

Provenance variability in establishment of native downy birch in a 14-year trial in southwest Iceland

DENNIS A RIEGE¹ AND AÐALSTEINN SIGURGEIRSSON²

¹University of Maryland University College, 2448 Sandburg St., Dunn Loring VA 22027 USA
(dennis.riege@faculty.umuc.edu)

²Icelandic Forest Service, Mógilsá, IS-162, Reykjavik, Iceland (adalsteinn@skogur.is)

ABSTRACT

Afforestation in southwest Iceland is hindered by eroded, infertile soils and salt deposition from strong oceanic winds. A trial plot of 25 provenances of native downy birch collected throughout Iceland was established in 1998 near Keflavik International Airport to identify the best adapted stock. Seedlings were fertilized in the early years; in 2003 lupine was transplanted into the plot. In 2012, the 25 provenances differed significantly in growth and survival. Both seedling height and survival correlated with latitude of provenance origin, but not with longitude, elevation, or distance from the Keflavik plot. Southern provenances performed better than other regions, with Þórsmörk best in both growth and survival. Local provenances were poorer in performance than many other southern provenances. For afforestation with downy birch, it is recommended that high-performing provenances be planted with initial artificial fertilization, accompanied by simultaneous seeding of lupine.

Keywords: afforestation, facilitation, native species, reclamation, Suðurnes, tree seedlings

YFIRLIT

Munur á afkomu kvæma af íslensku birki í 14-ára tilraun á Miðnesheiði.

Á Reykjanesskaga stendur ófrjósemi jarðvegs og sterkir hafvindar með saltákomu skógrækt fyrir þrifum. Árið 1998 var komið á fót samanburðartilraun við Keflavíkurlflugvöll, með 25 kvæmum af íslensku birki víðsvegar að af landinu, í þeim tilgangi að finna kvæmi sem best væru aðlöguð svæðinu. Borið var á trjáplönturnar í tilrauninni fyrstu árin eftir gróðursetningu. Árið 2003 voru lúpínuplöntur gróðursettar innan um birkið. Fjórtán árum eftir gróðursetningu (2012) reyndist marktækur munur í vexti og lifun kvæmanna. Bæði hæð gróðursettra plantna og lifun þeirra tengdust breiddargráðu upprunastaðar. Engin tengsl voru á milli hæðar og lifunar annars vegar og lengdargráðu, hæðar yfir sjávarmáli og fjarlægð frá tilraunastaðnum við Keflavíkurlflugvöll hins vegar. Sunnlensk kvæmi reyndust betur en kvæmi úr öðrum landshlutum og var hæð og lifun kvæmisins Þórsmörk best. Staðarkvæmi þrífust verr en önnur sunnlensk kvæmi. Þegar rækta á birkiskóg á ófrjósum jarðvegi á Suðurnesjum, er mælt með því að leggja áherslu á þau kvæmi sem sýnt hafa besta frammistöðu í tilrauninni. Einnig er mælt með að bera á plöntur fyrstu ár eftir gróðursetningu og um leið að sá lúpínu.

INTRODUCTION

Afforestation is difficult in the Suðurnes peninsula, which protrudes into the Atlantic Ocean in southwest Iceland. It is an area of strong winds, eroded soils, salt spray, and little soil nitrogen (Riege & Sigurgeirsson 2009).

Much of the peninsula is semi-barren or has a low cover of moss-heath. Afforestation projects in Iceland during the last half century have emphasized non-native species such as Siberian larch (*Larix sibirica* Ledeb.), Lodgepole pine

