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Hybridisation, Introgression and Phylogeography of Icelandic Birch

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1. Introduction

Birch woodland is an integral component of the tundra biome, which covers expansive areas of the Arctic and amounts to 20% of Earth's land surface. Arctic tundra is located in the northern hemisphere, encircling the North Pole and extending south to the coniferous forests of the taiga. In geographical Europe, this includes, from east to west, northern Russia, Fennoscandia (northern Scandinavia and Finland), the Svalbard archipelago and Iceland, which is the main focus of the present paper. Tundra is the coldest of all of the terrestrial biomes and is noted for its frost-moulded landscapes, extremely low temperatures, little precipitation, poor nutrients and short growing seasons with long days (Reece *et al*. 2011). The low temperatures in the Arctic are, however, highly variable from one area to another, due to the influence of different oceanic currents. For example, the Irminger Current, which branches from the North Atlantic Current at about 26°W (Bersch *et al*. 1999), transports warm (4–6 °C) water around the coast of Iceland, making the climate in Iceland more temperate than its far north location would suggest.

Tundra vegetation is mostly herbaceous, consisting of a mixture of mosses and lichens, grasses and forbs, along with some dwarf shrubs and trees. The vegetation structure of tundra is simple, with low species diversity, and among the shrubs and trees, birch (*Betula* L.) is a dominant woodland plant (**Fig. 1**). There are no deep root systems in the vegetation of the Arctic tundra; however, a number of plant species are able to tolerate the cold climates. These plants are adapted to sweeping winds and soil disturbance, and can carry out photosynthesis at low temperatures and low light intensities. Plants are low-growing and group together, and thus can tolerate cold temperatures and are protected by snow during the winter. As the growing seasons are short, most of these plants reproduce more vegetatively than sexually by flowering. The plants, especially pioneering species, are generally wind-pollinated and have acquired an effective means of dispersal in the open landscape of the Arctic tundra. Birch has all of the above-mentioned characteristics, and in addition it can disperse effectively with its light, winged seeds.

Birches are pioneer tree species which, with their tiny wind-blown seeds, often rapidly colonize open areas, heathlands and marginal and disturbed habitats, such as forest clearings. Birches establish most effectively on bare soils; even in the lowest vegetation they



Fig. 1. *Betula pubescens* in the woodland Brekkuskógur, south-western Iceland, showing its typical shrub-like feature and autumn colour. The cold stream in the background originates from under a lava field. Photograph taken by KAJ.

grow very poorly (Kinnaird 1974; Aradóttir 1991), presumably due to the lack of affinity for any particular soil type, their ability to grow on nutrient-poor soils and their intolerance of shade. This pioneering birch establishment begins a process of succession which eventually converts the area into woodland, provided there is no outside intervention in the form of grazing or human activities. Birch was one of the first tree species to become established in northern Europe after the last Ice Age retreated. It is also one of the dominant woodland trees in the more extreme climate of the Arctic tundra. Birch migrated rapidly after the Last Glacial Maximum (LGM) from southern and central Europe and quickly colonized northern Europe (Bennett *et al.* 1991; Paus 1995; Willis *et al.* 2000). However, it was not until the beginning of the Holocene that birch pollen appeared in lake sediments and peat in Iceland (10.2–9.6 cal ka BP) and birch woodland only became established from about 8.5 cal ka BP (Hallsdóttir 1995; Karlsdóttir *et al*. 2009). Birch arrived in Greenland a few thousand years later (Fredskild 1991).

The first objective of this paper is to review palynological and molecular evidence supporting the postglacial origin of Icelandic birch and its phylogeographical patterns, both within Iceland and in relation to Europe. Most of the studies have been carried out in my research group (e.g. Karlsdóttir *et al*. 2009; Thórsson 2008; Thórsson *et al*. 2010). Aspects discussed in this paper include when and how birch came to colonize Iceland, the history of birch vegetation in Iceland after the first colonization, birch woodland expansion and regression through time, climatic and geographical structures that may influence woodland

viability, as well as genetic and evolutionary factors that may have played critical roles in shaping the birch woodlands seen today.

The birch species currently found in Iceland are extremely variable, both morphologically and genetically. My own work, together with that of my research group during the past twenty years, has shown that introgressive hybridisation (introgression and gene flow) is probably the most significant drive towards the present-day variability in Icelandic birch. The second objective of this paper is therefore to review all evidence supporting hybridisation and introgression in *Betula*, notably interspecific hybrids from crossing experiments (Anamthawat-Jónsson & Tómasson 1990 and 1999), a qualitative and quantitative assessment of morphological variation of birch in natural woodlands (Thórsson *et al*. 2001 and 2007), triploid birch hybrids (Anamthawat-Jónsson & Thórsson 2003; Anamthawat-Jónsson *et al*. 2010) and birch palynology and Holocene hybridisation (Karlsdóttir *et al*. 2007, 2008 and 2009). All of this evidence indicates that Iceland could be considered as a birch hybrid zone, harbouring genetic variation which is likely to be advantageous in the arctic and subarctic environments. The present review provides an insight into the introgression and phylogeography of Icelandic birch which should lead to a better understanding of *Betula* in its broader geographical range, together with the bio- and phylogeography of plant species on oceanic islands (especially in the North Atlantic region) and the vegetation ecology and biodiversity conservation of the tundra biome.

2. Birch (*Betula* L.)

Betula is a genus of about 35–50 species distributed throughout the temperate, boreal and arctic regions of the Northern Hemisphere. There is no consensus on species limits in *Betula*, with different authors differing widely in what species they accept, from under 30 species to over 60. This is believed to be due to the fact that birches hybridise freely both in cultivation and in nature, resulting in continuous variation in morphology among the species involved, and hence making species delineation difficult.

According to Flora Europeae, only four *Betula* species are recognized for Europe (Walters 1964): two tree birch species, i.e. *B. pendula* Roth (silver birch) and *B. pubescens* Ehrh. (downy birch), and two small shrub birch species, *B. humulis* Schrank (shrub birch of Central and Eastern Europe) and *B. nana* L. (dwarf arctic birch); however, numerous other species present in Europe are considered to be conspecific to the above-mentioned species or are treated as subspecies, geographical variants and hybrids. Flora of North America recognizes 18 mostly native species of North America and the neighbouring northern regions (Furlow 1997). North American birches are considered to belong to three groups: (1) the Costatae group that consists of large trees, often with dark bark, such as the valuable timber tree species *B. alleghaniensis* Britt., (2) the circumboreal Betula group that consists of small and medium-sized trees, often with white bark, such as the paper birch *B. papyrifera* Marsh., and (3) the Nanae group of dwarf shrubby birches of the cold circumpolar region, such as the American dwarf birch *B. glandulosa* Michx.

Flora of China (Li & Cheng 1979; Li & Skvortsov 1999), on the other hand, has estimated a total of 50–60 species in the genus *Betula*. The flora describes 32 mostly Asiatic species, 14 of which are considered endemic to China. The geographical range covered by this flora is both vast and diverse. For example, *B. ermanii* Chamisso, which is a highly valuable hardwood tree, can

be found from the tundra of Kamchatka Peninsula in the Russian Far East to Japan and Korea, and more inland into Mongolia. *Betula utilis* D. Don, a valuable timber tree of commercial importance commonly found in temperate broad-leaved forests at high altitudes (2500–3800 m), has its distribution range from Inner Mongolia north of China to Yunnan province in the south and over the Himalayan region of Afghanistan, Bhutan, India and Nepal. The distribution of *B. chinensis* Maximovicz, on the other hand, is more limited to the broad-leaved forests in mountain valleys and rocky mountain slopes in the northern part of China and Korea. This species is one of the most valuable timber trees in North China. *Betula alnoides* Buchanan-Hamilton ex D. Don, one of the tallest birch tree species, has its distribution in the subtropical forests that range from Central China to South Yunnan province and further south in the montane forests of Bhutan, Myanmar, Thailand and Vietnam. *Betula utilis* and *B. alnoides* are among the most ecologically important broad-leaved tree species along the Himalayan range (Zobel & Singh 1997; Gardner *et al*. 2000). Although some of the Asiatic species may not have justifiable species status, due to being conspecific, subspecies or hybrids, there are others that have yet to be discovered, especially those in remote and inaccessible areas. For example, *Betula fujianensis*, a new species from subtropical evergreen and deciduous mixed forest in south-eastern China, has just recently been described (Zeng *et al*. 2008).

