



Evidence of hybridisation between *Betula pubescens* and *B. nana* in Iceland during the early Holocene

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ABSTRACT

The aim of this study was to find evidence of Holocene hybridisation between downy birch (*Betula pubescens*) and dwarf birch (*B. nana*) in Iceland. We measured *Betula* pollen from an early Holocene peat profile from Hella in Eyjafjörður, mid-northern Iceland, with 39 samples taken at ca. 100-yr intervals between ca. 10.3 and 7.0 cal. ka BP based on known tephra layers. Species proportions were estimated and compared with data on present-day birch pollen. We found that *Betula* pollen from old samples prepared in glycerol was larger than the pollen in parallel samples mounted in silicon oil by a factor of 1.2 to 1.6, depending on the age of the peat. Therefore the analysis of Hella peat profile was entirely based on size frequency distribution within samples. The size frequency distribution of *Betula* pollen changed throughout the profile. In all samples, two normal curves with different means gave good fit to the observed frequency distribution, which denoted small pollen of *B. nana* and large pollen of *B. pubescens*. A low proportion of *B. pubescens* pollen was found in the oldest peat samples and again around 7.8 cal. ka BP, when *B. nana* predominated. The proportion of *B. pubescens* pollen peaked approximately at 8.7 and 7.2 cal. ka BP. Evidence of *Betula* hybrids was found in several samples, especially simultaneously with the earlier *B. pubescens* peak. Pollen with low *D/P* ratios (hybrid pollen) was found at different frequencies throughout the profile. Non-triporate *Betula* pollen grains, which are frequent among present-day triploid hybrids, were observed in most samples. The frequency of non-triporate pollen in a period between 9.2 and 8.7 cal. ka BP far exceeded the average level produced by the present-day triploid hybrids. Climatic and ecological conditions may have favoured hybridisation of birch species during the expansion of downy birch over dwarf birch colonies in warm periods.

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1. Introduction

Two species of birch are found in natural habitats in Iceland: dwarf birch (*Betula nana* L., diploid with $2n = 2x = 28$) and downy birch (*B. pubescens* Ehrh., tetraploid with $2n = 4x = 56$). *Betula nana*, a circumpolar species (de Groot et al., 1997), grows up to about 1 m in height with procumbent, wide-spreading stems and a strong branching habit. It has orbicular or obovate-orbicular leaves which are regularly crenated and are rounded at both leaf tip and base. *Betula pubescens* is a European species (Atkinson, 1992), represented by the subspecies *pubescens* Ehrh., which may grow up to 25 m tall with single or many stems (monocormic or polycormic type), and subspecies *tortuosa* (Ledeb.) Nyman, which is a shrub or low tree found in the mountain regions of northern Europe and is therefore called “mountain birch”. The birch in Iceland (*B. pubescens*) has in

some occasions been referred to as mountain birch, due to its low stature and scrub-like growth form (e.g. Jónsson, 2004). Elkington (1968) compared birch from Iceland and Scotland and suggested that the morphological variability and the shrub-like appearance in Icelandic birch were due to genetic introgression from *B. nana* into *B. pubescens* via triploid hybrids between the two species. This was confirmed with both crossing experiments and population-based studies (Anamthawat-Jónsson and Tómasson, 1990; Anamthawat-Jónsson and Þórhsson, 2003). Furthermore, these studies revealed that the introgression occurred in both directions, i.e. also from the tetraploid to the diploid birch species, resulting in a high degree of variation in both species.

Birch species are common in sub-arctic vegetation and as birch is wind-pollinated, it produces a large quantity of pollen which can be found in sediments and peat. In Iceland, downy birch is the only tree species known to have formed forests and woodlands in the Holocene and is therefore a key ecological species in the history of vegetation. An assessment of several morphological traits of present-day Icelandic birch, focused upon leaf shape and size, has revealed continuous variation from a typical diploid *B. nana* appearance to tetraploid trees

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with *B. pubescens* traits (Thórrsson et al., 2007). The triploid hybrids also varied widely in their appearance but were often intermediate. Measurements of pollen from these trees and shrubs, which were differentiated by ploidy levels, showed small but significant differences in the average size and shape between the diploid and the tetraploid species (Karlsdóttir et al., 2007). Although abnormal pollen grains were found to be prevalent among the triploid hybrids, normal triporate pollen was also produced (Karlsdóttir et al., 2008). This triporate pollen was not intermediate in its appearance, but was on average as small as *B. nana* pollen while its vestibulum was as large as *B. pubescens* pollen. This type of pollen is presumably rare in the *Betula* pollen pool, but it may be viable and could therefore take part in the introgressive hybridisation process. Triploid plants (hybrids between diploid *B. nana* and tetraploid *B. pubescens*) make up about 10% of individual birch trees/shrubs in natural woodlands in Iceland today (Thórrsson et al., 2007). The presence of triploid hybrids in Icelandic birch populations indicates active hybridisation, which is likely to result in gene introgression if the triploid hybrids are not sterile.