(*Pinus contorta* Dougl. ex Loud.) and Sitka spruce (*Picea sitchensis* [Bong.] Carr.). In recent years, there has been growing use of native downy birch (*Betula pubescens* Ehrh.) for revegetation projects (Aradóttir & Eysteinnsson 2005), including an ambitious program (Hekluslógar) to reclaim ~1000 km² of tephra covered lands near Mt. Hekla (Aradóttir 2007). Downy birch is the only native tree species that forms natural woodlands in Iceland (Blöndal 1987). In some regions of Iceland it can be an aggressive pioneer that can rapidly colonize denuded soils and derelict land, if protected from sheep grazing. (Aradóttir & Eysteinnsson 2005). The few remnant birch woodlands that occur on the peninsula are composed of small, multi-stemmed, prostrate shrubs. Whether this is a result of the harshness of the environment, poor soils, past practices of intensive cutting for firewood, or inherent genetic constitution is not clear. While previous studies have compared a few downy birch provenances over broad geographic regions in Scandinavia (Sveinbjörnsson et al. 1993, Wielgolaski and Nilsen 2001, Övaska et al. 2005, Viherä-Aarnio et al. 2005), mostly in the context of climate change, published research in English is lacking on performance of birch provenances within Iceland, where such a study will benefit methods of afforestation to repair substantial desertification.

The main aim of our study was to find suitable, adapted birch provenances that will yield success in afforestation in the Suðurnes environment. For this, effects of location of provenance origin on seedling performance were examined to identify relationships that may be of practical use in provenance choice. Recent advances in fertilization procedures were applied, since afforestation on barren land without fertilization usually yields high mortality and long periods of stagnant growth in Iceland (Óskarsson & Sigurgeirsson 2001, Óskarsson et al. 2006, Óskarsson & Brynleifsdóttir 2009). Nootka lupine (*Lupinus nootkatensis* Sims) was transplanted into the trial five years after establishment, as a nearby study (Riege & Sigurgeirsson 2009) found that lupine facilitated

growth of downy birch seedlings in this stressful environment. Lupine has been found to improve tree seedling establishment by nitrogen fixation, addition of organic material, and amelioration of microclimate (Myrold & Huss-Danell 2003, Mattson et al. 2007). Development of methods that promote afforestation in southwest Iceland will be useful to counter soil erosion and to establish windbreaks around human habitation. Furthermore, the experiment may serve the region in the future as a source of well adapted and genetically variable seed.

MATERIALS AND METHODS

Study site

The study site (63°57'36.5"N, 22°36'52"W) is located just south of the Keflavik International Airport on the Suðurnes Peninsula. The climate is temperate, maritime, and windy, moderated by the Gulf Stream. Mean January temperature 1949-1995 was 0° C, July 10° C (former U.S. Naval Air Station Keflavik Meteorologic Office Climate Summary). Mean annual precipitation is 1074 mm, evenly spread throughout the year. Mean wind speed is 6 ms⁻¹, with extreme winds to 39 ms⁻¹. Soils are highly eroded and vegetation is sparse due to removal of woodlands and overgrazing since the time of the settlement in the late ninth century (Steindórsson 1957). The birch trial plot was established on rocky, eroded soil with patches of moss-heath cover dominated by *Racomitrium* moss, crowberry (*Empetrum nigrum*), and heather (*Calluna vulgaris*). More information about the site conditions at Reykjanes can be found in Riege & Sigurgeirsson (2009).

Birch provenance trial

In 1994-95, Icelandic Forest Research (IFR) carried out seed collections in over 40 woodlands throughout Iceland. At each location, seed was collected from 10-20 maternal parents. Trees chosen for seed collection were in most cases dominant, but not otherwise selected by their phenotype and separated by a distance of at least 20 meters. The seed samples were sown at the IFR nursery in 1997, and the seedlings were used for this experiment. For the Keflavik study,

