

Changes in air and soil temperatures in three Icelandic birch forests with different land-use histories

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ABSTRACT

Typically, temperature effects on plant communities are examined as external, large-scale climatic factors influencing ecosystem functions. Our study of three Icelandic birch woodland (*Betula pubescens* Ehrh.) sites suggests that local land-use activities can create site-specific feedback loops that change soil temperature regimes. Land-use history, air and soil temperatures, and moss thickness were examined at the upper forest limit and within three birch woodlands in East and North Iceland. Land-use activities were associated with moss thickness and soil temperature differences; moss thickness was significantly greater at the forest limit at Hallormsstaður, which has been protected from grazing for approximately 80 years, than at the two grazed, but otherwise comparable study sites. Correspondingly, maximum monthly soil temperatures were up to 3.5° C higher at the grazed sites than at Hallormsstaður. We conclude that changes in land use (i.e. introducing or excluding sheep grazing) can shift moss dominance and change soil temperature patterns in birch forests growing at the forest limit. These changes could not be deduced through analyses of air temperatures alone. Thus, monitoring soil temperature is important in ecosystems where temperature strongly controls plant and microbial structure and function, such as the birch tree line in Iceland. While it is appropriate to view large-scale climatic factors as a determinant of tree line dynamics, land-use history is a critical driving variable of site characteristics such as microclimate and, subsequently, the site's ecology.

Keywords: *Betula pubescens*, climate, grazing, land use, moss, tree line

YFIRLIT

Breytileiki í loft- og jarðvegshita í þremur íslenskum birkiskógum með mismunandi landnýtingarsögu

Yfirleitt eru áhrif hitafars á plöntusamfélög talin til utanaðkomandi þátta sem hafa afleiðingar fyrir virkni vistkerfisins. Rannsóknir á þremur íslenskum birkiskógum (*Betula pubescens* Ehrh.) benda hins vegar til þess að landnýting geti kallað fram svörum gróðurs sem breytir hitafari jarðvegs. Saga landnýtingar, loft- og jarðvegshiti og þykkt mosa voru rannsökuð við skógarmörk og innan þriggja skóglenda á Austurlandi. Þykkt mosa, sem var undir áhrifum frá landnýtingu, tengdist jarðvegshita. Mosalagið var marktækt þykkara við skógarmörk í Hallormsstaðaskógi, sem hefur verið friðaður fyrir beit í um 80 ár, en það sem mældist í tveimur ófriðuðum en að öðru leyti sambærilegum skógum. Þessu fylgdi að hámarks jarðvegshiti (mánaðarmeðaltal) var allt að 3,5°C hærri í beittu skógunum en í friðaða skóginum á Hallormsstað. Ályktað er að breytingar á landnýtingu (þ.e. sauðfjárbreit eða friðun fyrir beit) geti breytt því hversu ríkjandi mosi verði í svarðlaginu, sem breytir hitafari jarðvegs við skógarmörk í birkiskógum. Þessi áhrif koma ekki fram við mælingar á lofthita einum og því eru mælingar á jarðvegshita mikilvægar í vistkerfum þar sem hiti ræður miklu um vöxt og virkni plantna og örvera, t.d. við skógarmörk á Íslandi. Þótt víðeigandi sé að líta á loftslag sem helsta áhrifavald við skógarmörk, er saga landnýtingar mikilvæg breyta og áhrifavaldur varðandi ýmsa eiginleika svæðis svo sem örloftslag og þar af leiðandi vistfræði þess.

INTRODUCTION

Land uses and their associated legacies can have significant effects on ecological patterns and processes in vegetative communities (Sala et al. 2000). Furthermore, legacies of multiple disturbances can interact and/or accumulate in a landscape to profoundly alter its ecology (Beard et al. 2005). Although the location of the tree line is strongly driven by temperature patterns (Tranquillini 1979), tree line structure and function also may be significantly affected by other factors such as land-use activities. In particular, any land-use activity that alters temperature regimes will impact patterns of vegetative growth. Plant growth is affected by altered temperature regimes because temperature controls plant physiological functions, explaining in part why plants are adapted to particular climatic conditions.

The difficulty of separating the effects of several interacting disturbance factors has reduced the ability of researchers to understand how cumulative disturbances affect ecosystem resilience at both global and local scales. Especially in field experiments, it can be difficult to estimate the impact of different disturbance factors.

Climate has a significant impact on ecosystem processes at the forest limit in Iceland as elsewhere (Sveinbjörnsson 1993). Land use in Iceland has been well documented for several centuries, and large-scale anthropogenic dis-

turbances have only occurred since the Norse settlement in the early 870s C.E. (Amorosi et al. 1997). This makes Iceland an ideal location to examine the ecological impacts of multiple disturbances, such as the interactions between climate and human land-use legacies. Typically, there are so many layers of historical human disturbance at a site that it can be difficult to tell which disturbance legacies are driving current ecological patterns and processes. Additionally, the vegetative community structure is relatively simple in Iceland, which makes vegetation classification and tracking vegetative change more straightforward (see Ragnarsson & Steindórsson 1963). It was hypothesized that, in addition to the large-scale controls of global and regional climate, site-specific land-use history would affect soil temperatures through changes in plant community structures and processes. Thus, this research was designed to address the impact of multi-scale disturbances (both natural and anthropogenic) on vegetative communities at high altitude and latitude sites.

