both peaks are associated with peaks in *B. pubescens* PAR values, and this association conforms to the results we have published before from North and South-west Iceland, where periods of hybridization were also linked to *B. pubescens* pollen influx values higher than those characteristic for established *B. nana* populations. This is the first time birch hybridization has been detected in the Late Holocene.

The results of the present study, along with results from two previous studies on Holocene birch hybridization, indicate that the hybridization followed expansion of *B. pubescens* dominating woodlands, presumably during regional warming of the climate. An increase in annual mean temperature of around 5°C is predicted in the Arctic in the 21st century but summer temperatures are supposed to rise less, or around 2°C (Christensen et al. 2007). Such a change of climate would benefit vegetation and lead to establishment or expansion of birch woodlands, given there is available space for recruitments. In the process, a new wave of birch hybrids may be expected.

CONCLUSIONS

Periods of *Betula* hybridization were identified, based on pollen data from Thistilfjördur in North-east Iceland, supporting previous results from North and South-west Iceland. As found in the earlier studies, periods of hybridization were connected to the expansion of local *B. pubescens* populations. Our new data confirm that a period of hybridization occurred in the earlier half of the Holocene. Comparable periods of hybridization are also reported here in connection with birch expansion in the latter half of Holocene. Conditions in the oceanic North-east Iceland were near the lower limits of the temperature requirements of downy birch for most of the Holocene, resulting in a fluctuating *Betula* species balance. The effects of human settlement on birch in the area were small compared to climatic effects. Theories on a late HTM in Thistilfjördur, compared to other parts of Iceland, are partly supported, as birch woodlands peaked from 5.4-3.3 cal ka. Still a short period of warm climate, seen as a peak in PAR values for *B. pubescens* and land pollen in general, was detected near 7.5 cal ka and might represent the local HTM.

ACKNOWLEDGEMENTS

The authors would like to thank Sigurdur H. Árnason for help with the fieldwork; the residents at Ytra-Áland for access to the sampling site; Egill Erlendsson for his help and access to equipment for the loss on ignition test; Gudrún Larsen for advice on tephra identification; and an anonymous reviewer for useful comments and suggestions. The project was supported by the University of Iceland (Doctoral grant 2010–2013) and the University of Iceland Research Fund.

REFERENCES

Anamthawat-Jónsson K & Thórsson ÆTh 2003. Natural hybridisation in birch: triploid hybrids between *Betula nana* and *B. pubescens. Plant Cell, Tissue and Organ Culture* 75, 99-107.

Anamthawat-Jónsson K & Tómasson T 1990. Cytogenetics of hybrid introgression in Icelandic birch. *Hereditas* 112, 65-70.

Arnalds O 2004. Volcanic soils of Iceland. *Catena* 56, 3-20.

Axford Y, Miller GH, Geirsdóttir Á & Langdon PG 2007. Holocene temperature history of northern Iceland inferred from subfossil midges. *Quaternary Science Reviews* 26, 3344-3358.

Bhattacharya CG 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics* 23, 115–135.

Bennett KD 2009. Psimpoll 4.27: C program for plotting pollen diagrams and analysing pollen data. Available online from Queen's University of Belfast, Department of Archaeology and Palaeoecology. Accessed 2 May 2013 at www.chrono.qub.ac.uk/psimpoll/psimpoll.html.

Birchler JA & Veitia RA 2007. The gene balance hypothesis: From classical genetics to modern genomics. *The Plant Cell* 19, 395-402.

Caseldine C, Geirsdóttir Á & Langdon P 2003. Efstadalsvatn–A multi-proxy study of a Holocene lacustrine sequence from NW Iceland. *Journal of Paleolimnology* 30, 55-73.

Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon W-T, Laprise R, Magana Rueda V, Mearns L, Menendez CG, Räisänen J, Rinke A, Sarr A & Whetton P 2007. Regional climate projections. *Climate Change, 2007: The Physical Science Basis.* Contribution of Working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, pp. 847-940.

De Groot WJ, Thomas PA & Wein RW 1997. *Betula nana* L. and *Betula glandulosa* Michx. *Journal of Ecology* 85, 241-264.

Dugmore AJ, Cook GT, Shore JS, Newton AJ, Edwards KJ & Larsen G 1995. Radiocarbon dating tephra layers in Britain and Iceland. *Radiocarbon* 37, 379-388.

Dunbar A & Rowley JR 1984. *Betula* pollen development before and after dormancy: Exine and intine. *Pollen et Spores* 26, 299-338.

Edwards ME, Dawe JC & Armbruster WS 1991. Pollen size of *Betula* in northern Alaska and the interpretation of late Quaternary vegetation records. *Canadian Journal of Botany* 69, 1666-1672.

Elkington TT 1968. Introgressive hybridization between *Betula nana* L. and *B. pubescens* Ehrh. in North-West Iceland. *New Phytologist* 67, 109-118.

Fredskild B 1991. The genus *Betula* in Greenland-Holocene history, present distribution and synecology. *Nordic Journal of Botany* 11, 393-412.