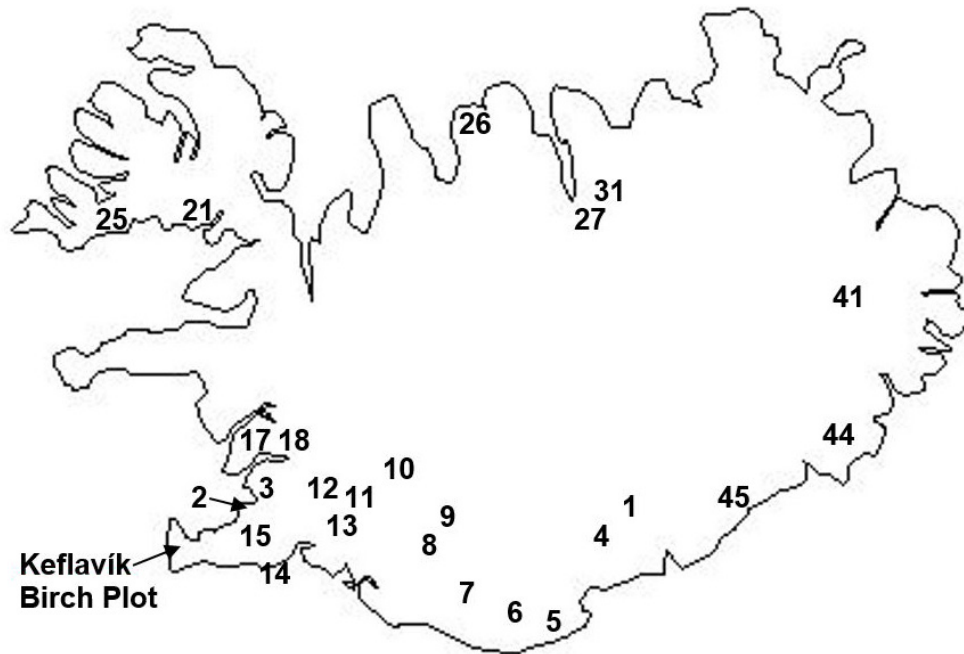


Figure 1. Location of origin of the 25 downy birch provenances in the Keflavík trial plot. Names of provenances are given in Table 1. Provenances nos. 2, 3 originated from stock from Bæjarstaðarskógur (location no. 1).

25 birch provenances were included, with most originating from lowlands in southern Iceland (Figure 1). The experiment was laid out with a randomized block design, with 20 seedlings per provenance in a block in row plots, and five adjacent replications of blocks (a total of 2500 seedlings). Seedlings were planted 2 m apart in late June/early July 1998 and fertilized with a 9-g teabag of RTI Booster-Pak (N-P-K-S-Ca-Mg-B: 18-6-6-5.7-8.5-0.71-0.18). During June 1999, the birch seedlings were scored for survival, and the initial heights of surviving seedlings in spring 1999 were measured. During October 2002, the seedlings were again scored for survival and measured for height. In 2002 the seedlings exhibited signs of nutrient deficiency. During the summers of 2003 and 2004, every seedling received an application of 40-50 g of Gróska II fertilizer, a mixture of NP easily soluble monoammonium phosphate (9-42-0) and controlled release fertilizer - Osmocote (32-0-0). During the summer of 2003, lupine seedlings of ~7 cm height were transplanted

next to every other birch seedling. By 2012, lupine had spread to cover most of the plot with thick growth.

During 28 August - 4 September 2012, the birch plants were scored for survival and measured for height (= tallest living branch). Effects of provenance on heights and survival of the seedlings were analysed via randomized block ANOVA. Results were considered significant if $p < 0.05$. Means were compared with the LSD test. Values for percent survival per provenance per block were arcsine transformed. Data were analysed with Statistix 9.0 software (www.statistix.com).

RESULTS

Survival of birch seedlings after 12 years (Table 1) was 74% in September 2012. The mean height of birch seedlings, which was 13.0 ± 0.4 cm in spring 1999 (data not shown), and reached 105.5 ± 0.8 cm in September 2012. Almost all birch seedlings had assumed a multistemmed, shrubby form.

