Impacts of sheep grazing on germinable seeds in the Icelandic Highlands

Paula Sierro Miguel

Faculty of Life and Environmental Sciences
University of Iceland
2017

Impacts of sheep grazing on germinable seeds in the Icelandic Highlands

Paula Sierro Miguel

12 ECTS thesis submitted in partial fulfillment of a
Baccalaureus Scientiarum degree in Biology

Supervisors
Ingibjörg Svala Jónsdóttir
Isabel Catalán Barrio

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Reykjavik, June 2017

Impacts of sheep grazing on germinable seeds in the Icelandic Highlands
12 ECTS thesis submitted in partial fulfillment of a *Baccalaureus Scientiarum* degree in Biology

Copyright © 2017 Paula Sierro Miguel
All rights reserved

Faculty of Life and Environmental Sciences
School of Engineering and Natural Sciences
University of Iceland
Askja, Sturlugata 7
IS-101, Reykjavik
Iceland

Telephone: 525 4000

Bibliographic information:
Paula Sierro Miguel, 2017, *Impacts of sheep grazing on germinable seeds in the Icelandic Highlands*, BSc thesis, Faculty of Life and Environmental Sciences, University of Iceland, pp. 38.

Printing: XX
Reykjavik, Iceland, 06 June 2017

Abstract

Iceland is nowadays the European country with more active soil erosion. Combined with harsh climatic conditions and frequent volcanic activity, sheep grazing has been pinpointed as one of the main reasons for the high degree of vegetation and soil degradation in Iceland. Beyond the direct damage to vegetation through feeding and trampling, sheep grazing can also influence vegetation recovery affecting the production and dispersion of seeds, or the occurrence of bare ground providing substrate for aeolian deposition. The goal of this study was to analyze the impact of sheep grazing on seed rain and aeolian deposition in summer rangelands of Iceland. We studied three sites (Auðkúluheiði, Skeiðarársandur and Þeistareykir), with different susceptibility to soil erosion. Within each site we placed 10-12 plots on each of 2 habitats with contrasting vegetation cover. Sheep grazing was excluded from half of the plots. We installed 3 seed traps in each plot, during 4 weeks in summer 2016 to collect seeds (counted by germination) and aeolian deposits. We found no effect of sheep exclusion neither on seed rain nor in aeolian deposition, but in general more seeds and less sand were recovered from the fenced plots. Seed rain and aeolian deposition were significantly greater in habitats with less vegetation cover. In Skeiðarársandur, rates of aeolian deposition were significantly greater. Further studies analyzing the number of seeds per specie and during longer periods are needed to characterize the habitats and sites and the effect of grazing on seed dispersal and aeolian deposition.

Table of Contents

List of Figures

List of Tables

Acknowledgements

I am immensely grateful to Isabel C Barrio for devoting me that much of her precious time, knowledge and patience apart from all her positive energy even when statistics come into play. Also to Ingibjörg Svala Jónsdóttir for sharing with me her wisdom and advice when I needed them more, in addition to her special sense for identifying seedlings. I would like to thank as well Bryndís Marteinsdóttir for her assistance with the germination method and the identification of the seeds, as well as for granting access to the sites in Skeiðarársandur, and Katrín Björnsdóttir for her help during the field season.

I am very thankful to Jaime Sierro Miguel and Ernesto Dieguez Casal for their support, comments and suggestions that were decisive in improving my manuscript and to Javier Sierro Martinez for his priceless statistical knowledge.

Finally, I want to thank Eduardo, Rosana and Ana, for helping me to develop the flotation method when I was lost in the laboratory and to Angel Luis da Silva Macias for his encouragement during the long afternoons processing samples and searching for references.

1 Introduction

With the establishment of the first human settlements in D.874, Iceland saw the onset of woodcutting and the introduction of livestock. Human impacts resulted in the disruption of the balance between the harsh climate and the erodible volcanic soils, and the sensitive vegetation of the island (Arnalds, 1987). From then on, vegetation and soil degradation have accelerated turning Iceland into the European country with more active soil erosion witnessed (Arnalds, 2000; Arnalds et al., 2001).

Nowadays, a large proportion of Iceland's vegetation cover has been lost, and land degradation is a critical environmental problem. Sheep grazing, together with harsh climate and frequent volcanic activity, is considered one of the main causes of extensive soil erosion in Iceland (Thorarinsson, 1961; Sigbjarnarson, 1969). However, sheep farming is still one of the main basis of Icelandic agriculture. To reduce environmental degradation and halt soil erosion, sustainable management plans that promote appropriate grazing densities for each site need to be implemented (Arnalds, & Barkarson, 2003). The design of such management plans should be informed by sound scientific evidence and studies are needed to assess the impact of sheep grazing in Iceland.