MATERIALS AND METHODS

Site selection

Sites were selected based on their climatic patterns and history of sheep grazing, two major determinants of vegetation composition and distribution in Iceland (Amorosi et al. 1997). Selected sites had a well documented history

of sheep grazing (or absence of sheep grazing) and were located well away from other sources of human-induced disturbance such as dwellings or other kinds of agricultural and human activities.

Site description

The three selected sites, 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, are forests composed of the only native forest-forming species in Iceland, *Betula pubescens* Ehrh. (Figure 1). Sites were selected along a gradient of ecological stress (i.e., levels of sheep grazing and climatic stress) with Site 1 having relatively little cumulative stress, and Site 3 having more cumulative stress than either of the other two sites.

Site 1 (Hallormsstaður) is located in eastern Iceland near the town of Egilsstaðir, and in a valley adjacent to Site 2. Thus, these two sites have similar climatic regimes, and the main difference between Sites 1 and 2 is their grazing history during the last century. Site 1 has a northwestern exposure, with the forest limit ranging from 222 to 254 meters above sea level and a latitude and longitude of 65° 5'N and 14°45'W, and slopes ranging from 10-20°. Site 1 belongs to and is managed by the Iceland Forest Service (Skógrækt Ríkisins)

and is one of the largest remaining birch forests in Iceland. In 1899, in response to the recognition that high levels of grazing were threatening the existence of birch forests, the Icelandic parliament passed an act to protect Hallormsstaður from grazing (Blöndal 1995). Fences to exclude sheep were built between 1905 and 1908 along the edges of the forest, traversing up the mountainside in two locations. In 1925, a fence was placed above the tree line to prevent sheep from entering the forest by way of higher elevations.

Site 2 (Eyjólfsstaðir) has never been effectively protected from grazing. However, its primary use is not for grazing as the land is owned and managed by the East-Iceland Forestry Society (Skógræktarfélag Austurlands). While there is still grazing at Site 2, the level of grazing today is not as intensive as it was in the past. Site 2 has a northwestern exposure, with the forest limit ranging from 247 to 273 meters above sea level, a latitude and longitude of 65° 10'N and 14°28'W, and slopes ranging from 10-20°.

Site 3 (Þórðarstaðir) is in the valley Fnjóskadalur in northern Iceland and is managed by the Iceland Forest Service. Site 3 has been subjected to high levels of grazing in the past, although the numbers of sheep

grazing today at this site have decreased, as they have across the rest of Iceland (Icelandic Farmers Association 2000). It differs from the other two sites in terms of its more northern latitude, higher elevation and shorter growing season. Þórðarstaðir is protected from grazing by a fence at its lower elevations, but the plots used for this research, at the forest limit and 100 m in elevation below the forest limit, have never been fenced to exclude sheep. Site 3 has a western exposure, with the forest limit ranging from 402 to 425 meters above sea level, a latitude and

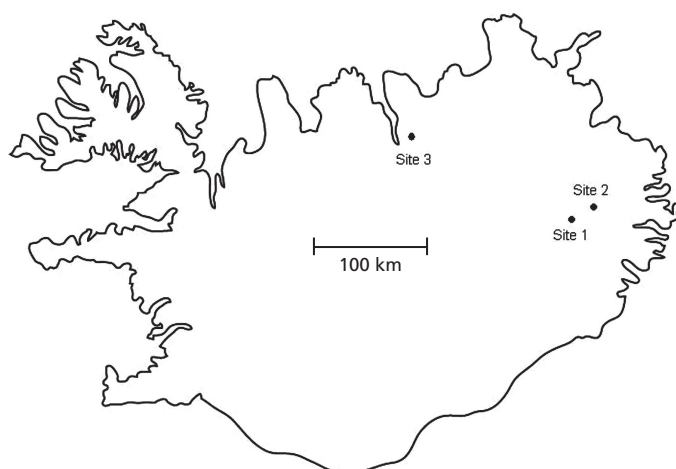


Figure 1. Locations of the field study sites. Site 1 is Hallormsstaðaskógur, Site 2 is Eyjólfsstaðaskógur and Site 3 is Þórðarstaðaskógur.

longitude of 65° 39'N and 17° 50'W, and slopes ranging from 15-25°.

While the levels of grazing at Sites 2 and 3 were not specifically quantified, broad patterns of free-ranging grazing in Iceland applicable to these sites have been tracked by the Icelandic Farmers Association. Since the mid 1970s, grazing levels have dropped across Iceland. For example, in 1978 there were 2,007,314 sheep (including lambs) grazing in Iceland. This number dropped to 1,073,542 in 1999. Icelandic land managers have been able to observe positive impacts on birch regeneration following overall reduction or exclusion of sheep. The positive impact of decreased grazing on the birch ecosystem was also observed after winter sheep grazing significantly declined in the mid 20th century (Eysteinnsson, pers. obs.).