Table 1. Characteristics of 25 *Betula pubescens* provenances in 2012, in order of mean height. Location, elevation, and distance from Keflavik study plot of provenance origin. Six northernmost provenances indicated by (N). Mean block height and survival. Means within a column that differ by a letter are significantly different (LSD test, $\alpha=0.05$).

no	provenance	coordinates	elevation (m.a.s.l.)	distance (km)	height (cm)	survival
7	Thórsmörk	63°41'N, 19°32'W	264	154	122.8 ^a	0.91 ^a
4	Núpsstaðarskógur	64°03'N, 17°28'W	236	251	121.8 ^{ab}	0.85 ^{abcd}
8	Galtalækur	63°59'N, 19°57'W	178	130	121.5 ^{ab}	0.72 ^{bcdef}
12	Thingvellir	64°14'N, 21°04'W	135	81	117.1 ^{abc}	0.86 ^{abc}
2	Embla*	64°08'N, 21°52'W	24	41	117.1 ^{abc}	0.85 ^{abc}
1	Bæjarstaðarskógur	64°03'N, 17°02'W	151	272	111.8 ^{bcd}	0.79 ^{abcde}
3	Mógilsá*	64°12'N, 21°42'W	16	52	111.3 ^{bcde}	0.74 ^{bcdef}
13	Öndverðanes	64°00'N, 20°57'W	51	81	110.2 ^{cdef}	0.73 ^{bcdef}
45	Steinadalur	64°09'N, 16°00'W	129	322	107.7 ^{cdefg}	0.85 ^{ab}
44	Stafafell í Lóni	64°26'N, 14°56'W	61	375	106.4 ^{defgh}	0.73 ^{bcdef}
5	Meðalland	64°34'N, 18°17'W	21	217	106.2 ^{defgh}	0.66 ^{defg}
14	Herdísarvík,	63°52'N, 21°50'W	46	40	105.8 ^{defgh}	0.69 ^{bcdef}
15	Vífilsstaðahlíð	64°03'N, 21°52'W	98	38	105.1 ^{defgh}	0.68 ^{bcdef}
9	Thjórsárdalur	64°07'N, 19°56'W	219	132	104.0 ^{defgh}	0.83 ^{abcde}
25	Norðdalur (N)	65°37'N, 23°21'W	244	187	102.8 ^{defgh}	0.62 ^{efg}
41	Hallormsstaður (N)	65°06'N, 14°43'W	116	398	101.9 ^{defgh}	0.73 ^{bcdef}
11	Laugarvatn	64°13'N, 20°44'W	91	96	101.3 ^{efgh}	0.78 ^{bcdef}
31	Vaglaskógur (N)	65°43'N, 17°53'W	221	297	100.9 ^{efgh}	0.70 ^{bcdef}
10	Haukadalur	64°20'N, 20°17'W	198	120	100.4 ^{fgh}	0.68 ^{cdefg}
6	Hrífunes	63°41'N, 18°31'W	168	204	98.5 ^{gh}	0.80 ^{abcde}
17	Hafnarskógur	64°30'N, 21°55'W	49	69	98.4 ^{gh}	0.80 ^{abcde}
18	Vatnshornsskógur	64°29'N, 21°22'W	134	84	95.9 ^{hi}	0.69 ^{bcdef}
27	Garðsárgil (N)	65°35'N, 18°00'W	79	310	85.0 ^{ij}	0.57 ^{fg}
21	Teigsskógur (N)	65°32'N, 22°14'W	76	176	77.9 ^j	0.46 ^g
26	Hrollleifsdalur (N)	65°59'N, 19°19'W	183	273	74.0 ^j	0.59 ^{efg}

* mostly from Bæjarstaðarskógur stock, with minor input from other Icelandic sites

Heights in 2012 of birch seedlings (Table 1) varied significantly by provenance (ANOVA: $F_{24, 1802} = 8.97$, $p < 0.0001$). The provenances also showed a significant difference in percent survival (Table 1) ranging from 46% to 91% ($F_{24,96} = 2.12$, $p < 0.01$). The rank order of provenances by height significantly correlated

with survival rate (Spearman's $r = 0.63$, $p < 0.001$). Among the 25 provenances, both height and survival correlated with the latitude of origin but not with longitude, elevation, or distance (Table 2). Lower survival and growth were observed among the six provenances from north and east Iceland, compared to those originating

Table 2. Rank correlation (Spearman's r) between height and survival of the birch provenances and geography of their origin ($n = 25$). Distance is from the Keflavik trial plot.

