

Photosynthetic temperature response of mountain birch (*Betula pubescens* Ehrh.) compared to two other broadleaved tree species in Iceland

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ABSTRACT

The temperature response of light- and CO₂-saturated net-photosynthesis (A_{max}) was measured on attached leaves of mature trees of the native mountain birch (*Betula pubescens* Ehrh.), the native mountain ash (*Sorbus aucuparia* L.) and the introduced grey alder (*Alnus incana* (L.) Moench.) in Hallormsstaður, eastern Iceland, in the summer of 2003. Mountain birch was found to have the highest optimum temperature, or 35.1 °C, followed by mountain ash and grey alder, which had optimum temperature at 32.5 and 30.8 °C, respectively. The photosynthetic capacity of birch at the mean 1961-1991 maximum temperature of the warmest month occurring at Hallormsstaður was only 71% of its capacity at optimum temperature. The results indicate that mountain birch is today growing where the environment is not necessarily at optimum for its growth and survival.

Key words: *Alnus incana*, *Betula pubescens*, gas exchange, photosynthesis, *Sorbus aucuparia*, temperature optimum

YFIRLIT

Kjörhitastig birkis samanborið við kjörhitastig tveggja annarra laufrjátægunda sem vaxa á Íslandi
Mælingar á kjörhitastigi birkis (*Betula pubescens*), ilmreynis (*Sorbus aucuparia*) og gráelris (*Alnus incana*) fóru fram í Hallormsstaðarskógi sumarið 2003. Til þessara mælinga var notaður færanlegur innrauður gasgreinir með áföstum mæliklefa þar sem hægt var að stjórna umhverfisaðstæðum svo sem inngæslun, lofthita, rakastigi og styrk koldíoxíðs í andrúmslofti. Birki hafði hærra kjörhitastig en hinar trjátægundirnar, eða 35,1 °C. Reynir og elri höfðu 32,5 og 30,8 °C kjörhita fyrir kolefnisupptöku, sem er fyrsta skrefið í vaxtarferli trjáa. Við meðal-hámarkshita í júlí á Hallormsstað (21,6 °C) gat birki ljóstillífað um 71% miðað við kjörhitastig. Ljóstillífun birkis við 10 °C var aðeins um 43% miðað við kjörhitastig. Niðurstöður þessarar rannsóknar komu talsvert á óvart, því birki hefur almennt verið talið vel aðlagð að vexti á kaldari og erfiðari svæðum. Það er því líklegt að samkeppni frekar en fullkomin aðlögun í ljóstillífun hafi valdið núverandi dreifingarmynstri birkis á Íslandi, en það finnst nú aðallega í 200-400 m hæð yfir sjó.

INTRODUCTION

Photosynthesis is the first step of the growth process in plants and their productivity may therefore be limited if the prevailing growing-season temperature in their natural environment is much above or below the optimum temperature for that process. It has been stated that the temperature optimum for photosynthesis of vascular plants generally matches the average daytime temperature encountered in the natural environment of the species (e.g. Salvucci & Crafts-Brandner 2004, Larcher 2003). However, most field studies on optimum temperature have been performed on species growing in a temperate climate, and less information is available on *in situ* measurements under boreal or sub-arctic conditions. At higher latitudes species often show northward or altitudinal distribution that is strongly related to isotherms of average temperature of the warmest month (Sjörs 1999, Carlsson et al. 1999). This may indicate that temperature is the main limiting environmental factor for growth and survival in those areas and that the temperature optimum of the species is not in balance with the local climate.

In Scandinavia, mountain birch (*Betula pubescens* Ehrh.) forms the forest limit and in Iceland it is the only tree species that forms extensive natural forests or woodlands (Aas & Faarlund 2001). It is therefore a key species to study in terms of the effects of climate change on growth and productivity in those areas. It was recently shown that during the past 100 years, growth of mountain birch in Southeast Iceland has been strongly correlated with changes in summer temperature during the same period (Eggertsson & Gudmundsson 2002). This seemed to contradict older findings, where mountain birch in northern Sweden was found to have a temperature optimum of only 11 °C (Sveinbjörnsson 1983). This apparent controversy inspired the authors to further study the photosynthetic processes of mountain birch in Iceland.