Temperature measurement and instrumentation

At each of the three sites, one weather station recorded air and soil temperature at the forest limit and one weather station recorded air and soil temperature at 100 m in elevation below the forest limit (in the forest). For simplicity, temperature recorded at an elevation of 100 m below the forest limit is referred to as "100m." Weather station locations were randomly assigned at each forest limit and 100m elevation. Temperature data were auto-

matically recorded every 15 minutes at each of the sites for one calendar year, beginning with the 2000 summer field season. Air and soil temperatures were measured using HOBO H8 Pro Series dataloggers (Onset Computer Corporation). Air sensors were located at 1.5 m above-ground (± 10 cm). Soil sensors were placed at a depth of 15 cm into the mineral soil (± 5 cm).

Vegetation classification

Sites were characterized with the vegetation classification system used by the Iceland Forest Service (Ragnarsson & Steindórrsson 1963) (Table 1) in late October to early November of 2002 (Table 2). Moss thickness was measured at 10 randomly selected locations in association with each weather station at the forest limit and at 100m.

Additionally, average tree height and crown cover were estimated at all three sites. Crown cover estimates used a four point classification system (0-10%, 10-33%, 33-66% and >66% crown cover) (Iceland Forest Service, unpublished management plans).

At the forest limit, average tree height was 2 m, 1.5 m and 1.5 m for Sites 1, 2 and 3 respectively, and birch crown cover was 33-66% at all three sites. Upright *Salix lanata* L. along with *Betula nana* L. were common shrubs at Site 1, but they were considerably smaller and less common at the other two sites. The birch

Table 1. Vegetation classification scheme, structured in classes S1, S2, and S3 by the Iceland Forest Service (Ragnarsson & Steindórrsson 1963).

Classification characteristic	Class S1	Class S2	Class S3
Birch forest understory classification	Herbaceous understory with no ericaceous species	<i>Vaccinium</i> sp. present (S2a) to dominant (S2b), but without <i>Empetrum</i> sp. or <i>Arctostaphylos</i> sp. (L.) Spreng.	<i>Empetrum</i> sp. and/or <i>Arctostaphylos</i> sp. present (S3a) to dominant (S3b)
Fertility characteristics associated with species	High fertility	Medium fertility	Low fertility associated with <i>Empetrum</i> sp.

at the forest limit consisted most commonly of young, multi-stemmed shrubs at all three sites, with some taller trees, especially at Site 1. Dead or dying trees were absent, indicating establishment of birch on the sites within the past few decades. Understory vegetation at the forest limit was dominated by *Vaccinium uliginosum* L. - *Empetrum nigrum* L. heath at Sites 1 and 2 and by *Vaccinium myrtillus* L. heath at Site 3 (Table 2).

At the 100m plots, average tree height was close to 4 m, with the tallest trees reaching 5-7 m, and crown cover was greater than 66% at all three sites. All three 100m sites were even-aged, middle-aged birch woods with few to no very old or standing dead trees and little regeneration either by stump sprouts or seedlings. *Vaccinium myrtillus* and *Deschampsia flexuosa* (L.) Trin. were dominant understory species in the 100 m plots at Sites 2 and 3, whereas Site 1

had an *Equisetum pratense* Ehrh. - *Hierochloa odorata* (L.) Beauv. - *Rubus saxatilis* L. dominated understory, characteristic of ungrazed birchwoods and a more fertile site (Table 2). The soils at all sites were Andosols, the most common soil type on mesic sites in Iceland (Arnalds 2006).

Data analysis

SPSS (version 10.0.5) was used to convert the 15-minutes temperature readings to calculate monthly air and soil temperature averages. Averages were based on a single calendar year that started 11 July, 2000 (when the weather station installation was completed at all three sites) and ended 10 July, 2001. Cross-site comparisons for July were kept consistent by using data from 11 to 31 July in 2000 and 1 to 10 July in 2001. SigmaPlot (2000) was used to plot monthly averages.

Table 2. Vegetation classification at the three selected sites: 1: Hallormsstaðir, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland. S1 is an herbaceous understory without ericaceous species. S2 has *Vaccinium* sp. either present (S2a) or dominant (S2b). S3 has *Empetrum* sp. or *Arctostaphylos* sp. either present (S3a) or dominant (S3b).