	height	survival
latitude	-0.63**	-0.56**
longitude	-0.14	-0.29
elevation	0.04	0.13
distance	-0.17	-0.11

** $p < 0.01$

from coastal regions of the south and southeast (Table 1, Figure 1). Mean height of seedlings of the southern provenances was 108.9 ± 0.9 cm versus 91.8 ± 1.9 cm for northern seedlings ($p < 0.0001$ by t -test, data not shown). Mean block survival was $77 \pm 2\%$ for southern versus $61 \pm 3\%$ for northern seedlings ($p < 0.001$ by t -test, data not shown). Thórsmörk was the most successful provenance for both height (123 cm) and survival (91%) in 2012 (Table 1).

DISCUSSION

The importance of using the right provenance for afforestation

Provenance matters in the selection of proper downy birch stock for afforestation programs in the Suðurnes region, as the provenances showed a significant gradation in performance (Table 1). Thórsmörk appeared to be the best adapted provenance of those tested, but not significantly better than some others (Table 1). An increase in provenance height and survival correlated with a decrease in latitude of origin of the Icelandic provenances (Table 2). On a larger geographic scale with provenances from Finland, Norway, and Iceland, Wielgolaski and Nilsen (2001) found faster growth in southernmost provenances of downy birch. With silver birch (*Betula pendula*) seeds from Finland and Estonia, Viherä-Aarnio et al. (2005) reported shorter growth periods in germinated seedlings as seed origins became increasingly northern, likely due to adaptations to photoperiod. However, with the relatively small latitudinal gradient in Iceland, adaptations to climate may be a larger factor

than photoperiod in the lower performance of northern provenances. The northern regions of Iceland are drier and colder than the south coast (Einarsson 1984). In altitudinal transects in Sweden and Iceland, Sveinbjörnsson et al. (1993) found that downy birch growth decreased with elevation. In the Keflavik site, there was no correlation between elevation of origin and height or survival among the 25 provenances. The relatively-small altitude gradient among the Icelandic provenances (Table 1) may be insufficient to cause differential adaptations.

The notion that “local is best” (or “safest”) when it comes to birch provenance selection for the region was not supported by our findings, as there was no correlation with distance of provenance origin from the Keflavik plot (Table 2). Herdísarvík (#14) and Vífilstaðahlíð (#15) were the nearest to being the “local” provenances in the experiment, with seed collected from low-growing coastal birch scrublands in southwest Iceland (Figure 1). The performance of these provenances was only average and similar to one another, both in terms of height and survival (Table 1). It is notable that three of the top seven provenances by height were from stock that originated in Bæjarstaðarskógur, a forest in Skaftafell National Park that contains birch up to 14 m tall (Eggertsson & Gudmundsson 2002). However, under the conditions of the Keflavik site, the three Bæjarstaðarskógur-provenances have thus far assumed a multistemmed, shrubby form, which is typical of most (Aradóttir & Eysteinnsson 2005), but not all (Jónsson 2004), Icelandic birch woodlands.

The lupine heights in the Keflavik plots were about 80-100 cm. Most birch branches did not extend much above the lupine. As the birch seedlings continue to rise above the lupine, it will be interesting to see if there is divergence in growth form or stature among the provenances. Jónsson (2004) found substantial differences from prostrate shrubs to trees in stature of downy birch in a study encompassing many stands throughout Iceland. The high degree of variation among downy birch provenances in Iceland may be the result of hybridization and gene flow from dwarf birch, *Betula nana* (Thórsson

et al. 2001, 2010), but genetic analysis of the provenances was beyond the scope of this study. *Best practice in afforestation at barren sites in southwest Iceland*