Birch (*Betula*) is a genus of monoecious trees or shrubs – a plant produces separate male and female catkins. *Betula* differs from its closely related genus *Alnus* Miller (alder) mainly in that the female (fruiting) catkins of birch are usually cylindrical in shape and the seeds have 3-lobed scales and fall with the fruit, whereas the female catkins of alder are ovoid in shape, woody and do not disintegrate at maturity, opening to release the seeds in a similar manner to that of many conifer cones (Walters 1964; Furlow 1997). Birch trees are not long-lived, rarely exceeding 80 years old. Birch woods may have a very diverse invertebrate life as the trees can support over 300 different species of insects and mites (Atkinson 1992; de Groot *et al*. 1997). This in turn attracts a variety of birds. Birch also has a number of fungi associated with it, especially beneficial soil mycorrhizal fungi that help to make the birch plants healthier and more resistant to insect herbivory, both above and below ground (Enkhtuya *et al*. 2003; Oddsdóttir *et al.* 2010). Birch is clearly vital to the viability and productivity of the tundra and forest ecosystems.

Birch is both ecologically and economically important. As can be seen in **Fig. 2**, research on *Betula* during the past 5–6 years has mostly been in the area of ecology and silviculture (261/339 publications or 77%). Examples of ecological papers include birch community and ecosystem analysis (Kleczewski *et al*. 2010; Deslippe *et al*. 2011; Takahashi *et al*. 2011), regeneration, vegetation succession and human influence (Shrestha *et al*. 2007; Erlendsson & Edwards 2009; Schofield & Edwards 2011), impact of climate change on plant performance and productivity (Levanic & Eggertsson 2008; Pudas *et al*. 2008; Sano *et al*. 2010), modelling of plant structure, growth and phenology (Linkosalo *et al*. 2010; Caffarra *et al*. 2011; Lintunen *et al*. 2011), environmental pollution and chemical ecology (Kontunen-Soppela *et al*. 2010; Franiel & Babczynska 2011; Morales *et al*. 2011). Although the category ecology-physiology appears to be the most published subject, a good proportion of the studies have direct application in silviculture and forestry.

Research on silviculture involves all aspects of establishment, growth, regeneration, composition, viability and quality of forests to meet diverse needs and values. Birch wood is

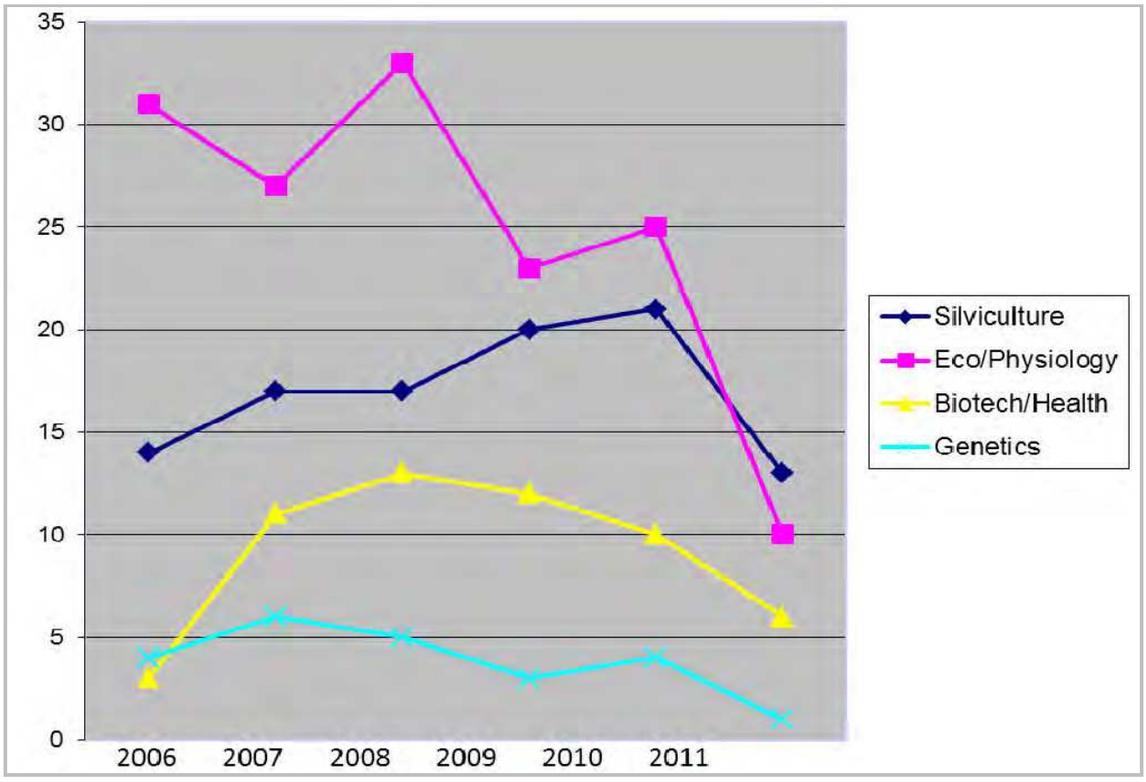


Fig. 2. Numbers and categories of publications revealed by a search in Web of Science using one keyword, Betula in Title, from 2006 to present. Note that 2011 is only up to September. The search found 339 publications, which were sorted manually into categories relevant to birch research after reading the content of the papers or the abstracts. Although the search is narrow, it shows a similar trend every year.

sought after for its fine quality, appearance, light colour, grain patterns, strength and durability. Birch is ranked among the highest quality timber for making furniture, in flooring and wall structure, and it also makes excellent plywood. There is great variation in the wood type and quality of different birch species, as there are diverse end-uses of birch wood. However, species that grow to medium- and large-sized trees (15–35 m in height) are the ones most used for commercial purposes. In Europe, silver birch (*B. pendula*) and downy birch (*B. pubescens*) probably produce the most valuable hardwood timber for the northern regions of Europe, including Scandinavia, Finland, Russia and the Baltic countries. Recent studies on these species include modelling and analysis of the growth and structure of forests and plantations (Hynynen *et al*. 2010; Kund *et al*. 2010; Lintunen *et al*. 2011); measuring and managing nutrient availability, retranslocation and fertilization (Mandre *et al*. 2010; Ruuhola *et al*. 2011); regeneration and seedling recruitment (Luostarinen *et al*. 2009; Sanz *et al*. 2011). In North America, paper birch (*B. papyrifera*), the medium-sized and fast-growing tree that forms pure stands or is otherwise found in mixed hardwood-conifer forests, is the most widely distributed birch species, especially in Canada. Its timber is used commercially for veneer, pulpwood and many speciality items. Recent studies on this birch are focused on timber quality in relation to tree growth, browsing, soil fertility and other factors (Droulin *et al*. 2010; Kleczewski *et al*. 2010; Belleville *et al*. 2011; Nielsen *et al*. 2011; Rea 2011). Asiatic and

subtropical birches, on the other hand, receive very little attention regarding silviculture, possibly due to the abundance and diversity of hardwood species that may be more valuable. Nevertheless, Asiatic species such as the northern species *B. ermanii* are important hardwoods for construction and furniture-making, and strong wooden tools can be made out of the Chinese species *B. chinensis*; however, research on silviculture of these species is still limited (Tabata *et al*. 2010). Furthermore, birch is one of several subtropical and tropical tree species that are now protected by local conservation laws and difficult access, for example the Himalayan birch *B. utilis* and the Southeast Asian birch *B. alnoides*.