The aim of this study was to measure the photosynthetic temperature response of the

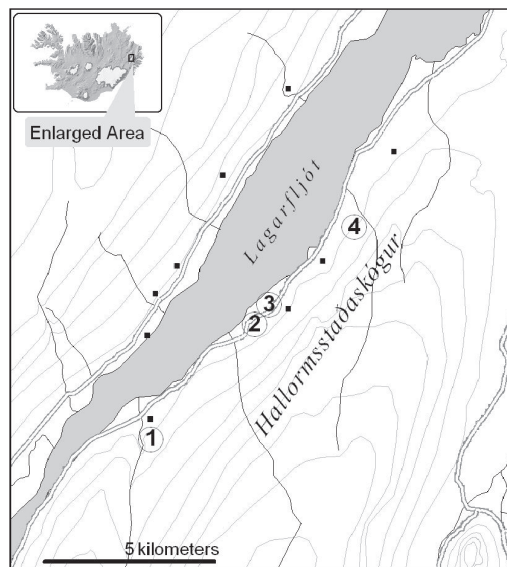


Figure 1. Location of the study sites in eastern Iceland. Mountain birch is denoted as 1, grey alder as 3 and mountain ash as 4. See Table 1 for further description of different stands.

native mountain birch and furthermore to compare the temperature response of mountain birch to native mountain ash (*Sorbus aucuparia* L.) and the introduced grey alder (*Alnus incana* (L.) Moench.) from Kvaefjord in South Troms, Norway. We expected to find the lowest temperature optimum for mountain birch and mountain ash followed by grey alder, corresponding to the average summer temperature in the place of their origin and northward distribution of these species (Table 1).

MATERIALS AND METHODS

Field site

The study was carried out in Hallormsstaðarkógur in eastern Iceland in the summer of 2003 (Figure 1, Table 1). The area contains Iceland's largest remains of the native mountain birch woodland and has been protected from livestock grazing since 1905-1907. Some individuals of the native mountain ash can be found in the old woodlands. At present the area is a mixture of mature mountain birch woodland

Table 1. Place of origin, mean January and July temperatures in place of origin, growing location and altitude, mean height and diameter at breast height of trees (DBH) chosen for gas-exchange measurements.

Species	Place of origin	Temperature, °C	Location	Altitude, m	Height, m	DBH, cm
Mountain birch	N65.06	-1.6, 10.2	N65.06	184	3.2±0.2	2.5±0.6
	W14.83		W14.83			
Mountain ash	N65.11	-1.6, 10.2	N65.11	240	4.0±3.3	8.9±15.4
	W14.69		W14.69			
Grey alder	N68.47	-2.8, 12.6	N65.09	205	6.9±1.1	17.0±3.6
	E16.10		W14.75			

and younger birch stands that have regenerated naturally following the protection from grazing. Also there are some stands of introduced species, such as black cottonwood and grey alder and others, planted by the Iceland Forest Service in the 20th century. The mean annual temperature (1961-1990) at the meteorological station at Hallormsstaður was 3.4 °C and the mean annual precipitation was 738 mm (The Icelandic Meteorological Office, pers. comm.). The mean 24-hour temperature for the same period varied between 10.2 °C in July to -1.6 °C in January, and the mean maximum daytime temperatures in June, July and August were 12.4, 14.1 and 13.4 °C, respectively (Figure 2). These were the average conditions around midday when photosynthesis is at the maximum. The mean monthly maximum daytime temperatures were 20.3, 21.6 and 19.5 °C for June, July and August, respectively (Figure 2). The highest temperatures experienced in June, July and August during the 1961-1990 period were 27.2, 26.2 and 25.2 °C, respectively.