For best results on mostly-barren soil in southwest Iceland, it is recommended that downy birch seedlings of the best-adapted provenances be accompanied by a packet of slow-release fertilizer upon transplantation to improve early survival (Óskarsson & Sigurgeirsson 2006, Riege & Sigurgeirsson 2009). Addition of lupine is recommended for longer term fertilization. In an experiment on five sites 1-3 km from the provenance plot, Riege & Sigurgeirsson (2009) found that lupine facilitated growth of transplanted downy birch seedlings. In a trial in Thjórsárdalur (inland south Iceland), Fischer (2010) also reported a positive effect of the lupine plants on birch seedling growth. However, in south Iceland Aradóttir (2004) noted a switch from facilitation to competition with increasing density of lupine. Riege & Sigurgeirsson (2009) found that survival of birch seedlings, but not growth of the survivors, was greatly reduced with thick lupine, especially when accompanied by dense grass cover. Thus, it is recommended that lupine be seeded, rather than transplanted, at the same time as downy birch seedlings are planted. This will slow the growth of lupine to promote its facilitative effects while lessening its competitive effects.

The Keflavík trial plot has successfully demonstrated that downy birch seedlings can survive and grow well in a stressful landscape in southwest Iceland. While these results have practical application for afforestation with birch in this environment, further research is needed on additional trial plots to determine the best performing provenances in other sections of the country.

ACKNOWLEDGEMENTS

We are indebted to David James of the Atlantic Division, U. S. Naval Facilities Engineering Command, for promoting afforestation research on Suðurnes Peninsula. Gudmundur Örn Jónsson supervised plot fertilization and addition of lupine. We are grateful to Bjarni D. Sigurdsson,

Hreinn Óskarsson, Thorsteinn Tómasson, and anonymous reviewers for critically improving the manuscript. Funding, field, and office support was generously provided by Iceland Forest Research, U. S. Naval Facilities Engineering Command, and the Environmental Division of the former Keflavík NATO Base.

REFERENCES

- Aradóttir ÁL 2004.** Does introduced Nootka lupin facilitate or impede colonization and growth of native birch in Iceland? In van Santen E & Hill GD. (eds.) *Wild and Cultivated Lupins from the Tropics to the Poles: Proceedings of the 10th International Lupin Conference*. International Lupin Association, Canterbury, New Zealand, pp. 184-190.
- Aradóttir ÁL 2007.** Restoration of birch and willow woodland on eroded areas. In: Halldorsson G, Oddsdóttir ES & Eggertsson O (eds.) *Effects of Afforestation on Ecosystems, Landscape and Rural Development*. TemaNord, Reykjavík, pp. 67-74.
- Aradóttir ÁL & Eysteinnsson T 2005.** Restoration of birch woodlands in Iceland. In: Stanturf JA & Madsen P (eds.) *Restoration of Boreal and Temperate Forests*. CRC Press, Boca Raton, pp. 195-209.
- Blöndal S 1987.** Afforestation and reforestation in Iceland. *Arctic and Alpine Research* 19, 526-529. <https://doi.org/10.2307/1551420>
- Eggertsson Ó & Gudmundsson HJ 2002.** Aldur birkis (*Betula pubescens* Ehrh.) í Bæjarstaðarskógi [Age of birch (*Betula pubescens* Ehrh.) in Bæjarstaðarskógur] *Skógrættarritið 2000* (2), 85–89. [In Icelandic].
- Einarsson MÁ 1984.** Climate of Iceland. In: van Loon, H (ed) *World Survey of Climatology: 15: Climates of the Oceans*. Elsevier, Amsterdam, pp. 673-697.
- Fischer S 2010.** *The Effect of Fertilizer and Mycorrhiza on the Growth and Survival of Planted Birch Seedlings on Lupine-fields and Non-lupine Fields*. B. Sc. thesis, Fakultät Ressourcemanagement, Göttingen. 78 p.
- Jónsson TH 2004.** Statures of sub-arctic birch in relation to growth rate, lifespan and tree form. *Annals of Botany* 94, 753-762. <https://doi.org/10.1093/aob/mch200>