Interestingly, 16% of publications on *Betula* during the past few years (**Fig. 2**) come under the category biotechnology and health. There are two main issues in this category. Firstly, extracts and glycosides from birch leaves, twigs and bark have been tested in biochemical, molecular and cellular experiments to show medicinal or pharmaceutical properties. For example, extracts from *B. pendula*, *B. pubescens* and *B. platyphylla* have shown anti-inflammatory effects, anti-proliferation of human cells and improved immune response *in vitro* (Freysdottir *et al*. 2011; Grundemann *et al*. 2011; Huh *et al*. 2011). A number of new biologically active compounds have recently been isolated, especially from Asiatic birch (Phan *et al*. 2011; Xiong *et al*. 2011). Secondly, birch pollen causes allergy. In northern latitudes, birch is considered to be the most important allergenic tree pollen, with an estimated 15–20% of hay fever sufferers sensitive to birch pollen grains. Modelling and prediction of the duration and intensity of birch flowering, measurement of pollen accumulation rates and the biochemical identification of pollen antigens are among the most recent studies on *Betula* (Kuopparmaa *et al*. 2009; Linkosalo *et al*. 2010; Erler *et al*. 2011).

On the other hand, publications on *Betula* genetics, phylogenetics, vegetation history, phylogeography, genecology and related fields are surprisingly limited (**Fig. 2**), even though birch is an ecologically and economically important plant. Research studies in this category are very diverse: from mapping the demographic variation of dwarf birch *B. nana* (Ejankowski 2010) and developing molecular markers for use in the breeding of tree-birch species such as *B. pendula* and *B. alnoides* (Guo *et al*. 2008; Jiang *et al.* 2011) to resolving phylogenetic relationships among *Betula* species using genome-wide markers, nuclear genes or DNA barcodes (Li *et al*. 2007; Schenk *et al*. 2008; Crautlein *et al*. 2011) and answering questions about the origin, hybridisation, introgression and phylogeography of a number of *Betula* species using molecular markers, botanical and statistical approaches, and macro- and microfossil evidence (Nagamitsu *et al*. 2006; Maliouchenko *et al*. 2007; Thórsson *et al*. 2007; Truong *et al*. 2007; Karlsdóttir *et al*. 2009; Anamthawat-Jónsson *et al*. 2010; Thórsson *et al*. 2010; Tsuda & Ide 2010). It is indeed our studies of *Betula* species from Iceland that have made a major contribution to a better understanding of birch hybridisation, introgression and phylogeography in general. The following sections in this review are therefore about the studies of Icelandic birch species.

3. Introgressive hybridisation as a major player in the maintenance of genetic variation in Icelandic birch

Two species of *Betula* co-exist in Iceland: the dwarf birch *B. nana* and the downy birch *B. pubescens* (Stefánsson 1901; Gröntved 1942; Löve & Löve 1956; Thórsson *et al*. 2001). *Betula nana* is a prostrate shrub up to one metre in height, whereas *B. pubescens* may grow up to

many metres tall. However, in Icelandic woodlands this tree birch species is often a shrub or low tree (**Fig. 1**). Both species are found together in most areas, although *B. pubescens* occupies lower elevations and a drier habitat compared with *B. nana*. In the forestry context, birch (i.e. *B. pubescens*) is the only tree-forming natural woodland in Iceland. Birch woodland in Iceland covers only about 1% of the total land area today, but birch is believed to have had an almost continuous distribution, covering most of Iceland's lowlands before the first settlement in the ninth century (Hallsdóttir 1995; Kristinsson 1995). During the last centuries, deforestation has been a continuous process, resulting in a highly fragmented distribution of birch populations.

Taxonomically, *B. nana* is represented by subspecies *nana* (Suk.) Hultén in Europe and western Asia, and by subspecies *exilis* (Suk.) Hultén in North America and central and eastern Asia (Hultén & Fries 1986). Only the subspecies *nana* is found in Iceland. *Betula pubescens* is a European species, represented by subspecies *pubescens* Ehrh., which may grow up to 25 m tall with single (monocormic) or many (polycormic) stems, and by subspecies *tortuosa* (Ledeb.) Nyman, which is a shrub or low tree found in the mountain regions of northern Europe (Walters 1964). The latter subspecies, so-called mountain birch, is believed to be the result of introgressive hybridisation with *B. nana* (Vaarama & Valanne 1973; Kallio *et al.* 1983); the same process that occurs with Icelandic birch (Anamthawat-Jónsson 1994 and 2003). In Iceland, *B. pubescens* tends to be in the form of 1–2 m low shrubs, especially in the regions with extreme oceanic climate and heavy coastal storms. Along the tree line in the mountains a zone of birch shrubs growing horizontally on the ground can be seen throughout the country. Due to the extensive and continuous morphological variation of birch in Iceland, the tree birch species is not divided into subspecies, but is treated in this review as *Betula pubescens* sensu lato.

Morphological variation in birch (*Betula*) is known to be extensive, due in part to frequent hybridisation in this genus (Woodworth 1929; Johnsson 1945; Walters 1964; Furlow 1997). This has made taxonomy of *Betula* problematic. Because of the difficulty in delineating species, morphological criteria for identifying interspecific hybridisation or hybrids can be extremely ambiguous. In the areas where the distribution of birch species overlaps, plants with intermediate morphology (presumed hybrids) have frequently been noted (reviewed in Atkinson 1992). Some of these putative hybrids have turned out to be part of the large range of variability within species. But hybrids between species with different ploidy levels can be confirmed cytogenetically. Such is the case with birch hybrids found in Iceland. Hybridisation between diploid *B. nana* and tetraploid *B. pubescens* produces triploid hybrids and this can be unequivocally confirmed by counting the chromosomes in somatic metaphase cells of the plants (**Fig. 3**). Triploid chromosome number has been confirmed among hybrids between *B. nana* and *B. pubescens* in crosses (Anamthawat-Jónsson & Tómasson 1990 and 1999) and among plants in natural woodlands (Thórsson *et al.* 2001 and 2007).

Triploid chromosome number indicating natural hybridisation between diploid and tetraploid birch species in Europe has been reported, but most of the plants are thought to be putative hybrids between silver birch (diploid *B. pendula*) and the tetraploid *B. pubescens* (Brown *et al.* 1982; Brown & William 1984). Natural triploid hybrids between *B. nana* and *B. pubescens* might have been among the plants with intermediate morphology found in Scotland (Kenworthy *et al.* 1972) and Fennoscandia (M. Sulkinoja, pers. comm.), but there was no cytogenetic confirmation. Birch chromosomes are extremely small and numerous,

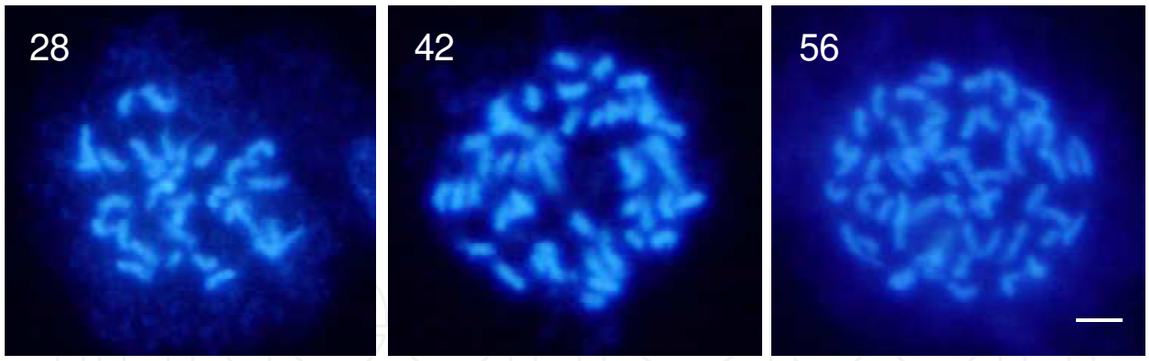


Fig. 3. Chromosome number of diploid Betula nana (2n = 2x = 28), triploid hybrid (2n = 3x = 42) and tetraploid B. pubescens (2n = 4x = 56). The chromosomes were isolated from leaf buds by Æ. Th. Thórsson, following the protocol of Anamthawat-Jónsson (2004), and stained with the fluorochrome DAPI. Scale bar represents 2 µm.

thus there is often uncertainty in counts from individual cells. Metaphase chromosomes of *B. pendula* (diploid) and four American tetraploid birch species are only 0.6–1.8 µm long (Taper & Grant 1973). Most of the *B. pubescens* chromosomes are less than one µm long (Anamthawat-Jónsson & Heslop-Harrison 1995). Birch genomes are also very small. Our recent investigation of Icelandic birch species (Anamthawat-Jónsson *et al*. 2010) shows that the average 1C genome size of the tetraploid *B. pubescens* (882 Mbp, 0.90 pg) is about twice the size of the genome of the diploid species *B. nana* (448 Mbp, 0.46 pg), while the triploid group has an average size of 666 Mbp (0.68 pg), which is mid-way between the two species. For comparison, the genome size of a diploid (2n = 2x = 14) barley *Hordeum vulgare* is 5.55 pg and that of a hexaploid (2n = 6x = 42) wheat *Triticum aestivum* is 17.33 pg (Bennett & Smith 1976). The latest compilation of angiosperm genome sizes (Bennett & Leitch 2011) includes new record holders for the smallest (1C = 0.0648 pg in *Genlisea margaretae*) and largest (1C = 152.23 pg in *Paris japonica*) genome sizes so far reported.