To this respect, it is of particular relevance for the design of the studies to take into account that several regions in Iceland differ greatly in their sensitivity to soil erosion. These differences are essentially founded on two factors.

One factor is the location relative to the volcanic active zone (outside or inside it), since volcanic activity results in the development of younger soils that are more prone to erosion and aeolian deposition (McDaniel et al., 2012). This is of particular relevance because Icelandic Andosols lack the phyllosilicates that procure other soils with cohesion, and they easily reach the liquid limit upon disturbance, changing their consistence from hard to liquid. This translates into potential massive erosion events if the soils are too saturated with water or if a disturbance occurs when the water content is high, even if they seem previously cohesive (Arnalds, 2015a).

Another factor is the vegetation cover. The lack of vegetation caused by different sorts of pressures, entails the presence of open areas of bare ground that are themselves more sensitive to erosion. In addition to that, some of this erosion processes generate advancing sand fronts that cover and damage vegetated areas generating new barren deserts in a positive feedback loop that further facilitates aeolian depositions (Arnalds, 2015b).

This in turns implies that sheep grazing impact on the ecosystem might vary across locations and therefore, the challenges to be faced when designing the management plans are varied and heterogeneous.

Sheep grazing has a strong impact on biodiversity, ecosystem function, plant biomass quantity and quality and soil stability (Ross et al., 2016). Up until now, most research has focused on how grazing by sheep affects the composition and structure of plant communities (Oom et al., 2008; Arnalds, 2015b) for example through its impact on the competitive interactions between plants (Jónsdóttir, 1991). However, fewer studies have investigated how sheep grazing affects natural revegetation processes.

There are two principal mechanisms considered to be involved in the revegetation process; plants may either be newly dispersed to the patch and colonize it, or survive disturbances in situ in the shape of adult plants, seeds, rhizomes, or viable propagules (Forbes et al., 2001). For its part, during the colonization process, different mechanisms come into play from which seed dispersal is particularly important in the denuded lands, since the establishment of propagules is a tougher challenge in this environment (Forbes et al., 2001). Seed dispersal is indeed, one of the major factors influencing plant community assembly (Marteinsdóttir, 2014). In the earlier phases of primary succession, long-distance dispersal generates the greatest income of seeds. It is only after some time that the constitution of a seed bank takes place and gradually becomes nurtured by the local seed production (Wood & Del Moral, 2000). Seed dispersal can be driven by endo- and exozoochory, anemochory, hydrochory, or autochory (Howe & Smallwood, 1982). In our study, we have focused more specifically in the seed rain (referring to the seeds dispersed by the wind and by autochory) as an indicator of seed limitation and potential for recovery of plant communities.

The aim of this study was to evaluate (1) the impact of sheep grazing on seed rain in different plant communities in summer rangelands of Iceland. To address this question, I conducted a field experiment excluding sheep grazing from plots located in two habitats with contrasting vegetation cover, at three sites in Iceland with differential erosion potential. To evaluate the seed rain I placed seed traps in the plots to recover the gathered seeds later on. My hypothesis was that sheep may affect seed production by selectively foraging on flowers or seeds, decreasing the amount of individuals of those species that are more palatable (Jónsdóttir, 1984). Therefore, I expected that in grazed areas seed rain might be constrained by the scarcity of flowers inducing a lower amount of seeds trapped compared to the fenced plots that were free of grazing pressure. In relation with that, I wanted also to assess the impact on the seed rain of other traits that are likely to shape seed dispersal: (2) vegetation cover and (3) aeolian deposition. In this vein, I expected vegetation cover to increase seed production and therefore seed dispersal. On the other hand, aeolian deposition could have a negative effect on seed dispersal trough suffocating vegetation, which would reduce its cover and productivity. With this objective, I performed also a preliminary analysis of the aeolian depositions that take place in the study sites comparing the amount of sand recovered in the seed traps. My presumption was that the type of habitat is conditioning aeolian deposition expecting that the presence of barren areas triggers erosion and consequently more sand would be recovered from the habitats with lower vegetation cover. In the same way, I hypothesized that sheep grazing could also be related with a greater erosion degree as a result of weakening the vegetation.

2 Methodology

2.1 Study sites

This study is part of a larger project aimed at analyzing the impact of livestock grazing in summer rangelands in Iceland. The project looks into different ecosystem components, and this study is focused on the effect of sheep grazing on seed dynamics. The study was conducted at three sites that differ in their susceptibility to soil erosion. The basis of site and habitat selection lays on two of the main features that determine the ecological conditions in Iceland: volcanic activity and vegetation cover.