- Mattson S, Bergsten U & Mörling T 2007.** *Pinus contorta* growth in boreal Sweden as affected by combined lupin treatment and soil scarification. *Silva Fennica* 41, 649-659
- Myrold, DD. & Huss-Daniel K 2003.** Alder and lupine enhance nitrogen cycling in a degraded forest soil in Northern Sweden. *Plant and Soil* 254, 47-56.
- Óskarsson H & Sigurgeirsson A 2001.** Fertilization in Icelandic afforestation: Evaluation of results. *Scandinavian Journal of Forest Research*, 16, 536-540.
<https://doi.org/10.1080/02827580152699367>
- Óskarsson H & Sigurgeirsson A 2004.** Effects of fertilization on tree seedling establishment and growth in a lupin field in southern Iceland. In van Santen E & Hill GD. (Eds.) *Wild and Cultivated Lupins from the Tropics to the Poles. Proceedings of the 10th International Lupin Conference*. International Lupin Association, Canterbury, New Zealand, pp. 203-205.
- Óskarsson H, Sigurgeirsson A & Rauland-Rasmussen K 2006.** Survival, growth, and nutrition of tree seedlings fertilized at planting on Andisol soils in Iceland: six-year results. *Forest Ecology and Management* 229, 88-97.
<https://doi.org/10.1016/j.foreco.2006.03.018>
- Óskarsson H & Brynleifsdóttir SJ 2009.** The interaction of fertilization in nursery and field on survival, growth and the frost heaving of birch and spruce. *Icelandic Agricultural Sciences* 23, 58-68.
- Osaska JA, Nilsen J, Wielgolaski FE, Kauhanen H, Partanen R, Neuvonen S, Kapari L, Skre O & Laine K. 2005.** Phenology and performance of mountain birch provenances in transplant gardens: latitudinal, altitudinal, and oceanality-continentiality gradients. In: Wielgolaski FE, Karlsson PS, Neuvonen S, & Thannheiser D. (eds) *Plant ecology, herbivory, and human impact in Nordic mountain birch forests*. Springer Berlin Heidelberg, pp. 99-115.
- Riege DA & Sigurgeirsson A 2009.** Facilitation of afforestation by *Lupinus nootkatensis* and by black plastic mulch in south-west Iceland. *Scandinavian Journal of Forest Research* 24, 384-393.
<https://doi.org/10.1080/02827580903117404>
- Steindórsson S 1957.** Um gróður í Reykjaneshraunum. [On vegetation in the Reykjanes lava field.] *Ársrit Ræktunarfélags Norðurlands*, 54, 137-150. (In Icelandic).
- Sveinbjörnsson B, Sonnesson M, Nordell OK, & Karlsson PS. 1993.** Performance of mountain birch in different environments in Sweden and Iceland. In: Alden J, Mastrantonio JL & Ødum S. (eds) *Forest development in cold climates*. Plenum Press, New York, pp. 79-88.
- Thórsson, ÆH, Salmela E, & Anamthawat-Jónsson K 2001.** Morphological, cytogenetic, and molecular evidence for introgressive hybridization in birch. *Journal of Heredity* 92,404-408.
- Thórsson, ÆH, Pálsson, S, Lascoux M, & Anamthawat-Jónsson K 2010.** Introgression and phylogeography of *Betula nana* (diploid), *B. pubescens* (tetraploid) and their triploid hybrids in Iceland inferred from cpDNA haplotype variation. *Journal of Biogeography* 37:2098-2110.
<https://doi.org/10.1111/j.1365-2699.2010.02353.x>
- Viherä-Aarnio A, Häkkinen R., Partanen J Luomajoki A, & Koski, V 2005.** Effects of seed origin and sowing time on timing of height growth cessation of *Betula pendula* seedlings. *Tree Physiology*, 25, 101-108.
<https://doi.org/10.1093/treephys/25.1.101>
- Wielgolaski FE, & Nilsen J 2001.** Coppicing and growth of various provenances of mountain birch in relation to nutrients and water. In: Wielgolaski FE (ed.) *Nordic mountain birch ecosystems. Man and biosphere series* 27. UNESCO Paris and Parthenon, New York, pp. 77-92.

Manuscript first received 26 February 2014

Resubmitted 5 December 2017

Accepted 8 February 2018