Review of Palaeobotany and Palynology 181 (2012) 1–10

Contents lists available at SciVerse ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Research paper

Early Holocene hybridisation between *Betula pubescens* and *B. nana* in relation to birch vegetation in Southwest Iceland

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ARTICLE INFO

Article history:
Received 1 November 2011
Received in revised form 25 April 2012
Accepted 1 May 2012
Available online 10 May 2012

Keywords:
birch
Betula
Iceland
Holocene
hybridisation
pollen

ABSTRACT

The aims of the present research were to gain better insight into the early Holocene vegetation history of *Betula* in South Iceland and to investigate whether hybridisation between downy tree-birch (*Betula pubescens*) and dwarf birch (*Betula nana*) could be discovered in this region, similar to that previously found in North Iceland. A peat monolith spanning the period from about 10.3 to 7.6 cal ka BP from Eyvík, Southwest Iceland, provided 44 samples for pollen analysis. The samples were dated by known tephra layers, Saksunarvatn and Seydishólar tephras, and two ^{14}C datings. The macrofossil and spore/pollen results showed several progressive phases of vegetation development in the area until birch woodland became established around 9.5 cal ka BP. The timing of birch colonisation is in good agreement with results from other sites in Iceland. From these Eyvík samples, all morphologically normal *Betula* pollen grains were size-measured and abnormal pollen grains recorded. Species proportions within samples were estimated statistically on the basis of pollen size. As birch woodland in this area became established rather late, statistical analysis of *Betula* pollen size was only possible in the uppermost 18 samples, approximately spanning the period between 7.6 and 9.5 cal ka BP. The frequency distribution of pollen size indicated populations of *B. nana* predating those of *B. pubescens*. The proportion of *B. pubescens* pollen was oscillating but increased with time. In two samples at the top of the peat monolith, more than half of the measured *Betula* pollen grains belonged to *B. pubescens*. Evidence of hybridisation based on high frequencies of non-triporate *Betula* pollen was found in two samples dated at about 8.8 and 7.7 cal ka BP. Conditions appeared to be comparable to the corresponding hybridisation events previously reported for North Iceland, i.e. in warm periods when downy birch was expanding near dwarf birch habitats.

1. Introduction

Downy birch (*Betula pubescens* Ehrh., tetraploid with 2n = 4x = 56) has its main distribution in central and northern Europe (Atkinson, 1992), whereas dwarf birch (*Betula nana* L., diploid with 2n = 2x = 28) has a circumpolar distribution (de Groot et al., 1997). Distributions of the two species overlap in most of northern Europe and Iceland (Hultén and Fries, 1986). In the zones where the two species coexist, they cross-pollinate and produce triploid hybrids (Thórsson et al., 2001). Although the fertility of triploid hybrids is severely reduced, due to meiotic pairing abnormalities, the plants are not totally sterile and can produce viable diploid or tetraploid gametes (Ramsey and Schemske, 1998). This is the case with birch, as interpreted from crossing experiments (Anamthawat-Jónsson and Tómasson, 1990), and with birch in natural woodlands (Anamthawat-Jonsson and Thórsson, 2003). Triploids which produce viable gametes can facilitate gene flow between the parental species via back-crossing of the gametes — this is the most likely mechanism driving the bidirectional introgression observed between *B. pubescens* and *B. nana* in Iceland (Thórsson et al., 2007).

Birch is wind pollinated and produces ample quantities of pollen found in sediments and peat. The need to accurately differentiate pollen from different birch species, particularly when it is to be used for tracing different vegetation histories, past ecological and climatic requirements, has led to further research on the differences in pollen size and shape based on pollen from living plants (Mäkelä, 1996; Karlsdóttir et al., 2007). These studies showed not only that there is significant difference in the relative size of *Betula pubescens* and *Betula nana* pollen, but that triploid hybrids also have their own morphology that can be recognised and, more importantly, they produce large numbers of abnormal pollen grains (Karlsdóttir et al., 2008).

These results were utilised in our analysis of an early Holocene peat section from Hella in Eyjafjördur, mid-northern Iceland (Karlsdóttir et al., 2009). In the process of measuring *Betula* pollen from Hella, we found that type or age of the peat affected final pollen size. We therefore avoided comparison of pollen sizes between samples and focussed on

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doi:10.1016/j.revpalbo.2012.05.001

analysis of pollen size frequencies within each sample. Utilizing the methods of Bhattacharya (1967) and Járaí-Komlody (Prentice, 1981), we calculated an estimate for the proportion of pollen from each species in total *Betula* pollen within each sample and thereby obtained an overview of the ratios between birch species over time. The counting and classification of abnormal pollen grains showed peaks of interspecific hybridisation i.e. the presence of triploid hybrids. From the study of Hella peat section, we concluded that hybridisation was likely to have occurred when *Betula pubescens* was expanding its distribution in habitats where *Betula nana* had predominated. These results, even though strongly suggestive, were limited to a study representative of only one geographical region. We therefore repeated the procedure in the present study with a peat section from a different region covering roughly the same period as before, or the first few thousand years of the Holocene. We aim to answer questions regarding the history of birch in the area of study, its colonisation and the interaction of the two birch species. For the period covered by the present study, very little is known about vegetation history of this area as most studies to date are about regions in North Iceland. Of special interest to us is the question of hybridisation, and if we can see comparable indications to that in the North. Apart from the search for hybrid pollen, we compared periods of each species progression in order to find out if the timing would have been synchronous between North and South Iceland and also looked for comparable environmental factors associated with the dynamics of birch ecology and hybridisation. As far as our data allow, we try to link the birch pollen curve to known climatic variations of the period.