Gas exchange measurements

Light- and CO₂-saturated net photosynthesis (A_{max}) at varying leaf temperature, *i.e.* temperature response curves, were measured on attached leaves in the upper half of the canopy (sun leaves) of mature mountain birch, mountain ash and grey alder trees (Table 1). For each species, measurements were made of one leaf from each of three to four trees, *i.e.*, three

to four replicate curves were made for each species.

The gas exchange measurements were made by means of the CIRAS 2, open path portable photosynthesis system, with PLC6 Universal leaf cuvette (PP Systems, Hitchin, Hertfordshire, UK). The PLC6 cuvette allowed automatic control of ambient CO₂ concentration ([CO₂]), water vapor concentration ([H₂O]), air or leaf temperature (T_{air} and T_{leaf}) and irradiance, measured as photosynthetic active radiation (PAR). Inserts were used in

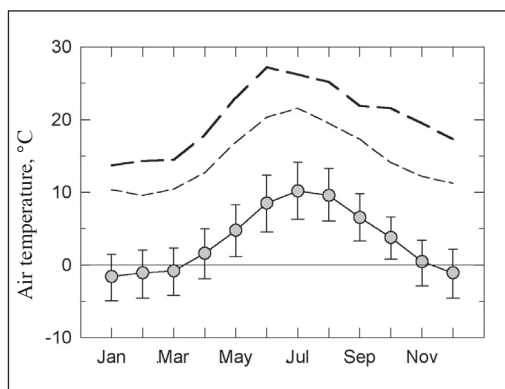


Figure 2. Mean monthly 24-hour air temperature at Hallormsstaður during 1961-1990 (symbols) and mean maximum daytime and minimum nighttime temperatures (error bars). Also shown are mean monthly maximum temperature (short-dashed line) and maximum measured temperature during the period (long-dashed line; The Icelandic Meteorological Office, pers. comm.).

the PLC6 cuvette to measure exactly 4.5 cm² of foliage (25 × 18 mm) for all species except for mountain ash, for which inserts with 1.75 cm² (25 × 7 mm) aperture were used, because of narrower leaves.

Each curve consisted of ca. 3 measurements of A_{max} made at eight different T_{leaf} . The measurements were started after ca. 30 min acclimation period at T_{leaf} of 5 °C, and then the T_{leaf} was increased stepwise to 10, 15, 20, 25, 30, 35 to 40 °C, with ca. 5 min intervals between temperature change and measurements. During the measurements [H₂O] was kept at 80% of ambient humidity, PAR at 1000 μmol m⁻² s⁻¹ (light saturation) and [CO₂] was kept at 1000 μmol CO₂ mol⁻¹ air. If stomata started to close at higher temperatures, due to increased transpiration, with a corresponding decrease in calculated intracellular [CO₂], the cuvette [CO₂] was increased to maintain ca. 900 μmol CO₂ mol⁻¹ air intracellular [CO₂] (CO₂ saturation).

Data and statistical analyses

Each individual temperature response curve was first normalized to 25 °C ($A_{max, rel}$ of 1 = A_{max} at 25 °C). An Arrhenius-type temperature-model was then used to derive the temperature dependencies of light- and CO₂-saturated photosynthesis by non-linear least-squares regression in the Sigmaplot 8.0 software (Harley & Baldocchi 1995, Harley et al. 1996):

$$A_{max, rel} = \frac{e^{\frac{\Delta H_a(T_k - T_s)}{R T_k T_s}}}{1 + e^{\frac{\Delta H_d(T_k - C)}{R T_k T_s}}}, \quad (1)$$

where T_k is the measured leaf temperature in Kelvin, T_s is the leaf temperature to which data are normalized (298 K or 25 °C), R is the gas constant (8.314 J K⁻¹ mol⁻¹), H_a is the activation energy (J mol⁻¹) and H_d deactivation energy (J mol⁻¹), and C is an empirical scaling coefficient (°K). Activation energy is a measure of the minimum energy needed by the photosynthesis system to react and deactivation energy is the maximum energy the system can cope with before the reaction decreases (Brady 1990).