Site characteristic	Site 1	Site 2	Site 3
Understory vegetation classification at the Forest Limit	S3a: <i>Vaccinium uliginosum</i> , <i>Empetrum nigrum</i> , <i>Deschampsia flexuosa</i> (with <i>Betula nana</i> , <i>Salix lanata</i>)	S3a: <i>Vaccinium uliginosum</i> , <i>Empetrum nigrum</i> , <i>Deschampsia flexuosa</i>	S2b: <i>Vaccinium myrtillus</i> , <i>Deschampsia flexuosa</i> (with low growing <i>Betula pubescens</i>)
Understory vegetation classification at 100m	S1: <i>Equisetum pratense</i> , <i>Hierochloa odorata</i> , <i>Rubus saxatilis</i> (with <i>Ranunculus acris</i> L., <i>Agrostis tenuis</i> Sibth., <i>Taraxacum</i> sp. Wigg.)	S2b: <i>Vaccinium myrtillus</i> , <i>Deschampsia flexuosa</i> , <i>Vaccinium uliginosum</i>	S2b: <i>Vaccinium myrtillus</i> , <i>Deschampsia flexuosa</i>
Main moss species present	<i>Hylocomium splendens</i> (Hedw.) Br. Eur., <i>Rhytidiadelphus squarrosus</i> (Hedw.) Warnst.	<i>Hylocomium splendens</i> , <i>Rhytidiadelphus squarrosus</i>	<i>Hylocomium splendens</i> , <i>Rhytidiadelphus squarrosus</i> , <i>Rhacomitrium canescens</i> (Hedw.) Brid.

SPSS was used to calculate daily temperature averages, which were then used to calculate degree days and number of days above 0°C. Degree days were calculated by taking the sum of the daily temperature averages minus a base value (0°C) over the course of a selected time period (one calendar year).

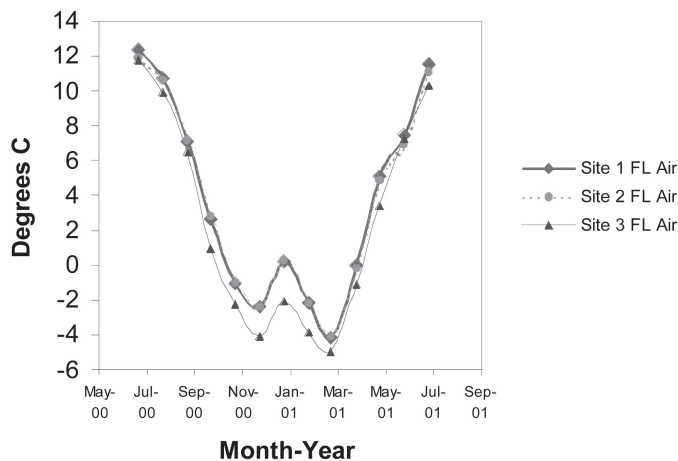


Figure 2. Plots representing mean monthly air temperatures (1.5m aboveground) at the forest limit (FL Air) recorded in 2000 and 2001 in at Sites 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland.

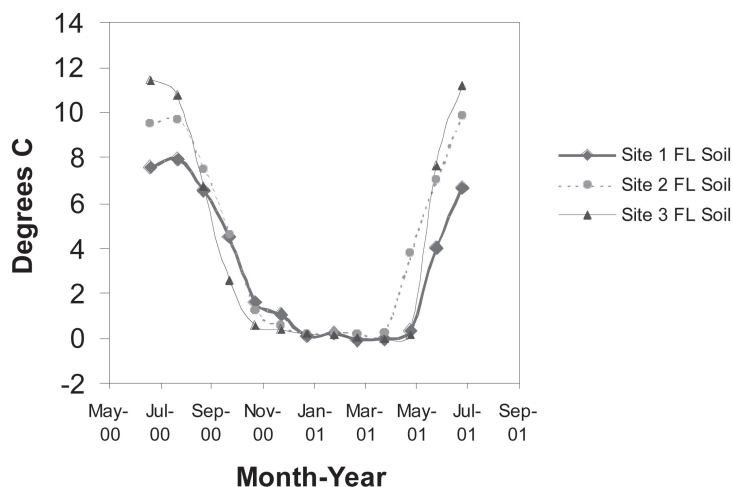


Figure 3. Plots represent mean monthly soil temperatures (15 cm depth in the mineral soil) at the forest limit (FL Soil) recorded in 2000 and 2001 at Sites 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland.

RESULTS

At the forest limit, a cross-site comparison of air temperatures revealed the following patterns: monthly air temperatures at Sites 1 and 2 did not differ from each other during the study year, whereas Site 3 air temperatures were consistently lower, especially during winter (Figure 2). A comparison of soil temperatures

showed that monthly averages at all three sites were different from one another throughout the growing season but similar from December through April (Figure 3). During the growing season, Site 1 had the lowest average monthly soil temperatures, while Site 3 had the highest (Figure 3). Although average monthly soil temperatures were higher at Site 3 during the growing season than at the two other sites, this was not the case at the beginning of the growing season. In May, the average soil temperatures at Sites 1, 2, and 3 were 0.4°C, 3.8°C, and 0.2°C, respectively. Site 3 had the fastest cooling of the soil at the end of the 2000 growing season (August through November), while Site 2 had the earliest warming of the soil at the beginning of the 2001 growing season (Figure 3). The most rapid warming of the soil in the spring was observed at Site 3. Patterns of change in monthly soil temperatures did not track the air temperature patterns recorded at the forest limit.