Even though most of the soils in Iceland are of volcanic nature, only one part of the island is currently volcanic active. Within the volcanic active zone, there are sandy desert surfaces that are referred as aeolian environments (Arnalds, & Kimble, 2001). These areas are a source of dust and sediment particles that are dispersed by the wind in different ways with a dramatic influence in soils and ecosystems. In Iceland, due to the extreme wind speeds and the low density of the tephra, particles of several millimeters of diameter are transported (mainly by saltation movement), producing highly destructive wind erosion in the surroundings (Arnalds, 2015b; Arnalds, 2015c). Taking that into account, we chose three sites that differ in their susceptibility to soil erosion and their position relative to the volcanic active area which runs through the country form the south-west to the north-east. Þeistareykir lies within the volcanic active zone, Auðkúluheiði and Skeiðarársandur are outside the volcanic active zone, but the latter lies on a glacier outwash plain composed by very erodible materials (Figure 2.1) (Magnússon, 1997).

.

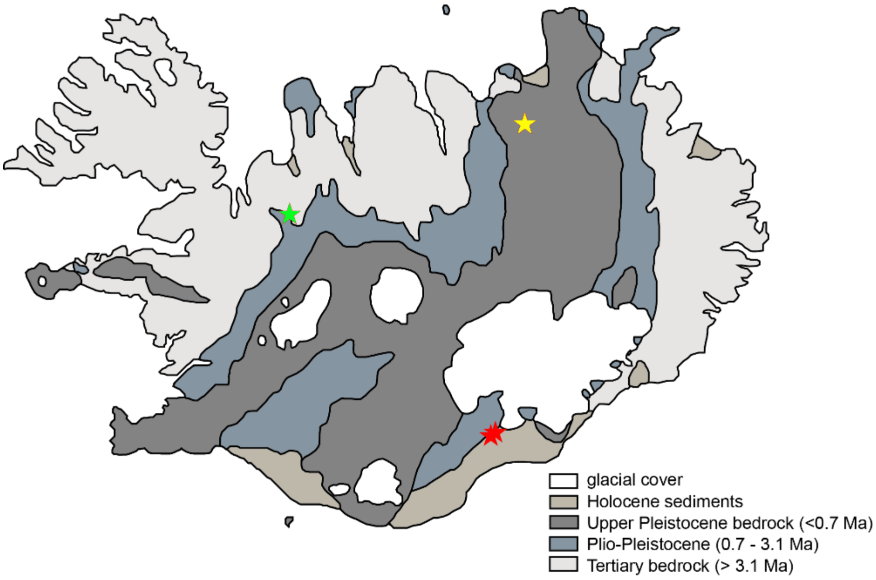


Figure 2.1 *Iceland geological map showing the study sites: ★ Þeistareykir, ★ Auðkúluheiði and ★ Skeiðarársandur. Dark grey area indicates young bedrock materials within the volcanic active zone of Iceland. Adapted from Kleine et al (in prep) with permission.*

On the other hand, one of the most relevant classifications of Icelandic soils relies on the differences in vegetation cover, sorting them into desert soils (vitric soils) and soils under vegetation (andosols). The main difference between them is that the andosols have more carbon and allophane than vitrisols, which deeply conditions their fertility. Following that approach we selected two different habitats in Auðkúluheiði and Þeistareykir: with vegetation cover (heath) and without vegetation cover (melur).

- **Melur** (also known as gravel desert): it has less than 10% of vegetation cover, mostly integrated by forbs (mainly *Arabidopsis petraea* and *Silene uniflora*) and grasses.
- **Heath**: the vegetation cover reaches more than 90% of the surface and is comprised mostly shrubs, more specifically *Betula nana*.

In Skeiðarársandur a single habitat was sampled.

2.1.1 Auðkúluheiði

Auðkúluheiði is located on the north-western highlands (65.13 N 19.67W) at 480 m elevation, above the potential tree line. It is a basaltic bedrock with loose glacial deposits on top.

Soils in Auðkúluheiði are classified as brown andosols. As such, their distinctive feature is the high content in carbon (above the minimum of 1.5 % C in the surface horizon), allophane (15% - 30%) and ferrihydrite (Feo 1% - 8%). They are also characterized by a high cation exchange capacity (CEC) and high water retention (>50% at wilting point) due to its porosity (Arnalds, 2004). Soil pH is in the neutral range (5-7) and C/N ratio is low, making the soil more favorable for plant growth (Jónsdóttir et al., 2005).