Analysis of variance (ANOVA) was conducted to test for species effects (SAS system 8.2, SAS Institute Inc., Cary, NC, USA), where the unit of replication was the individual temperature response curve. When the ANOVA model gave $P < 0.10$, pair-wise differences between species were analyzed by Fisher's least-significant-difference tests (LSD). Pair-wise differences were only considered significant if $P < 0.05$. The parameters that were analyzed were T_{opt} (temperature optimum of photosynthesis), H_a (the activation energy of photosynthesis), H_d (the deactivation energy of photosynthesis), C (an empirical coefficient) and A_{max} at temperature 10, 15, 20, 25, 30 and 35 °C as a fraction of A_{max} at optimum temperature (relative loss in photosynthetic capacity).

RESULTS

Mountain birch

Figure 3 shows the actual rate of light- and CO₂-saturated net photosynthesis of mountain birch, mountain ash and grey alder at varying leaf temperatures. Mountain birch A_{max} was 19.7, 33.5, and 43.6 μmol m⁻² s⁻¹ at 10, 20 and 30 °C, respectively. When the photosynthesis was expressed as $A_{max, rel}$ i.e. photosynthetic capacity relative to 25 °C ($A_{max, rel}$ of 1 = A_{max} at 25 °C), it was apparent that mountain birch increased its photosynthesis almost linearly from 5 to 27 °C, where it began to level off, reaching its maximum at 35.1 °C (optimum temperature) and thereafter decreasing (Figure 4). The photosynthetic capacity at mean maximum temperature for Hallormsstaður in July (14.1 °C, Figure 2) was only 51% that of optimum temperature (Table 2). Similarly, it was found that the monthly mean maximum daytime temperature in July (21.6 °C) and the absolute maximum July temperature (26.2 °C) led to photosynthetic capacity that was only 71% and 83% of the photosynthetic capacity at optimum temperature, respectively (Table 2). The activation energy of the temperature response of mountain birch was 31 kJ mol⁻¹ and the deactivation energy (ΔH_d) 152 kJ mol⁻¹ (Table 3).

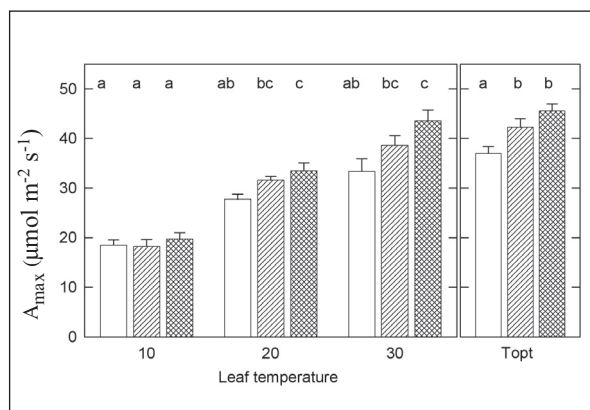


Figure 3. Actual light- and CO₂ saturated photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at 10, 20, 30 °C and at optimum temperature (T_{opt}) for grey alder (blank), mountain ash (right hatched) and mountain birch (cross hatched). Shown are mean values \pm s.e. Shared letters indicate no significant difference ($P > 0.05$) at a given temperature.

Table 2. A_{\max} at different temperatures as a fraction of A_{\max} at optimum temperature (T_{leaf} , relative loss in photosynthetic capacity), and optimum temperature, °C (T_{opt}) for three tree species growing in eastern Iceland. Shown are mean values \pm SE for $n=3-4$. Shared letters indicate no significant difference ($P > 0.05$).