At 100 m below the forest limit, average monthly air temperatures were very similar at all three sites throughout the growing season (Figure 4). Monthly changes in soil temperatures throughout the

year were parallel to patterns recorded at the forest limit sites, though less pronounced. Similar to the soil temperature patterns recorded at the forest limit, Site 1 had the lowest average monthly soil temperatures during the growing season and Site 3 had the highest (Figure 5). This pattern was also apparent during the winter months. Again, patterns of change in monthly soil temperatures did not track air temperature patterns at 100m.

The three sites had very different numbers of degree days depending on whether air or soil temperatures were examined (Table 3). When only considering air temperatures at the forest limit and 100m, Site 3 had the fewest degree days, Site 2 was intermediate, and Site 1 had the greatest number of degree days. In contrast, soil temperatures at 100m had the reverse pattern; Site 3 had the greatest number of degree days and Site 1 had the fewest. At the forest limit, the greatest number of degree days for soil temperatures was recorded at Site 2. A similar pattern to that observed with degree days was seen if days above 0°C was the selected variable (Table 3).

Daily snow depth measurements made at Lerkihlíð and Grímsárvirkjun, the two weather stations closest to the study sites, indicated that snow cover at Site 3 was likely continuous from 31 October, 2000 to at least 7 May, 2001. Sites 1 and 2, on the other hand, had as many as six snow-free periods during the winter, three of them lasting two weeks or more. The first snow at Sites 1 and 2 fell at roughly the same time as at Site 3

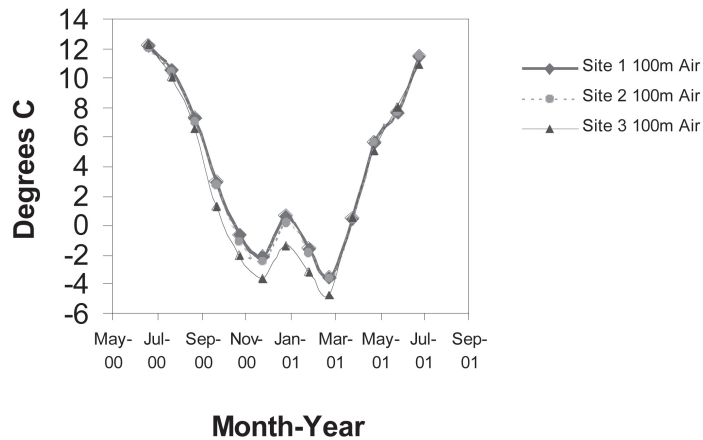


Figure 4. Plots represent mean monthly air temperatures (1.5 m above ground) at 100 m in elevation below the forest limit (100m Air) recorded in 2000 and 2001 at Sites 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland.

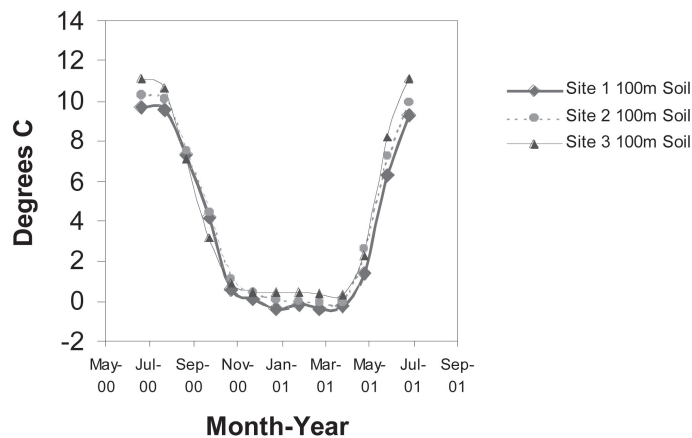


Figure 5. Plots represent mean monthly soil temperatures (15 cm depth in the mineral soil) at 100 m in elevation below the forest limit (100m Soil) recorded in 2000 and 2001 at Sites 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland.

(1 November, 2000) but the last snow disappeared on 27 April, 2001, at least 10 days earlier than at Site 3 (Icelandic Meteorological Office, unpublished data).

There was a significant difference in the thickness of moss layers across sites. At the forest limits, the thickest moss layer was recorded at Site 1 and the thinnest at Site 3

Table 3. Degree days (calculated using a base value of 0°C), number of days above 0°C recorded in 2000 at the forest limit and 100 m in elevation below the forest limit (100m), and precipitation data at Sites 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland. Precipitation data from the Icelandic Meteorological Office website (2007) and Iceland Forest Service website (2007).

	Site 1	Site 2	Site 3
Degree days (air)			
Forest limit	1570	1534	1284
100m	1630	1593	1462
Degree days (soil)			
Forest limit	1033	1381	1243
100m	1202	1341	1386
Number of days above 0°C (air)			
Forest limit	253	250	205
100m	263	255	234
Number of days above 0°C (soil)			
Forest limit	314	365	340
100m	231	288	365
30 year (1961-1990) mean annual precipitation at closest weather station (mm)	690.3	765.6	709.3

(Table 4). At 100m, moss layers were significantly thicker at Site 2 than Sites 1 and 3.