Fægri K & Iversen J 1989. *Textbook of pollen analysis*. In: Fægri K, Kaland PE, Krzywinski K (eds.), 4th edn. John Wiley and Sons, Chichester. 328 p.

Gudmundsdóttir ER, Larsen G & Eiríksson J 2012. Tephra stratigraphy on the North Icelandic shelf: Extending tephrochronology into marine sediments off North Iceland. *Boreas* 41, 719-734.

Hallsdóttir M 1987. *Pollen analytical studies of human influence on vegetation in relation to the*

Landnám tephra layer in southwest Iceland. Ph.D. thesis. LUNDQUA thesis 18, Lund University, Department of Quaternary Geology, 45 p.

Hallsdóttir M 1995. On the pre-settlement history of Icelandic vegetation. *Búvísindi* 9, 17-29.

Hallsdóttir M & Caseldine CJ 2005. The Holocene vegetation history of Iceland, state-of-the-art and future research. In: C. Caseldine, A. Russell, J. Hardardóttir, Ó. Knudsen (eds.) *Iceland: Modern Processes and Past Environments.* Elsevier, Amsterdam, pp. 319-334.

Hättestrand M, Jensen C, Hallsdóttir M & Vorren KD 2008. Modern pollen accumulation rates at the north-western fringe of the European boreal forest. *Review of Palaeobotany and Palynology* 151, 90-109.

Kapp RO, King JE & Davis OK 2000. *Ronald O. Kapp's Pollen and Spores*. 2nd ed. American Association of Stratigraphic Palynologists Foundation Publication, Texas, 279 p.

Karlsdóttir L, Thórsson ÆTh, Hallsdóttir M, Sigurgeirsson, Eysteinsson Th & Anamthawat - Jónsson K 2007. Differentiating pollen of *Betula* species from Iceland. *Grana* 46, 78-84.

Karlsdóttir L, Hallsdóttir M, Thórsson ÆTh & Anamthawat-Jónsson K 2008. Characteristics of pollen from natural triploid *Betula* hybrids. *Grana* 47, 52-59.

Karlsdóttir L, Hallsdóttir M, Thórsson ÆTh, Anamthawat-Jónsson K 2009. Evidence of hybridisation between *Betula pubescens* and *B. nana* in Iceland during the early Holocene. *Review of Palaeobotany and Palynology* 156, 350-357.

Karlsdóttir L, Hallsdóttir M, Thórsson ÆTh & Anamthawat-Jónsson K 2012. Early Holocene hybridisation between *Betula pubescens* and *B. nana* in relation to birch vegetation in Southwest Iceland. *Review of Palaeobotany and Palynology* 181, 1-10.

Kaufman DS, Ager TA, Anderson NJ, Anderson PM, Andrews JT, Bartlein PJ, Brubaker LB, Coats LL, Cwynar LC, Duvall ML, Dyke AS, Edwards ME, Eisner WR, Gajewski K, Geirsdóttir A, Hu FS, Jennings AE, Kaplan MR, Kerwin MW, Lozhkin AV, MacDonald GM, Miller GH, Mock CJ, Oswald WW, Otto-Bliesner BL, Porinchu DF, Ruüland K, Smol JP, Steig EJ & Wolfe BB 2004. Holocene thermal maximum in the western Arctic (0–180 W). *Quaternary Science Reviews* 23, 529-560.

Kershaw AP 1997. A modification of the Troels-Smith system of sediment description and portrayal. *Quaternary Australasia* 15, 63-68.

Körner C & Paulsen J 2004. A worldwide study of high altitude treeline temperatures. *Journal of Biogeography* 31, 713-732.

Larsen G 1984. Recent volcanic history of the Veidivötn fissure swarm, southern Iceland – an approach to volcanic risk assessment. *Journal of Volcanology and Geothermal Research* 22, 33-58.

Larsen G & Eiríksson J 2008. Late Quaternary terrestrial tephrochronology of Iceland - Frequency of explosive eruptions, type and volume of tephra deposits. *Journal of Quaternary Science*, 23, 109-120.

McCormick S 1993. Male gametophyte development. *The Plant Cell* 5, 1265-1275.

Morgan JH 2005. A computer method for resolving mixed normal distributions. *Ringing & Migration* 22, 145-152.

Nilsson T 1961. *Kompendium i kvartärpaleontologi och kvartärpaleontologiska undersöknings-metoder* [Compendium in Quarter paleontology and Quarter paleontological research methods]. University of Lund, Lund, 2 volumes, 238 p. + 63 plates. [In Swedish]

Norddahl H & Pétursson HG 2005. Relative Sea-Level Changes in Iceland: New Aspects of the Weichselian Deglaciation of Iceland. In: Caseldine C, Russel A, Hardardottir J & Knudsen O (eds.) *Iceland – Modern Processes and Past Environments*, Elsevier, Amsterdam, pp. 25-78.