T_{leaf} , °C	A_{\max}/A_{\max} at optimum temperature		
	Mountain birch	Mountain ash	Grey alder
10	0.43 \pm 0.02 a	0.47 \pm 0.03 ab	0.53 \pm 0.02 b
15	0.54 \pm 0.02 a	0.59 \pm 0.03 ab	0.65 \pm 0.02 b
20	0.66 \pm 0.02 a	0.72 \pm 0.03 ab	0.78 \pm 0.02 b
25	0.80 \pm 0.02 a	0.87 \pm 0.03 ab	0.92 \pm 0.02 b
30	0.93 \pm 0.01 a	0.97 \pm 0.02 ab	0.99 \pm 0.01 b
35	1.00 \pm 0.00 a	0.96 \pm 0.02 ab	0.91 \pm 0.04 b
Optimum temperature, °C			
T_{opt}	35.1 \pm 0.62 a	32.5 \pm 1.27 ab	30.8 \pm 1.01 b

The other species

Mountain ash and grey alder showed a general response of A_{\max} to leaf temperature similar to that of mountain birch (Figure 3). At 10 °C A_{\max} for mountain ash and grey alder was 18.3 and 18.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$, respectively. Similarly,

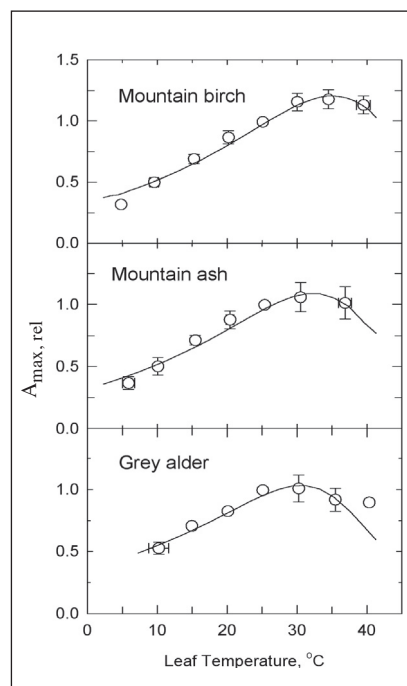


Figure 4. Temperature response curve of $A_{\max, \text{rel}}$ (relative photosynthetic capacity to 25 °C) for mountain birch, mountain ash and grey alder. Shown are mean values \pm s.d. for 3-4 curves, which each consisted of 2-4 measurements at each temperature.

the species A_{\max} were 31.6, 27.8 and 38.7, 33.4 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at 20 °C and 30 °C, respectively.

The photosynthetic response was linear between 5 °C and 25 and 23 °C for the two species, respectively, and reached its maximum at 32.5 and 30.8 °C, respectively (Figure 4). The photosynthetic capacity of mountain ash and grey alder at the daily mean maximum

July temperature (14.1 °C) was only 57% and 63%, respectively, of photosynthesis at optimum temperature (Table 2). The photosynthetic capacity at monthly mean maximum July temperature (21.6 °C) was 77% and 82%, respectively. The maximum tempera-

Table 3. The activation energy ΔH_a , deactivation energy ΔH_d and empirical scaling coefficient C ($^{\circ}\text{K}$) for three tree species growing in eastern Iceland. Shown are mean values \pm s.e. for $n=3-4$. Shared letters indicate no significant difference ($P>0.05$).

	Mountain birch	Mountain ash	Grey alder
ΔH_a (kJ mol $^{-1}$)	31.09 \pm 2.44 a	31.06 \pm 2.52 a	28.09 \pm 0.55 a
ΔH_d (kJ mol $^{-1}$)	152.3 \pm 6.5 a	160.5 \pm 9.1 a	172.3 \pm 24.2 a
C ($^{\circ}\text{K}$)	315 \pm 1.1 a	313 \pm 1.4 a	311 \pm 1.3 a

tures recorded in July during 1961-1990 (26.2 $^{\circ}\text{C}$) would have yielded 89% and 93% of the maximum photosynthetic capacity for the two species, respectively. The activation energy for mountain ash and grey alder was 31 and 28 kJ mol $^{-1}$, respectively, and the deactivation energy for the two species was 161 and 172 kJ mol $^{-1}$, respectively, (Table 3).