As stated previously, birch chromosomes are numerous and minute. Furthermore, the conventional squash method of root-tip chromosome preparation is often ineffective because rooting of birch is very difficult. But by using the protoplast dropping method of chromosome preparation developed for *Betula* (Anamthawat-Jónsson 2004), it is possible to obtain high-quality metaphases from young leaf buds collected in the field at any time of the growing season. This has made chromosome counting accurate and cytogenetic investigation of birches at a population level possible.

By having the means to accurately identify triploidy among birch plants in the field, we are able to investigate the occurrence of natural hybrids in Iceland where two birch species, *B. nana* and *B. pubescens*, coexist and the growing season is short enough for their flowering to be relatively synchronous. Hybridisation is known to be an important factor that influences evolution in a variety of ways (Barton 2001); for example many plant species have a hybrid ancestry (Rieseberg 1997; Rieseberg & Willis 2007), including *Betula* (Nagamitzu *et al.* 2006). The most common form of hybrid speciation is probably allopolyploidy, whereby interspecific or intergeneric hybridisation gives rise to new species following chromosome doubling and reproductive isolation from the parental species. Natural hybridisation can also lead to gene flow between species through backcrossing of the hybrid with its parental

species; this process is known as hybrid introgression, introgressive hybridisation, or simply introgression (Heiser 1973). Such is the case with birch hybridisation described in this review. Only a few partially fertile hybrids are sufficient for introgression to occur, and therefore these hybrids may not have been detected. Introgressive hybridisation allows for the transfer of neutral or adaptive traits from one species to another and can increase genetic polymorphism in one or both parental species, but it may have a negative outcome, such as an evolution of aggressive weeds, or result in the extinction of a species. Numerous cases of introgressive hybridisation have been documented, including plants in natural habitats and under cultivation (e.g. Arnold 1992; Ellstrand *et al*. 1999; Jarvis & Hodgkins 1999; Minder & Widmer 2008).

Introgression in birch was examined originally using morphological characters, in particular introgression between *B. nana* and *B. pubescens* in Iceland, northern Scandinavia and Greenland (e.g. Elkington 1968; Vaarama & Valanne 1973; Sulkinoja 1990). Most studies described introgressive modification of the tree-birch species as a distinct type, which became recognized as mountain birch (*Betula pubescens* ssp. *tortuosa*). But our studies using botanical, cytogenetic and molecular approaches revealed that the introgression in birch is bi-directional, resulting in gene flow between the two species via triploid interspecific hybrids (Anamthawat-Jónsson & Thórsson 2003; Thórsson *et al*. 2001, 2007 and 2010). Such gene flow is likely to be an important mechanism in maintaining genetic variation in both species.

We have examined the morphological variation systematically; the results are summarized here in **Fig. 4** (modified from Thórsson *et al*. 2007). The study includes more than 400 birch plants, randomly chosen regardless of morphology, from all major birch woodlands in Iceland. Chromosome counts from mitotic metaphases of all individuals under study produce three unambiguous groups of birch: diploid (2n = 2x = 28), triploid (2n = 3x = 42) and tetraploid (2n = 4x = 56). Of the 461 plants examined, 176 plants (38.2%) are diploid, 241 plants (52.3%) are tetraploid and 44 plants (9.5%) are triploid hybrids. The three ploidy groups are confirmed by genome size analysis on a subset of samples based on flow cytometry and DNA densitometry (Anamthawat-Jónsson *et al*. 2010). No aneuploid was found. Aneuploids have never been found among birch plants in nature, or from crosses. Triploid hybrids between *B. nana* and *B. pubescens* were backcrossed using *B. pubescens* as pollen donor – only triploids and tetraploids were discovered among the backcrossed progeny (Anamthawat-Jónsson & Tómasson 1990 and 1999). I therefore hypothesized that viable gametes produced by the triploid plants, although in extremely low frequencies, must have been "euploid" gametes with n = 14 or 28, most probably derived via a meiotic non-disjunction.

By looking at the plant morphology, i.e. analysing species-specific botanical characters, we can separate the diploid and the tetraploid groups most of the time (**Fig. 4**). The diploid group consists mostly of dwarf birch *B. nana*, whereas the tetraploid group predominantly includes *B. pubescens*-like plants. The triploid plants, most interestingly, resemble *B. nana* or show intermediate morphology. They rarely resemble *B. pubescens*. Morphological characters, especially in the leaf shape, are useful for species identification as they are relatively independent of environmental changes. Leaves of *B. pubescens* have been taxonomically described as being cordate with dentate margins, whereas *B. nana* leaves are orbicular with crenate margins. In order to define morphological variation within and across the species, a set of species-specific characters that can be visually scored has been

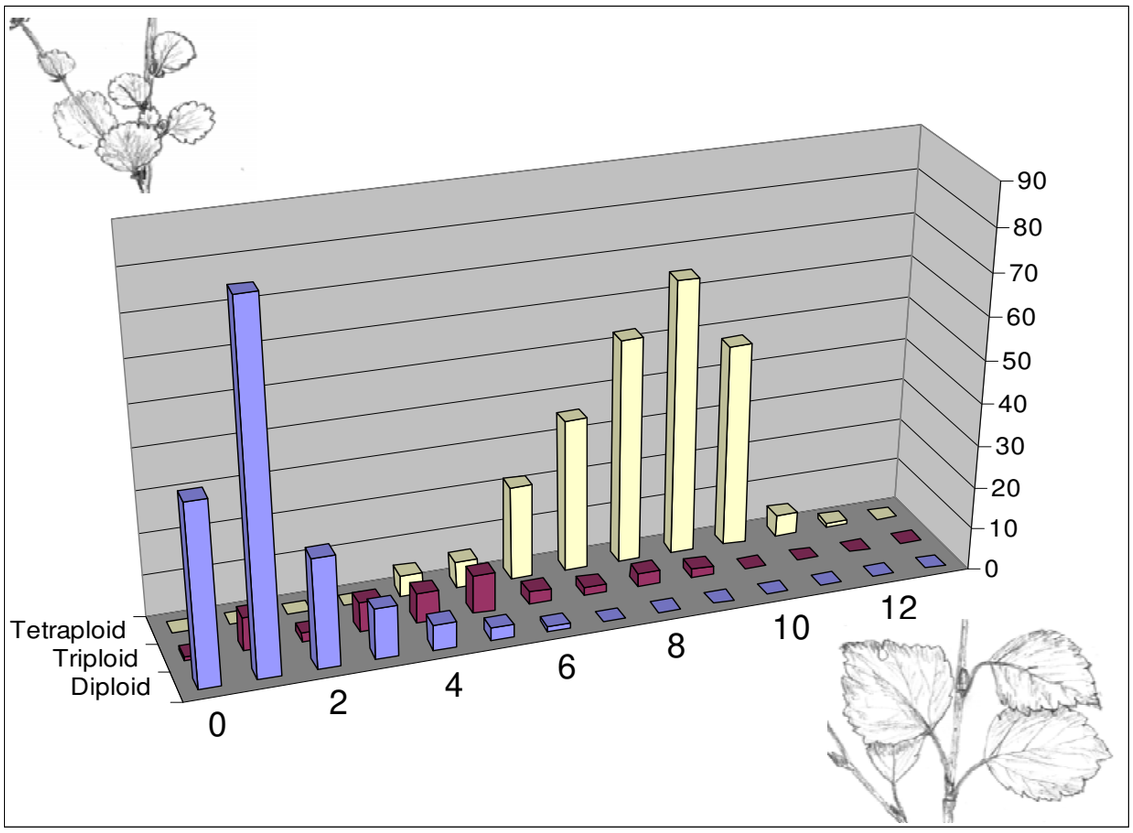


Fig. 4. Morphological distribution of 461 birch plants from 14 major woodlands throughout Iceland (modified from Thórsson 2008). Drawings by K. Anamthawat-Jónsson show a typical *Betula nana* plant (upper left corner) and *B. pubescens* (lower right corner). X-axis: Morphology indices from 0 (*B. nana*) to 13 (*B. pubescens*) based on species-specific botanical characters (see text). Y-axis: Number of plants belonging to each group by morphology index. The diploid, triploid and tetraploid groups had average scores of 1.3, 4.1 and 8.3 respectively. Introgression in Icelandic birch is evidently bi-directional.