2. Materials and methods

2.1. Location

The sampling site was a pasture near the farm Eyvík in Southwest Iceland, at 64°03.3′ N, 20°41.6′ W and approximately 65 m asl (Fig. 1). A drainage ditch, which opens into a small river called Grjótá, had exposed a peat section and provided easy access to the peat stratigraphy. The landscape of the area is rather flat, with the exception of the low mountains of Hestfjall (322 m) and Vördufell (392 m) at a

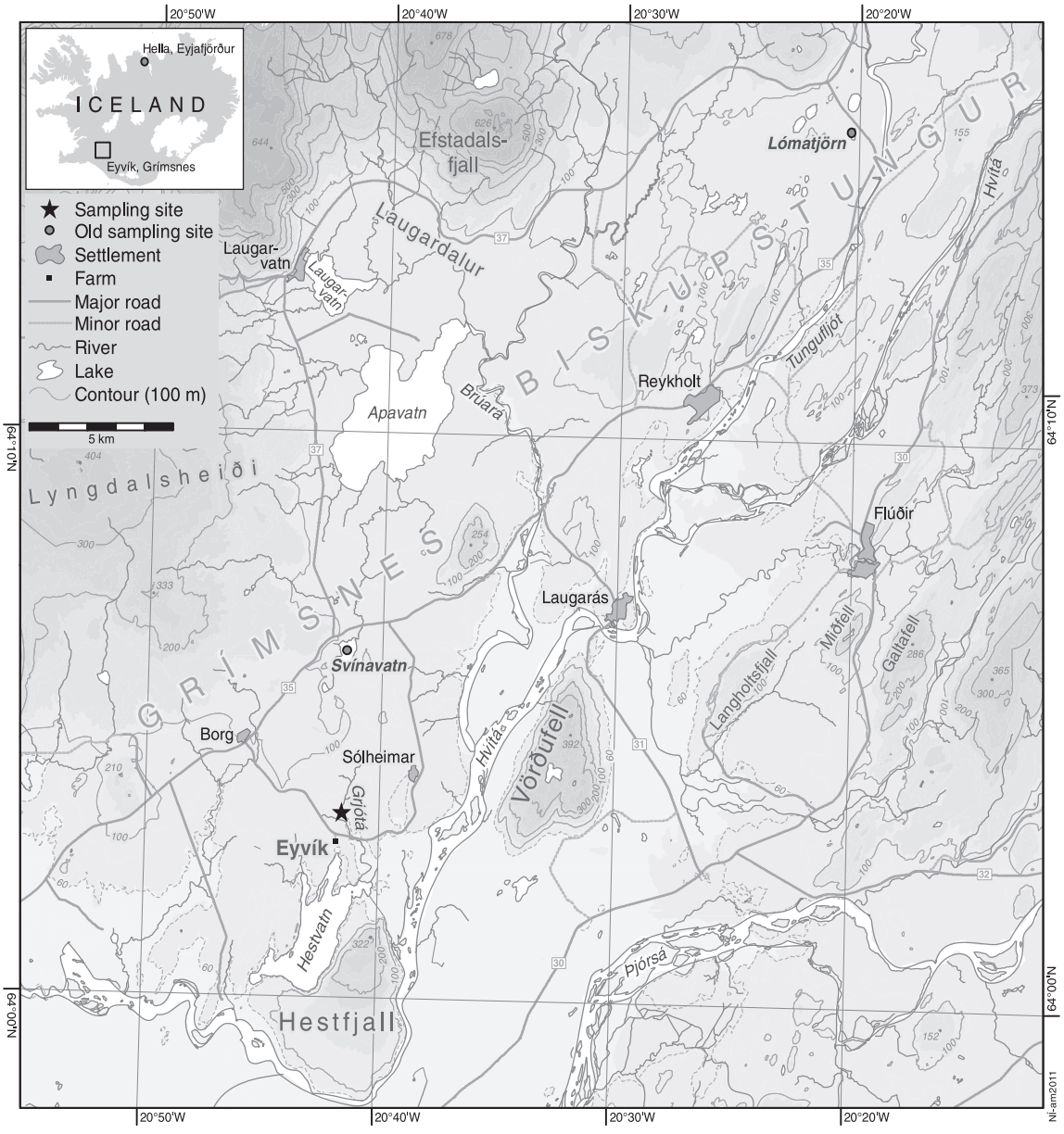

Fig. 1. Map of Iceland showing location of the sampling site at Eyvík (indicated with a star) in Grímsnes, Southwest Iceland. Source: National Land Survey of Iceland.