Species differences

Mountain birch was found to have the highest optimum temperature for light- and CO_2 saturated photosynthesis, or 35.1 $^{\circ}\text{C}$ (Table 2). This was a higher temperature optimum than for grey alder (30.8 $^{\circ}\text{C}$; $P=0.05$), but not significantly different from mountain ash (32.5 $^{\circ}\text{C}$; Table 2).

Because of the higher T_{opt} of birch than alder, birch was significantly more limited by temperature (relative to optimum temperature) in the range between 5 $^{\circ}\text{C}$ to 30 $^{\circ}\text{C}$ ($P<0.05$). Only at the high temperature of 35 $^{\circ}\text{C}$ did the birch have a significantly higher $A_{\text{max, rel}}$ than alder ($P<0.05$; Table 2). No significant differences were found between birch and mountain ash or alder and mountain ash at any measured temperature (Table 2).

At optimum temperature, the actual photosynthetic capacity was 18.7% and 7.3% higher in birch than in alder and mountain ash, respectively (Figure 3). The above differences were significant between birch and alder ($P<0.05$), but not between birch and mountain ash. However, when compared at 10 $^{\circ}\text{C}$ the three species had approximately the

same actual photosynthetic rate (Figure 3). At 20 $^{\circ}\text{C}$ and 30 $^{\circ}\text{C}$ there were significant differences in the actual photosynthetic rate between birch and alder ($P<0.05$), but there was neither a significant difference between birch and mountain ash nor alder and mountain ash (Figure 3).

In spite of some significant differences in the optimum temperature and relative temperature limitations between the three species, there were no significant differences found in the basic physical constants of the temperature response curves, ΔH_a (activation energy), ΔH_d (deactivation energy) or C (an empirical coefficient; Table 3).

DISCUSSION

Mountain birch had the highest optimum temperature of the three tree species tested and grey alder had a lower optimum temperature than mountain ash (Table 2). This was not what was expected from the differences in northward distribution in Scandinavia and in mean summer temperatures at the place of origin (Table 1). All species had higher temperature optima than could be expected from the local climate at the place of origin (Table 1). These results indicate that the general assumption that plant species usually have a temperature optimum for photosynthesis that matches the average daytime temperature encountered in the species' natural environment (e.g. Larcher 2003) may not be valid for species close to their northern growth limit or close to the altitudinal tree line.

In most of Scandinavia, mountain birch ecosystems are limited to a narrow altitudinal belt, just above the coniferous forest and below the tree line on mountain slopes (Aas & Faarlund 2001, Carlsson et al. 1999). In Iceland, birch is also most commonly found at higher altitudes above the lowland, 200-400 m a.s.l. (Steindórsson 1964). It could therefore

be expected that the species should be well adapted to the harsh alpine environment, with low temperature requirements. The finding in the present study that optimum temperature of mountain birch was as high as 35.1 °C was therefore a surprise. The optimum was identical to the reported temperature optimum of light- and CO₂ saturated photosynthesis of the closely related but more boreal species, silver birch (*Betula pendula* L.; Dreyer et al. 2001). Earlier studies on mountain birch have reported temperature optima of net-photosynthesis ranging from 11 – 16 °C (Sveinbjörnsson 1983, Skre 1993). Jurik et al. (1985) also reported a lower temperature optimum of 24 °C for the North American paper birch (*Betula papyrifera* Marsh.). These earlier studies, however, measured temperature responses at non-saturated [CO₂]. Hence the photosynthetic response to higher temperatures could have been confounded by stomatal limitation, due to high evaporative demand. Such temperature response curves may not show the actual temperature optimum of leaf photosynthesis.