developed, based on botanical characteristics (Clapham *et al*. 1962; Elkington 1968; Kenworthy *et al*. 1972), and was used in this study. The growth form and habit can be assessed in the field, but the leaf characters are usually scored from 30 randomly collected leaves per plant. Leaf shape characters are highly uniform within plants. The scores have been assigned to place *B. nana* at the lowest ranks (zero) and *B. pubescens* at the highest (13) as follows: shrub (0) or tree (1); growth habit procumbent (0) or erect (1); petiole sessile (0), intermediate (1) or non-sessile (2); leaf tip obtuse (0), sub-acute (1) or acute (2); leaf base rounded (0), cordate (1) or cuneate (2); leaf margin crenate (0), serrate (1) or dentate (2); leaf shape orbicular (0), obovate (1), or ovate (2); and leaf teeth single (0) or multiple (1). For each plant, the scores of all characters are combined into a single value called a morphology index, and this was plotted against ploidy of the plants.

Based on the qualitative analysis of species-specific characters (**Fig. 4**), diploid and tetraploid plants form separate peaks of morphology index distribution, representing *B. nana* and *B. pubescens* respectively. The *B. nana* peak includes the scores from 0 to 6 (average

score 1.3). About 80% of diploid plants fall within the narrower morphology index range of 0–1 and only 23% of these have the minimum score zero, which is taxonomically equivalent to being pure *B. nana*. The scores 2–6 extend into the intermediate region of the total distribution, meaning that about 20% of the diploid plants look more like hybrids and much less like *B. nana*. At the high end of the morphology index, a broader peak of 4–12 scores (average 8.3) belongs to the tetraploid group, the *B. pubescens* group. About 83% of the tetraploid plants have most of the *B. pubescens* morphology (scores 7–10); about 15% are hybrid-like (scores 4–6) and could be mistaken for triploid birch; and only some 2% score higher than 10. Taxonomically, the maximum score for *B. pubescens* should be 13, but none of our tetraploid plants have this morphology. In other words, we have not found pure *B. pubescens* in natural birch woodlands in Iceland so far. Only one *B. pubescens* individual (out of 241 tetraploid plants) has a score of 12. Based on the average score of 8.3, most of the Icelandic tetraploid birch plants looked more like hybrids and much less like the typical European *B. pubescens*. And if we look at plants with intermediate morphology, with a score of 4 in particular, the plant can be diploid, triploid or tetraploid. Introgressive hybridisation is obviously evident among Icelandic birches.

The species-specific botanical characters of this group of 461 plants have also been measured quantitatively (Thórsson *et al*. 2007; Thórsson 2008), using the leaf morphology analysis program WinFolia (Regent Instruments, Quebec, Canada). Multivariate analysis of variance (MANOVA) was used to test the differentiation among ploidy groups and among sites within each group, whereas the linear discriminant analysis (LDA) was conducted to evaluate how the variables can be used to classify the different individuals. The principle of both methods is based on a linear combination of variables that maximizes the ratio of between-groups variance to within-groups variance (Quinn & Keough 2002). The homogeneity of variances of each variable was tested with the Bartlett test (Sokal & Rohlf 1995). The overall results strongly support the introgression study based on the morphology index described above. The linear discriminant analysis reveals significant separation among the three ploidy groups and the model assigned 96% and 97% of the *B. nana* and *B. pubescens* individuals correctly. The triploid hybrids are difficult to predict since only half of them could be assigned correctly. Among the species-specific leaf characters, leaf length is the most useful variable for identifying triploid hybrids.

Most interestingly, there is a clear indication of geographical structure among the woodlands investigated when the ploidy groups were analysed separately. The multivariate data analysis (Thórsson 2008) reveals geographical patterns within the ploidy groups, which could partly be explained by differences in mean July temperature. In the woodlands where summer is cold (often associated with glacial sites or the interior highlands), the leaf morphology in all ploidy groups tends to be closer to the minimum LDA values and has a low morphology index. On the other hand, the woodlands in lowland areas tend to have morphology closer to the maximum LDA values with a high morphology index. Shrub-like birch with intermediate or hybrid-like morphology is also known to be common in regions characterized by cold climates, such as Fennoscandia, the highland areas of Scandinavia, other mountain regions of Europe, and southern Greenland (e.g. Kallio *et al.* 1983; Gardiner 1984; Sulkinoja 1990; Jetlund 1994). In the northern part of the Urals and Western Siberia, in the region of forest tundra-taiga, changes in leaf parameters in *B. pubescens* including shape and complexity were found to correlate with climatic conditions such as long-term average

temperatures (Migalina *et al.* 2010); this may have physiological advantages, especially in photosynthesis. Such morphological differentiation is likely to be driven by the introgressive hybridisation process, if the introgressant types are more adaptable (or more tolerant) to environmental pressure and habitats such as those found in Iceland and elsewhere in the subarctic regions. This introgressed birch can have certain advantages: for example the ability to spread vegetatively and form a large multicormic shrub could ensure survival of the plant in extreme environments. A molecular study on alpine sedge has shown that genotype integrity is maintained in optimal habitats, whereas introgressed individuals are favoured in marginal habitats (Choler *et al*. 2004). Our future work on birch introgression will most likely be in the area of experimental genecology.

4. Introgression, origin and molecular phylogeography of Icelandic birch

Introgressive hybridisation has been shown to be associated with demographic history of the species. For tree and woody species, a number of molecular studies have revealed dynamic patterns of demographic history in relation to the glacial histories of Europe, Asia and North America, as well as in the arctic–alpine regions (Taberlet *et al.* 1998; Petit *et al*. 2002; Skrede *et al*. 2006; Alsos *et al*. 2007; Fussi *et al*. 2010; Tsuda & Ide 2010; Seiki *et al*. 2011). These studies infer changes, including population expansion, plant migration and hybridisation, which lead either to allopolyploid speciation or introgression.

Icelandic birch samples from the morphological introgression study described above have been analysed molecularly, together with new samples collected in northern Scandinavia, Scotland and Greenland, amounting to 463 birch plants/trees in total (Thórsson 2008; Thórsson *et al*. 2010). The objective was to find direct genetic evidence supporting introgressive hybridisation between tetraploid tree birch (*Betula pubescens*) and diploid dwarf birch (*B. nana*) via triploid hybrids, and to investigate an association between the introgression and phylogeographical distribution of Icelandic birch. No genetic data was available on the origin and phylogeography of *Betula* in Iceland. In our study, chloroplast (cp) DNA haplotypes across different ploidy groups in two species of Icelandic birch were examined and the results were analysed in an attempt to relate the extent of introgression to the historical and current geographical distribution. Individual plants were first classified by their ploidy status after direct chromosome counting, according to the chromosome isolation protocol of Anamthawat-Jónsson (2004). The haplotypes were identified using the polymerase chain reaction-restriction fragment length polymorphism (PCR-RFLP) universal primers for non-coding regions of plant chloroplast genomes from Taberlet *et al.* (1991) and Demesure *et al.* (1995), following the protocol modified from Palmé *et al.* (2004). The geographical distribution of the haplotypes obtained was mapped, and subsequently the haplotype variation and introgression ratios (*IG)* were analysed statistically.