Anamthawat-Jónsson and Tómasson (1990) showed that seed progeny of open-pollinated triploid plants consisted of diploid, triploid and tetraploid individuals, confirming the role of triploid hybrids as seed parents in the introgressive hybridisation process. There is no study to date showing that triploid plants contribute directly to this process as pollen parents. On the other hand, the characterization of pollen produced by triploid plants has provided a reliable means for identification of introgressive hybridisation between the two birch species in the past.

There have been questions about the origin of Icelandic birch. The dwarf birch (*B. nana*) may have survived some cold periods of the late Pleistocene (Rundgren and Ingolfsson, 1999) but more likely it was a Holocene immigrant coming from Europe, like *B. nana* in north-eastern Greenland (Bennike et al., 1999). Even for the high-Arctic species like *Campanula uniflora*, one of the most likely glacial survival candidates in the Icelandic flora, there is no molecular evidence for glacial survival (Ægisdóttir and Thórhallsdóttir, 2004). Downy birch (*B. pubescens*), on the other hand, is believed to have dispersed from Europe (western

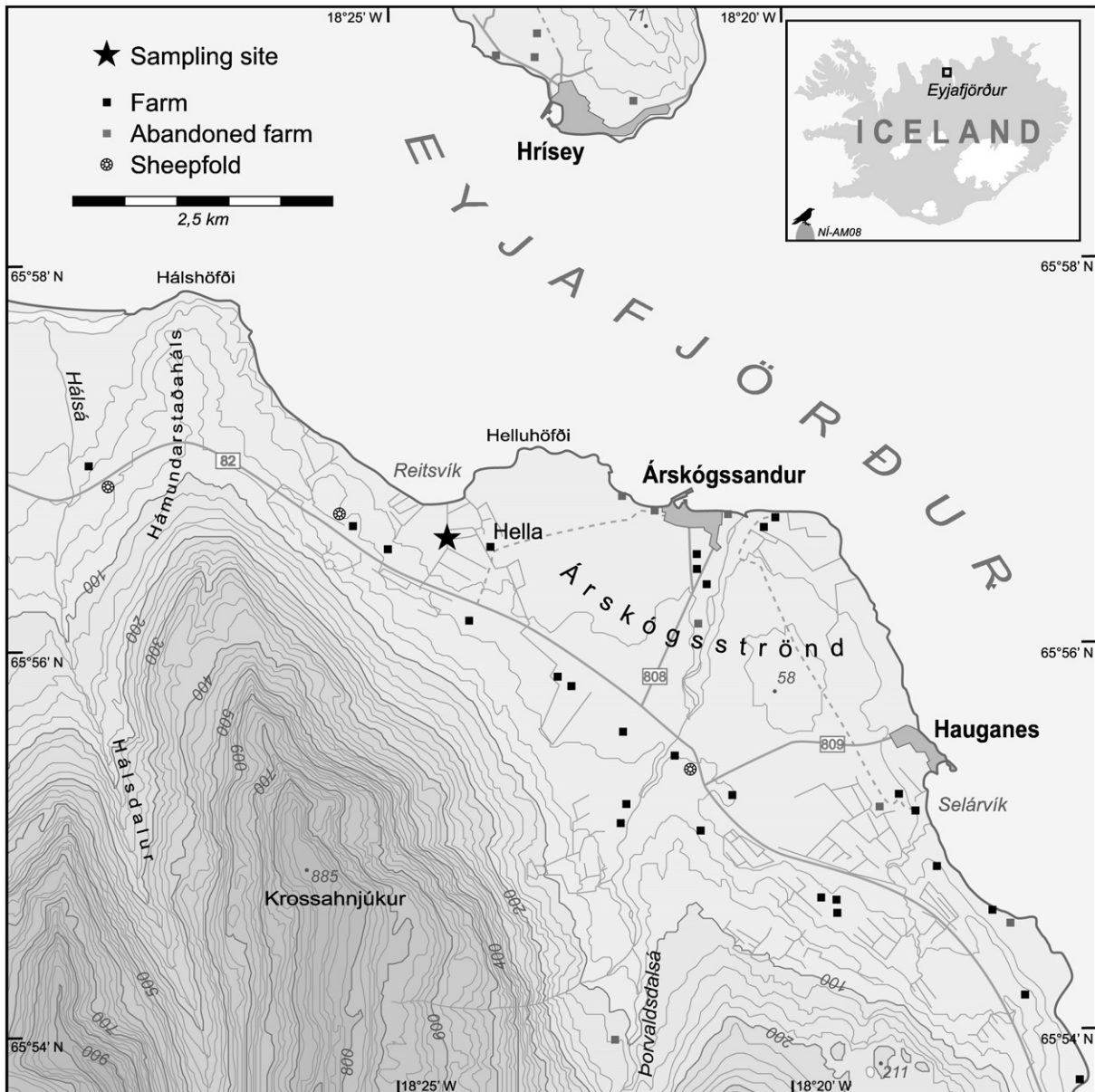


Fig. 1. Map of Iceland showing location of the sample site at Hella in Eyjafjörður, northern Iceland. Source: National Land Survey of Iceland.

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