DISCUSSION

Most studies interpret temperature data in the context of large-scale global, regional, and seasonal factors that control plant community structure and function. While such factors are critical to ecological patterns and processes, this research suggests that land-use activities may also play an important role in a site's temperature regimes and therefore should also be considered. In most cases, it has been difficult to separate the impacts of different disturbances and other driving factors on ecosystem function. The unique attributes of Iceland's land-use history and climatic regime have allowed us to explore how the combination of large-scale climatic factors and site-specific

anthropogenic disturbances, such as land use, may create internal ecosystem feedback loops that alter soil temperature regimes and other ecosystem attributes. In particular, because soil temperature patterns did not track air temperature patterns at any of the three study sites, we have good reason to hypothesize that factors in addition to large-scale climatic and seasonal impacts are influencing soil temperatures.

The air temperatures recorded during this study reflected both the altitudinal and latitudinal location of the research sites and did not vary from expected ranges. As expected, air temperatures at Sites 1 and

2 were similar, and Site 3 had lower air temperatures and a shorter growing season than the other two sites. These data affirm previous hypotheses on seasonal temperature dynamics in northern and eastern Iceland, namely that the growing season in northern Iceland is approximately one week shorter than it is in eastern Iceland, based on repeated observations on the timing of bud burst and leaf senescence at Hallormsstaður and Vaglir (Iceland Forest Service unpublished records).

The soil temperature data did not parallel these air temperature patterns. In fact, soil temperature patterns were the opposite of those recorded for air temperatures, with soil temperatures during the growing season highest at Site 3 and lowest at Site 1. However, soil temperature patterns at the forest limit paralleled

Table 4. Moss depth in 2002 at the three selected sites: 1: Hallormsstaður, 2: Eyjólfsstaðir, and 3: Þórðarstaðir, Iceland. Mean values (\pm SE) followed by the same letter were not significantly different ($p \leq 0.05$). Analyses of significant differences were conducted across sites at the forest limit and 100m.

Moss depth	Site 1	Site 2	Site 3
Average moss depth (\pm SE) - Forest Limit	9.4 (\pm 0.9) a	4.2 (\pm 0.4) b	0.7 (\pm 0.3) c
Average moss depth (\pm SE) - 100m	0.3 (\pm 0.2) a	4.6 (\pm 0.3) b	0.8 (\pm 0.3) a

soil temperature patterns at 100m, suggesting that other variable(s) besides seasonal air temperatures were likely driving these consistent trends. This is significant, given that some hypotheses concerning the impact of climate on the tree line are based on air temperature alone (Köerner 1998). For this study, monitoring air temperature alone would have missed important microclimatic changes in the soil that are likely affecting vegetative community growth and persistence. Monitoring soil temperature is important when assessing the impact of global change factors on vegetative and microbial community structure and function.

The aspect of the sites might in part explain the different patterns observed in soil and air temperatures, as Site 3 has a western exposure, while Sites 1 and 2 have a northwestern exposure. However, since the aspects of Sites 1 and 2 are very similar, it is unlikely that aspect is driving the observed difference in soil temperature patterns between these two sites. A more plausible explanation for the cross-site patterns of soil temperature change is the significant differences in moss layer thickness recorded at the three sites, with Site 1 having the thickest moss layers and Site 3 the thinnest (Table 4). The thin moss layers at Site 3, which offer little buffering to soil temperature change, likely contributed to the observed rapid soil cooling after the 2000 growing season. It is also likely that the higher elevation and more northerly location (i.e., seasonal temperature affects) of Site 3 played an important role in rapid autumn cooling of the soil. However, in spite of the fact that air temperatures were similar at all three sites in the spring, and snow melt occurred approximately ten days later at Site 3 than at the other two sites, the most rapid soil warming was observed at Site 3, probably also driven by the limited buffering capacity of the thin moss layer. Thus, seasonal dynamics cannot be the only driving variable of soil temperature at Site 3. Interestingly, at the forest limit, the earliest increase in soil temperature was recorded at Site 2 (the more southerly of the two grazed sites) during the spring of 2001. These temperature changes at Site 2 also support the

hypothesis that a thin moss layer decreases the temperature buffering capacity of the soil and, furthermore, one would expect to observe this pattern earlier in the growing season at a more southerly site where snowmelt had occurred earlier. The thicker moss layer at Site 1 had the same insulating effect as the later snow melt at Site 3, delaying the start of spring soil warming. Taken together, these data suggest that soil temperatures are driven by a combination of seasonal dynamics and shifts in vegetation cover related to land use.