Thirteen haplotypes have been identified among 345 Icelandic samples (**Fig. 5**), along with five haplotypes from 118 samples from outside Iceland including three haplotypes shared with the Icelandic set of samples. These three are also the most common haplotypes in Iceland, with haplotypes T, C and A found in 49%, 19% and 15% of the plants respectively. Haplotypes D and F are represented by 4–6% of the plants, whereas other haplotypes (eight in total) are considered rare (less than 2%). All common haplotypes are shared between the triploid group and the parental species (**Fig. 5**), clearly indicating introgressive hybridisation.

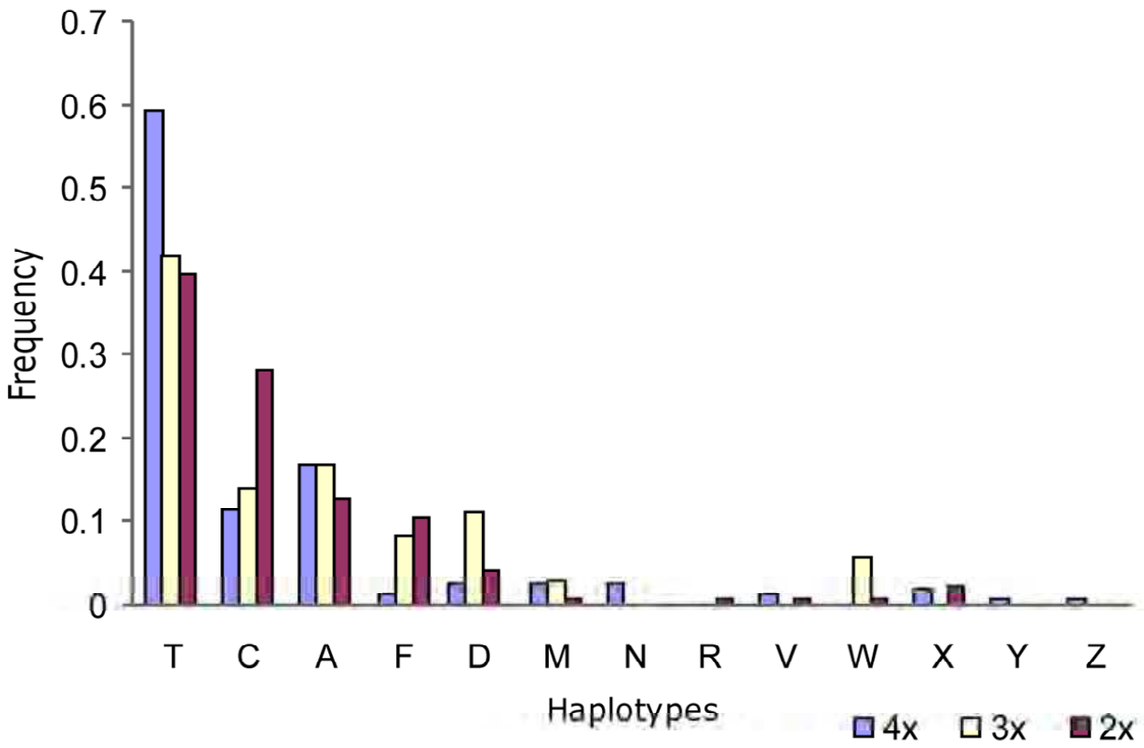


Fig. 5. Frequencies of chloroplast PCR-RFLP cp-DNA haplotypes in birch from three ploidy groups in Iceland (modified from Thórsson 2008): tetraploid (4x) *Betula pubescens*, diploid (2x) *B. nana* and triploid (3x) hybrid between the two birch species.

Introgressive hybridisation, as shown by the extensive sharing of common haplotypes across ploidy groups (**Fig. 5**), is supported by the statistical analysis of *IG* indices and the variation components. In this study, the observed and expected introgression ratios (*IG* and IG^e respectively) were calculated according to Belahbib *et al.* (2001), whereby *IG* reflects the amount of locally shared (within site) haplotypes between two species and IG^e represents the expected value if the haplotype sharing is not geographically structured. As gene flow among sites may be extensive, a modified ratio *IG** was also applied to contrast a species within a site with the other species pooled over all localities. Furthermore, modified ratios *IGR* and *IGR** (Palmé *et al.* 2004) were applied to this data set in an attempt to distinguish recent introgression from ancestral polymorphism (shared polymorphisms due to incomplete lineage sorting), although not as quantitatively. The results are as follows (see numerical results in Thórsson *et al.* 2010): (**1**) There is significant introgression in the Icelandic birch populations, which supports the haplotype sharing observed here and the morphological analysis described in the previous section. (**2**) There is indeed a geographical structure of introgression, for example the populations that are least introgressed are those woodlands in which summers are cold and often associated with glacial sites or the interior highlands, whereas the woodlands in optimal climatic environments harbour a great deal of gene flow. (**3**) The population differentiation appears to be more pronounced in *B. nana* than in *B. pubescens* with regard to introgression. (**4**) The overall introgression index for Iceland (all woodlands together) is nearly twice as large as the value for northern Scandinavia.

When the statistical analysis of *IG* indices and the dissection of haplotype variation components are combined, considerable differences are found to exist among samples in Iceland, shaped by isolation by distance and local introgression.

An east-west phylogeographical distribution in Iceland can be deduced from this molecular study. The overall geographical distribution of haplotypes in Iceland (see illustrations in Thórsson 2008) shows that the T haplotype (the most common haplotype, with 49% occurrence) is present in all woodlands examined, and often in all three ploidy groups. This haplotype is also prevalent in northern Scandinavia, where it is apparently associated with *B. nana*. Therefore the T haplotype might have been distributed over all woodlands and across ploidy groups via introgression and hybridisation. On the other hand, the distribution of all other haplotypes in Iceland is found to be associated with the geographical location of woodlands, i.e. forming an east-west separation pattern. Haplotype A (15% land occurrence) occurs mainly in western Iceland, especially in the north-west fjords where it is recorded at high frequency and in all ploidy groups. This haplotype is significantly correlated with longitudes. It is also a common haplotype among tree-birch species in Europe (Palmé *et al*. 2004) and is confirmed in the present study. Two rare haplotypes unique to Iceland (M and N) are found mainly in the western coastal woodlands. On the other hand, a greater diversity of haplotypes is observed from the eastern and north-eastern woodlands. Haplotype C (19% land occurrence, the second most common haplotype in Iceland after T), which also exists in all ploidy groups, is a dominant haplotype of the eastern woodlands. Interestingly, this is the most common birch haplotype in Europe (Palmé *et al*. 2004) and is also the most common haplotype among birch samples we collected from Northern Scandinavia and Scotland, yet it is essentially absent from Greenland. Of the ten haplotypes unique to Iceland, eight of them, including haplotypes D and F (4–6% occurrence) together with all other rare haplotypes, occur almost exclusively in the eastern sites. The higher number of rare haplotypes in the east could indicate that the eastern (and north-eastern) populations are more ancient in origin than the western (and south-western) woodlands. The east-west separation of haplotypes is also reflected clearly in the statistical analysis of phylogenetic association among haplotypes discovered in Iceland (Thórsson *et al*. 2010). The observed east-west haplotype distribution within Iceland may indicate different population histories or multiple origins of Icelandic birch.