Bearing in mind the high temperature optimum of mountain birch in the present study, it seems most probable that it is rather a strong competition with other tree species (Scandinavia) or with lowland land use (Iceland) that has created the current distribution patterns than adaptation to a harsh climate. Mountain birch is able to take up nutrients at lower soil temperatures than most other tree species and the nutrient availability seems to be the limiting factor that controls the treeline in Iceland and northern Sweden (Sveinbjörnsson et al. 1992, 1993, Weih 1998). The ability to survive at low temperatures, even if the growth is severely limited by low carbon uptake by photosynthesis, gives mountain birch a competitive advantage over other plant species of lower stature that can colonise this harsh habitat. This enables mountain birch to form relatively stable ecosystems under these conditions (Aas & Faarlund 2001). However, it does not mean that mountain birch today is mainly found where the environment is optimal for its growth and survival.

Inhibition of photosynthesis of vascular plants by high temperature has generally been attributed to an impairment of electron transport activity (light reactions), caused in part by changes in membrane fluidity (e.g. Murakami et al. 2000, Larcher 2003). It was assumed that this also applied to the three tree species of the present study. Therefore the photosynthetic measurements were done at saturating CO₂ levels, which allowed us to decouple the response to temperature from the response to high transpiration demand (stomata limitation). There are, however, some recent reports showing some plant species being more limited at high temperatures by some Calvin cycle reactions (dark reactions), specifically the inactivation of the Rubisco enzyme (e.g. Salvucci & Crafts-Brandner 2004). This is unlikely to have affected the present results for mountain birch, since the closely related silver birch has been found to have a higher temperature optimum for dark reactions than for light reactions (Dreyer et al. 2001).

Recently, Hjelm and Ögren (2003) reported that mountain birch can adjust its photosynthetic capacity to a 30 day low temperature treatment by a 30% increase in capacity at 10 °C. Furthermore, paper birch and silver birch have been found to acclimatise to high temperatures (Ranney 1994). Hence, birch has a certain capacity to adapt its photosynthetic system to long-term changes in temperature. These acclimation processes seem, however, not to be able to bring the photosynthetic system of the Icelandic mountain birch or the other two species into equilibrium with the local climate close to their northern growth limit.

Mountain birch seedlings are known to grow vigorously in nurseries in Iceland. They may grow as much in one or two years, when kept under glass or in greenhouses, as during 5-10 years in the field. This has commonly been related to better nutrient availability in the nursery than in the field. The present study, however, indicates that this could also, indeed, be due to the high temperature optimum of birch. A few degrees' increase in temperature

in the greenhouse may, in combination with good nutrient and water availability, have large interactive effects on the carbon uptake and growth. Mountain birch is also known to show strong growth differences with altitude and have large site-to-site differences in Iceland (e.g. Sveinbjörnsson et al. 1993). Jónsson (2004) has shown that differences in growth rate are one of the main explanations for height differences in Icelandic birch. Again, the high temperature optimum may contribute to the apparent plasticity of the growth rate of the species.

ACKNOWLEDGEMENTS

The authors thank the staff of the Forest Service station at Hallormsstaður for help in the field and Bjarni Th. Kjartansson for the making the site map. This work was a part of a larger study, ICEWOODS, which included studies on the ecology and the physiology of mountain birch, and was also a part of a M.Sc. study of the first author at the University of Copenhagen, under the supervision of Professor Helge Ro Poulsen and Bjarni D. Sigurdsson. The Central Bank of Iceland, the Icelandic Research Council and the Icelandic Agricultural Fund are acknowledged for financially supporting the fieldwork of the first author in 2003.

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Manuscript received 21 February 2005

Accepted 14 June 2005