Exclusion of grazers in some arctic and sub-arctic communities is correlated with increases in the thickness of the moss layer, thereby affecting soil temperature dynamics (Van der Wal et al. 2001). It has also been observed in eastern Iceland that excluding grazing can result in the development of a thick moss layer (Guðleifsson et al. 1997). Alternatively, clearing of vegetation in boreal systems has been shown to cause increases in soil temperature (Van Cleve et al. 1993). Furthermore, grazing can have a significant effect on the species composition of an ecosystem, since grazers select the species they prefer to consume (Bryant & Chapin 1986, Fischer & Wipf 2002). This selective grazing can also affect the nutrient cycling of an ecosystem. Shifts in nitrogen cycling at Hallormsstaður, Eyjólfssstaðir, and Þórðarstaðir were in fact correlated with soil temperature, moss thickness, and land-use history (Hecht & Heltne 2005). At Sites 2 and 3, the impact of sheep on the composition of vegetation was apparent from the sheep trails which were deeply grooved and retained no vegetation, as well as from the grazing of birch leaves in the lower parts of the canopy (Hecht, pers. obs.).

The contiguousness and thickness of moss in the understory layer could conceivably be affected by a number of factors besides grazing; the most likely factors being precipitation, soil moisture, and competing vegetation. However, precipitation is similar at the three sites based on measurements of meteorological data taken near Sites 1, 2, and 3 (at Hallormsstaður, Grímsárvirkjun and Vaglir,

respectively) (Table 3). Although soil moisture was not measured, vegetation indicated that it did not differ much among the sites, none of them being excessively wet or dry. With the exception of the 100m plot at Site 1, understory vascular plant vegetation was similar in height and density among the sites. The dense herbaceous understory vegetation at Site 1 100m probably explains the lack of a well developed moss layer. We conclude that grazing effects, including trampling, most likely explain the differences in moss cover among the sites, especially at the forest limit. Since moss is also known to modulate soil temperature regimes (Van der Wal et al. 2001), the differences in moss thickness among the three forest limit sites likely explain the majority of differences in soil temperatures during the growing season recorded during this study.

Moss thickness cannot explain all the soil temperature changes observed during this study. For example, at the 100m plots, moss layers were significantly thicker at Site 2 than at Sites 1 and 3. However, Site 1 at 100m nonetheless had the lowest average monthly soil temperatures during the growing season and Site 3 at 100m had the highest. This seeming anomaly can be explained by the fact that the 100m plots at Site 1 had a completely different understory species composition, dominated by a dense cover of herbaceous vascular plants, including a layer of plant residues from previous years that had built up in the absence of grazing and which appeared to have a soil temperature buffering capacity similar to moss. The data also show that the differences in soil temperatures among the three 100m sites were less than the differences observed at the forest limit.

Excluding sheep grazing entirely (as is the case at Site 1) is likely to result in the development of a thick moss layer. This change in moss thickness will result in colder growing season soil temperatures, which will in turn reduce microbial activity. These changes may to some extent retard the expansion of the tree line to higher elevations. This conclusion is supported by the fact that the forest limit at

Site 1 is lower in elevation than the other two sites, despite its higher air temperatures. In comparison, a moderately grazed landscape may allow the forest limit to persist or expand to higher elevations, both because of thinner moss layers and as scarification increases contact of birch seeds and mineral soil (Magnússon & Magnússon 1990). A thinner moss layer at the forest limit is also correlated with higher soil temperatures during the growing season, which will increase the activity of the microbial community and therefore increase decomposition rates. Such changes should increase nutrient availability for the birch, allowing it to expand its range. In contrast, in a highly grazed landscape, thin moss layers (or the absence of moss) could increase microbial activity to the point that competition for nitrogen would occur between the more active soil microbial community and the birch. Under such conditions of increased decomposer activity, high soil temperatures may actually contribute to birch decline. Indeed, there was evidence of competition between microbes and birch for nitrogen at higher soil temperatures (Hecht & Heltne 2005). This is significant, given that there is strong competition for nitrogen in most boreal ecosystems (Archibold 1995). The absence of grazing at elevations close to the forest limit (i.e., 100 m in elevation below the forest limit) can have significant effects on the understory species composition found in each forest. In this study, understory dominance shifted from being ericaceous-dominated in a moderately grazed landscape to an Equisetum-dominated understory in the absence of grazing.

It is well known that biological activity is regulated by temperature. Within a certain temperature range, i.e., below values where heat damage occurs, metabolic rates increase with increasing temperature such that a coefficient (Q_{10}) has been developed to express the rate of change that occurs with an increase of 10°C (Kramer & Kozlowski 1979, Larcher 1995). It is also well established that temperature is a significant driving variable in tree line and forest limit ecology (Tranquillini 1979, Köerner 1998, Tuhkanen 1998, Sveinbjörnsson 2000).

Typically, the temperature variables most often thought to be important to tree line dynamics are the low air temperatures that limit plant growth and the short growing seasons that limit the time available for a plant to fix sufficient carbon to maintain its growth (Köerner 1998). However this research suggests that historical and current land-use activities in Iceland may be shifting soil temperature patterns critical to tree line growth in ways not previously considered. While global and regional climate are certainly a strong determinant of tree line, legacies of historical and present grazing patterns (including protection from grazing) can affect both the composition of the understory vegetation and the soil microclimate.