Present-day birch in Iceland is most probably post-glacial in origin, i.e. having colonized Iceland in the early Holocene. The first colonization of Holocene birch is believed to have occurred in the north and north-eastern valleys and this is thought to be the result of different deglaciation patterns in that area, together with early-Holocene warming in northern Iceland. The Holocene vegetation history constructed from pollen records from lake sediments and macroscopic remains in peat (Hallsdóttir 1995; Hallsdóttir & Caseldine 2005) supports the hypothesis that birch woodland (dominated by the tree-birch species *B. pubescens*) started to form in the north-eastern valleys of Skagafjördur and Eyjafjördur in the Late Boreal and progressed into the western fjords and southern Iceland towards the end of the Atlantic period. We measured *Betula* pollen from an early Holocene peat profile from Hella in Eyjafjördur, mid-northern Iceland, with 39 samples taken at ca. 100-year intervals between ca. 10.3 and 7.0 cal ka BP based on known tephra layers, including the Saksunarvatn tephra at 10.2 cal ka BP (Karlsdóttir *et al*. 2009). The study shows two periods with large quantities of *B. pubescens* pollen (i.e. birch woodland expansion): the earlier

period from approximately 9.3 to 8.3 cal ka BP and the later from approximately 7.3 cal ka BP to the end of the profile, with a peak at 7.2 cal ka BP. The early onset of vegetation development in northern Iceland is thought to be the result of different deglaciation patterns in that area (Norddahl 1991), together with early-Holocene warming in northern Iceland (Rundgren 1998; Caseldine *et al.* 2006). The Holocene Thermal Maximum (HTM) in terrestrial Iceland has been estimated between 10.3 and 5.6 cal ka BP (Kaufman *et al*. 2004) and the peak may have been about 7.1 cal ka BP, with the summer temperatures almost 1.5 °C above the averages of the 20th century (Wastl *et al*. 2001). The early Holocene peaks of *B. pubescens* pollen in northern Iceland, as represented by the Hella peat profile (Karlsdóttir *et al*. 2009), coincide with warming periods of the Boreal based on the Greenland ice-core project (Bond *et al*. 1997).

Our molecular studies seem to indicate that birch – particularly *B. pubescens* – colonized Iceland more than once during the early Holocene. The east-west separation of cpDNA haplotypes described above is so far the strongest indication of multiple origins in Icelandic birch. The higher number of rare haplotypes in the east could indicate that the eastern (and north-eastern) populations are more ancient in origin than the western (and south-western) woodlands. The two common haplotypes, i.e. A (west) and C (east), have clearly not crossed the geological boundary which includes the central highland and glaciers. The T haplotype, on the other hand, is distributed all over Iceland, which may be explained if this haplotype was *B. nana*-specific in the first place. *Betula nana* is an arctic-alpine species that colonized Iceland long before *B. pubescens* (Hallsdóttir 1995; Rundgren 1998), while new pollen records (L. Karlsdóttir, unpublished) indicate that *B. nana* established itself as early in the north (north-east) as in the south (south-west). Chloroplast genes, which are maternally inherited, could easily be transferred across species via hybrids, as *B. nana* is known to be a predominant seed parent in such hybridisation (Eriksson & Jonsson 1986; Anamthawat-Jónsson & Tómasson 1999).

Our current and ongoing work uses bi-parentally inherited nuclear DNA markers to further resolve the phylogeographical pattern of birch in Iceland. Tsuda & Ida (2010) found north-south separation of chloroplast DNA variation in *Betula maximowicziana* endemic to Japan, whereas the analysis using microsatellite (SSR) nuclear markers on this birch (Tsuda & Ide 2005) revealed dispersal by pollen across the boundary, at least in one direction. Genome-wide nuclear markers offer excellent within-species resolution, and are hence useful for dissecting genetic variation due to founder effects, genetic drift, bottleneck effects, gene flow and other evolutionary forces. Amplified fragment length polymorphic (AFLP) genome-wide markers have been used successfully to identify glacial survival of two west-arctic species, while the sequencing of non-coding regions of chloroplast DNA revealed only limited variation (Westergaard *et al*. 2011a).

The unique feature of our *Betula* research is that we have karyotyped plants in natural woodlands, meaning that our continuing molecular studies, for example using nuclear markers, can also answer specific questions about hybridisation and introgression. Once correlated to present-day and past biogeography, it will be possible to predict future changes due to human influences and global warming. We have already found evidence of hybridisation between *B. nana* and *B. pubescens* in Iceland as early as the first woodland establishment in the early Holocene (**Fig. 6**; Karlsdóttir *et al*. 2009), by using morphometric

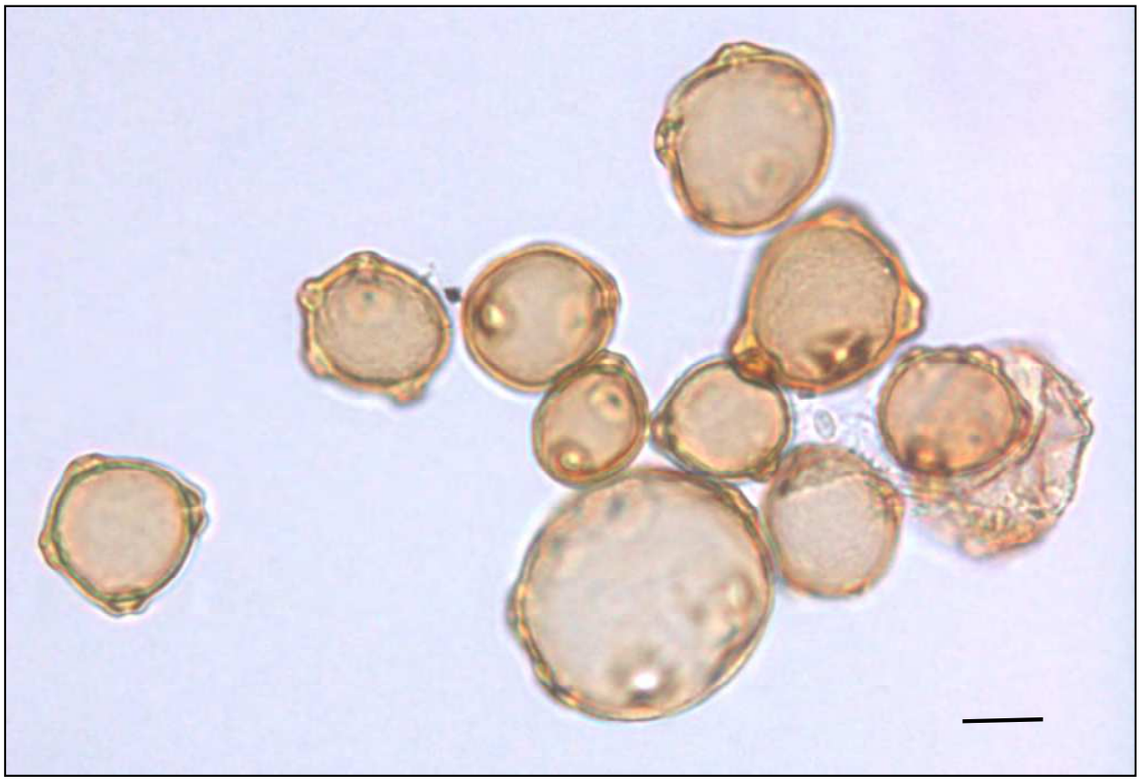


Fig. 6. Examples of pollen grains produced by triploid *Betula* hybrids (scale bar represents 10 μm). Triploid hybrids produce pollen with distinctive characteristics which may be used to detect hybridisation in sub-fossil samples. Several anomalies in pollen morphology, especially an unusual number of pores (4 or more), are significantly more frequent in pollen samples from triploid hybrids than from diploid and tetraploid species.

standards of pollen measurements obtained from karyotyped present-day birch plants. The frequency of non-triporate pollen (the strongest evidence of hybridisation) in the period between 9.2 and 8.7 cal ka BP, during the first birch woodland establishment in the north of Iceland, 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 birch woodlands in warm periods.

One of the most important questions to us is where the Icelandic birch came from, and how. Our study of cpDNA variation (Thórsson *et al*. 2010) indicates that Icelandic birch is most likely European in origin and had colonized Iceland in the early Holocene. All three most common haplotypes found in Iceland (T, C and A haplotypes) are widespread in Europe (Palmé *et al.* 2004). Microsatellite data of Maliouchenko *et al*. (2007) also supports this similarity. Our study shows further that these cpDNA haplotypes are not prevalent at all sites investigated. Haplotype T, the most common haplotype in Iceland, dominates the northern Scandinavian sites and seems to be associated with *B. nana*, as suggested earlier in this section. Haplotype C (Icelandic eastern haplotype) is also found in Sweden and Scotland but is absent from Greenland. This haplotype is the most common and probably the oldest haplotype of birch in Europe, occurring in all three *Betula* species (i.e. *B. pendula*, *B. pubescens* and *B. nana*), and is most prevalent on the European mainland (Palmé *et al.*

2004). On the other hand, the A haplotype, which is prevalent among the western Icelandic populations, is also detected in birch samples from Greenland, Scotland and Scandinavia. It is the second most common haplotype of birch in Europe, occurring essentially in the tree-birch species, *B. pendula* and *B. pubescens*, and mainly in the western part of Europe, including the British Isles and Scandinavia (Palmé *et al.* 2004).