Norddahl H, Ingólfsson Ó, Pétursson HG & Hallsdóttir M 2008. Late Weichselian and Holocene environmental history of Iceland. *Jökull*, 58, 343-364.

Óbyggdanefnd 2005. *Úrskurður Óbyggðanefndar mál nr. 4/2005, Svalbarðshreppur, Þórshafnarhreppur og Skeggjastaðahreppur.* [Verdict of The Wilderness Committee, Case nr. 4/2005 Svalbarðshreppur, Þórshafnarhreppur and Skeggjastaðahreppur], Reykjavík, Óbyggðanefnd, 241 p. [In Icelandic].

Odland A 1996. Differences in the vertical distribution pattern of *Betula pubescens* in Norway and its ecological significance. In: Frenzel, B. (ed). *Holocene treeline oscillations, dendrochronology and palaeoclimate*; Gustav Fischer, Stuttgart, p. 43-59.

Pauly D & Caddy JF 1985. *A modification of Bhattacharya's method for the analysis of mixtures of normal distributions*. FAO Fisheries Circular 781. Rome: FAO, 16 p.

Pétursson HG 1991. The Weichselian glacial history of West Melrakkaslétta, Northeastern Iceland. In Maizels JK & Caseldine C. (eds.) *Environmental Change in Iceland: Past and Present.* Springer, Netherlands. pp. 49-65.

Prentice IC 1981. Quantitative birch (*Betula L.*) pollen separation by analysis of size frequency data. *New Phytologist* 89, 145-157.

Ramsey J & Schemske DW 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29, 467-501.

Rasmussen SO, Vinther BM, Clausen HB & Andersen KK 2007. Early Holocene climate 10 oscillations recorded in three Greenland ice cores. *Quaternary Science Reviews* 26, 1907-1914.

Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Burr GS, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Hajdas I, Heaton TJ, Hogg AG, Hughen KA, Kaiser KF, Kromer B, McCormac FG, Manning SW, Reimer RW, Richards DA, Southon JR, Talamo S, Turney CSM, van der Plicht J & Weyhenmeyer CE 2009. IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* 51, 1111-1150.

Reitsma TJ 1969. Size modification of recent pollen grains under different treatments. *Review of Palaeobotany and Palynology* 9, 175-202.

Seppä H & Hicks S 2006. Integration of modern and past pollen accumulation rate (PAR) records across the arctic tree-line: A method for more precise vegetation reconstructions. *Quaternary Science Reviews* 25, 1501-1516.

The Icelandic Meteorological office 2013. Tímaraðir fyrir valdar veðurstöðvar [Time series for selected weather stations]. Accessed 2 July 2013 at www.vedur.is/vedur/vedurfar/medaltalstoflur [In Icelandic]

Thomas ER, Wolff EW, Mulvaney R, Steffensen JP, Johnsen SJ, Arrowsmith C, Whited JWC, Vaughn B & Popp T 2007. The 8.2 ka event from Greenland ice cores. *Quaternary Science Reviews* 26, 70-81.

Thorarinsson S 1961. Uppblástur á Íslandi í ljósi öskulagarannsókna. [Soil erosion in Iceland in the light of tephra research]. *Ársrit Skógræktarfélags Íslands* 1960–61, 17-54 [In Icelandic, English summary]

Thorarinsson S 1971. Aldur ljósu gjóskulaganna úr Heklu samkvæmt leidréttu geislakolstímatali. [The age of the light Hekla tephra layers according to corrected C14-datings]. *Náttúrufrædingurinn* 41, 99-105 [In Icelandic].

Thórsson ÆTh, Pálsson S, Sigurgeirsson A & Anamthawat-Jónsson K 2007. Morphological variation among *Betula nana* (diploid), *B. pubescens* (tetraploid) and their triploid hybrids in Iceland. *Annals of botany* 99, 1183-1193.

Troels-Smith J 1955. Characterization of unconsolidated sediments. *Danmarks Geologiske Undersøgelse* IV 3, 1-73.

Vasari Y &Vasari A 1990. L'histoire Holocène des lacs Islandais [The Holocene history of Icelandic lakes]. In: Devers, S. (ed.), *Pour Jean Malaurie.* Editions Plon, Paris, pp. 277–293 [In French].

Vinther BM, Clausen HB, Johnsen SJ, Rasmussen SO, Andersen KK, Buchardt SL, Dahl-Jensen D, Seierstad IK, Siggaard-Andersen M-L, Steffensen JP, Svensson AM, Olsen J & Heinemeier J 2006. A synchronized dating of three Greenland ice cores throughout the Holocene. *Journal of Geophysical Research* 111, D13102. DOI: 10.1029/2005JD006921

Wöll C 2008. Treeline of mountain birch (*Betula pubescens* Ehrh.) in Iceland and its relationship to temperature. Department of Forestry: Technical University Dresden. 125 p.

Zutter C 1997. *The Cultural Landscape of Iceland: A Millennium of Human Transformation and Environmental Change*. Doctoral dissertation, University of Alberta USA, 239 p.

Manuscript received 11 March 2014
Accepted 03 June 2014