In conclusion, microclimate and land use can be closely linked, and land-use patterns can create an internal ecosystem feedback loop, modifying site microclimatic patterns. Thus, this study underscores the importance of considering how legacies of land-use history drive current ecological patterns and processes.

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REFERENCES

- Amorosi T, Buckland P, Dugmore A, Ingimundarson JH & McGovern TH 1997.** Raiding the landscape: Human impact in the Scandinavian North Atlantic. *Human Ecology*. 25: 491-518.
- Archibold OW 1995.** *Ecology of World Vegetation*. London: Chapman and Hall. 528 p.
- Arnalds Ó 2006.** *Skógarmold* [Forest soil]. In Halldórsson, G. (ed.), *Skógarbók Grænni Skóga*. Landbúnaðarháskóli Íslands. pp 77-80 (In Icelandic).
- Beard KH, Vogt KA, Vogt DJ, Scatena FN, Covich AP, Sigurdardóttir R, Siccama TC, & Crowl TA 2005.** Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. *Ecological Monographs*, 75, 345-361.
- Blöndal S 1995.** *Innfluttar trjategundir í Hallormsstaðaskógi* [Exotic tree species in Hallormsstaður forest]. Iceland Forest Service, Hallormsstaður, Iceland. 56 p. (In Icelandic).
- Bryant JP & Chapin III FS 1986.** Browsing-woody plant interactions during boreal forest plant succession. In VanCleve K, Chapin III FS, Flanagan PW, Viereck L A & Dyrness CT (eds.), *Forest Ecosystems in the Alaskan Taiga*. Springer-Verlag, 213-225.
- Fischer M & Wipf S 2002.** Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biological Conservation* 104, 1-11.
- Guðleifsson BE, Hallgrímsson H & Lárusson Þ 1997.** Gróðurskemmdir í Fljótsdal 1996 og 1997 (Vegetation damage in Fljótsdal 1996 and 1997). *Skógræktarritið* 1997, 111-116. (In Icelandic).
- Hecht B & Heltne P 2005.** Case 2.4. Icelanders and their forest history: A thousand year-old humans and nature history controlling resilience and species composition in forests today. In Vogt KA, Honea JM, Vogt DJ, Edmonds RL, Patel-Weynand T, Sigurðardóttir R & Andreu MG (eds.),

- Forests and Society: Sustainability and Life Cycles of Forests in Human Landscapes*. CABI Publishing, England, 54-59.
- Icelandic Farmers Association 2000**. Icelandic Agricultural Statistics 2000. Reykjavik: The Farmers Association of Iceland.
- Iceland Forest Service website 2007**. <http://www.skogur.is/?PageID=213>
- Icelandic Meteorological Office website 2007**. http://www.vedur.is/vedurfar/yfirlit/m6190/Grimsarvirkjun_575_med6190.txt
- Köerner C 1998**. A re-assessment of high elevation tree line positions and their explanation. *Oecologia* 115, 445-459.
- Kramer PJ & Kozlowski TT 1979**. *Physiology of Woody Plants*. Academic Press. 411 p.
- Larcher W 1995**. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups*. 3rd ed. Springer-Verlag, 506 p.
- Magnússon SH & Magnússon B 1990**. Birkisáningar til landgræðslu og skógræktar [Direct seeding of birch for land reclamation and afforestation]. *Skógræktarritið* 1990, 9-18. (In Icelandic).
- Ragnarsson H & Steindórsson S 1963**. Gróðurannsóknir í Hallormsstaðaskógi [Vegetation research in Hallormsstaður forest]. *Skógræktarritið* 1963, 32-59. (In Icelandic).
- Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oosterheld M, Poff NL, Sykes MT, Walker BH, Walker M & Wall DH 2000**. Global biodiversity scenarios for the year 2100. *Science* 287, 1770-1774.
- Sveinbjörnsson B 1993**. Performance of mountain birch in different environments in Sweden and Iceland: Implications for afforestation. In: Alden J, Mastrantonio JL, & Ødum S. (eds.), *Forest development in cold climates*. Plenum Press, 79-88.
- Sveinbjörnsson B 2000**. North American and European tree lines: External forces and internal processes controlling position. *Ambio* 29, 388-395.
- Tranquillini W 1979**. *Physiological Ecology of the Alpine Timberline*. Springer-Verlag. 137 pp.
- Tuhkanen S 1999**. The northern timberline in relation to climate. In: Kantiaanpää S, Tasanen T & Sutinen M-L (eds.) Sustainable development in northern timberline forests. *Finish Forest Research Institute. Research Papers* 734, 29-61.
- Van Cleve K, Yarie J, Erickson R & Dyrness CT 1993**. Nitrogen mineralization and nitrification in successional ecosystems on the Tanana river floodplain, interior Alaska. *Canadian Journal of Forest Research* 23, 970-978.
- Van der Wal R, Van Lieshout SMJ & Loonen MJJE 2001**. Herbivore impact on moss depth, soil temperature, and arctic plant growth. *Polar Biology* 24, 29-32.

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