The most likely scenario could be that the first birch colonization (*B. nana* in particular) in the north and north-eastern part of Iceland came from Western Europe, and perhaps Scandinavia, to Iceland and eastern Greenland via the North Atlantic current. This is thought to be the most probable means of biota dispersal during the early Holocene (Buckland *et al.*, 1981). Bennike *et al.* (1999) carbon-dated plant and animal remains in sediments from north-eastern Greenland locations and concluded that woody plant species, including the dwarf birch *B. nana*, were Holocene immigrants and that the first immigrants came from north-west Europe. A number of molecular studies have shown that circumpolar species tend to split into Eurasian and North American lineages, and that the Eurasian lineage (the amphi-Atlantic species in particular) often has its distribution from Eurasia (western Siberia), northern Scandinavia and Iceland to eastern Greenland. Examples include *Juniperus* (Adams *et al.* 2003), *Saxifraga* (Abbott *et al.* 2000), *Vaccinium* (Alsos *et al.* 2005) and *Carex* (Westergaard *et al*. 2011b). An analysis of the history of the North Atlantic biota (Brochmann *et al*. 2003; Alsos *et al.* 2007) indicated that the majority of endemic species have undergone extensive migration and are post-glacial in origin.

Betula pubescens is also thought to have arrived in Iceland from Western Europe, but a few hundred years after *B. nana*. As shown earlier in this section, the first birch woodland establishment was in the northern (north-eastern) valleys. The eastern and north-eastern cpDNA haplotypes in Iceland seen today must have originated earlier than the western haplotypes, i.e. from the first dense woodlands in the Late Boreal, thus having enough time to evolve into the high haplotype diversity that contains several new and unique haplotypes seen today. On the other hand, the western and south-western haplotypes might have arrived much later, during the southern woodland establishment in the Atlantic period or during the regeneration of birch woodland in the lowlands of the south in the latter half of the Holocene. Pollen studies of early Holocene peat from south-western Iceland (e.g. Vasari 1972) appear to indicate fragmented or scattered woodlands in the area at the time. This is most likely due to a different geological history and palaeoenvironment during the early Holocene in South Iceland (Geirsdóttir *et al*. 2000), as a consequence of substantial sea-level changes during the Weichselian deglaciation (Norddahl & Pétursson 2005). The cpDNA haplotype diversity in western and south-western populations, which is only one-third of that found among the eastern and north-eastern woodlands, indicates more recent origin. But as the western haplotypes are essentially exclusive to western and south-western woodlands, there is only one explanation: birch in these woodlands originated from a different colonization, though also from Europe.

The migration of birch (*B. nana* and *B. pubescens*) to these regions could have come about easily by long-distance wind dispersal, as the winged seeds of birch are lightweight. The alternative route of Holocene dispersal, which is especially important for species lacking a wind-dispersal mechanism, is by ice-rafting and wood-drifting with the transpolar current from Siberia to northern Scandinavia, Iceland and eastern Greenland (Johansen & Hytteborn 2001). The arctic flora appears to be highly mobile (Alsos *et al*. 2007), as some dispersal vectors may be particularly efficient in the Arctic as a result of the open landscape, strong winds and extensive snow and ice cover.

Birch migrated rapidly after the Last Glacial Maximum (LGM) from southern and central Europe and quickly colonized northern Europe. Towards the end of the LGM, the arctic-alpine dwarf birch *B. nana* already covered much of central and eastern Eurasia (Tarasov *et al.* 2000). Based on macrofossil data (Fredskild 1991), dwarf birch occupied the North Atlantic coast of Scotland and south-western Norway around 11.2–10.3 cal ka BP. However, based on new macrofossil data (Birks & van Dinter 2010), *B. nana* had already arrived and spread by the Allerød period (13.5–12.9 cal. ka BP) at the Tjørna site, south-western Norway, then disappeared during the Younger Dryas but appeared again at the transition towards the Holocene, about 500 years before the arrival of *B. pubescens* in the area at around 11.4 cal ka BP. Note that the calibrated year BP is based on the early tephra horizons with Saksunarvatn tephra (Icelandic origin, ca. 10.2 cal ka BP), forming a horizon in the late Pre-Boreal of Northern Europe, and with Vedde ash (also Icelandic in origin, ca 12.0 cal ka BP). According to Paus (1995), *B. pubescens* existed in southern Norway as early as 10.8 cal ka BP. Both *Betula* species were found in the Shetland Islands in ca. 8.6 cal. ka BP (Fredskild 1991), but note that this estimation was based on macrofossil rather than pollen data. New evidence inferred from high-resolution plant macrofossil and pollen data (Hannon *et al.* 2010) showed that *B. nana* was already prevalent in the Faroe Islands during the earliest part of the Holocene (11.3–10.3 cal. yr BP). As shown by palynological studies (especially Karlsdóttir *et al*. 2009), *B. nana* had already appeared in northern Iceland before the Saksunarvatn tephra fall in 10.2 cal ka BP, whereas *B. pubescens* appeared in the same area around 9.8 cal ka BP with birch (*B. pubescens*-dominated) woodland establishment at approximately 9.3–8.3 (peak 8.7) cal ka BP. Birch arrived in Greenland much later: the dwarf birch *B. nana* was found in eastern Greenland around 7,600 yr BP, whereas the tree-birch species *B. pubescens* only arrived in south-western Greenland sometime before 3,500 yr BP (Fredskild 1991). The Holocene route of birch migration is clearly westwards from Europe, across the Atlantic Ocean to Iceland, and then on to Greenland. In order to elucidate these migration routes better, we plan to study the phylogeography of *Betula* species in the British Isles and Greenland in the next phase of our project.

5. Conclusions

Our botanical, cytogenetic, palynological and molecular studies reviewed here show clearly that hybridisation between *B. nana* and *B. pubescens* is widespread in Iceland; the resulting gene flow via introgressive hybridisation is bi-directional; and that the process is continuous through time and space. Iceland could be considered a birch hybrid zone, harbouring genetic variation which may be advantageous in subarctic regions. Despite extensive introgression across species and ploidy levels, a biogeographical pattern has been observed which indicates different population histories or multiple origins of Icelandic birch. Present-day birch in Iceland is most probably post-glacial in origin, migrating from Western Europe and colonizing Iceland in the early Holocene.

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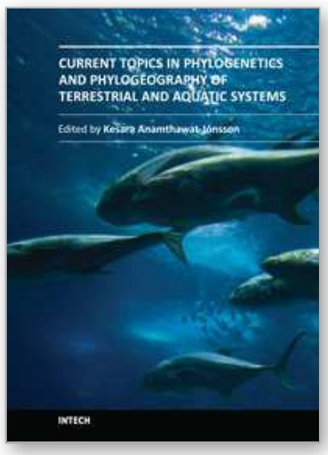
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Mapping phylogenetics on geographical scales is one of the most important scientific aspects of bioscience research. Changes in the environment have evidently shaped the geographical distribution of organisms on land and in the oceans seen today. Overexploitation of key species has caused not only changes in the distribution and diversity of organisms and composition of the ecosystems, but is also leading to species extinction at accelerating rates. It is our duty as scientists to find ways of protecting the species endangered with extinction and preventing other species from entering the endangered stage. To manage this effectively, we need to map species distribution, understand life-history traits, define genetic variation within species and populations, identify lineages - especially at the molecular level - and correlate the historical, phylogenetic components with the spatial distributions of gene lineages. In this book, phylogenetics and phylogeography of a diverse range of organisms are reviewed: from microorganisms causing gastroenteritis in humans, fishes in the Southwest Atlantic Ocean and spiders of the western Indian Ocean, to mountain tapirs in South America and birch tree species of the Arctic tundra.

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