The climate is oceanic-subarctic-alpine, with long, usually very cold winters, and short, cold to mild summers.

The vegetation in the heath consists of a dwarf shrub community dominated by *Betula nana* with high abundance of bryophytes and lichens (Jónsdóttir et al., 2005). In the melur, however, vegetation cover is less than 10% and is dominated by forbs (*Arabidopsis petraea, Armeria maritima, Cerastium alpinum, Silene uniflora*) and graminoids (*Juncus trifidus, Festuca rubra*), with a prominent scarcity of shrubs.

2.1.2 Þeistareykir

Þeistareykir is located in the northeast region of Iceland, at the northern extension of the volcanic active zone (65.89 N 17.08 W) about 300 m above sea level, and also above the tree line. This site was chosen because it was within the volcanic active zone but with similar conditions to Auðkúluheiði in terms of habitat and sheep densities. However, this site is at lower elevation and closer to the coast, what leads to some differences in snow cover.

As in Auðkúluheiði, the soils are well-drained basaltic andosols with all the associated characteristics. The pH is higher than usual for this kind of soils; given dryness of the northeast part of Iceland and despite the high amount of aeolian additions that it receives, the leaching is minimal so there is not increment of the acidity (Arnalds, 2015d). At a nearby location, soil carbon was 0.3% at 38.4°C soil temperature. (Elmarsdóttir, Vilmundardóttir, & Magnússon, 2015).

The vegetation is similar to Auðkúluheiði with some distinctive features, such as a considerable greater abundance of *Empetrum nigrum* or the presence of some distinctive species like *Calluna vulgaris*.

2.1.3 Skeiðarársandur

Skeiðarársandur is located in the south of Iceland, (site A: 63°57′N, 17°09′W, site B: 63°56′N, 17°12′W). It is a large outwash plain (1,000 km^2) at the foot of the glacier Skeiðarárjökull.

The soil is 74% sand, 20% gravel and 6% silt/clay. It is classified as arenic vitrisol, characterized by a lower organic matter and allophane content than andosols. These soils also have less water holding capacity and CEC with a pH usually around 7 (Arnalds, 2004; Arnalds, 2015a; Arnalds, 2015d; Arnalds, 2015e). The mineralogy is dominated by volcanic glass. It is infertile, with low mean nitrogen and carbon concentrations (0.01% and 0.05%, respectively) (Marteinsdottir, 2007).

The climate in Skeiðarársandur is maritime, with cold summers and mild winters. In 2016, the mean annual air temperature was 6.0°C and the mean temperature between late August and late September was 9.4°C. Mean annual and summer precipitation was 1593 and 469 mm respectively in 2005, and 2070 and 433 mm respectively in 2006 (Icelandic Meteorological Office 2007, Fagurhólsmýri station).

It is a very sparsely vegetated area (<5% cover) in a pioneering successional stage, (Marteinsdóttir, Svavarsdóttir, & Thórhallsdóttir, 2010) developing towards a moss heathland community with herbs and a few small shrubs, such as willow (Kofler, 2004) or mountain birch (*betula nana*) that has started to colonize the area in recent years. (Hiedl, Þórhallsdóttir, & Svavarsdóttir, 2014).

2.2 Experimental design

The experiment followed a hierarchical design (Figure 2.2). The experimental set-up was similar in two of the sites, Þeistareykir and Auðkúluheiði. These study sites are part of a larger research project aimed at evaluating the impacts of sheep grazing on highland ranges. For the present study, I included an additional study site in Skeiðarársandur. This site is also part of a long-term research project investigating the effects of sheep grazing on primary vegetation succession (Marteinsdóttir, Svavarsdóttir, & Thórhallsdóttir, 2010).

Within Þeistareykir and Auðkúluheiði two main habitats were targeted: melur and heath. In Skeiðarársandur two habitats with contrasting vegetation cover were also selected, but cover was dominated mostly by mosses in both of them.

In Þeistareykir and Auðkúluheiði six pairs of plots were set up in each of the two habitats (24 plots per site) in the Spring 2016. In Skeiðarársandur there were 5 pairs of plots per habitat, hence 20 plots in total, that were established more than 10 years ago. One plot of each pair was protected from grazing by fencing, while the other one was not protected, so sheep had free access during the course of the experiment, constituting the control. Each of the plots was 12 by 12 m (40 by 40 m in Skeiðarársandur) and the fences were 1 m high. The plots in each pair were situated one next to the other (separated 3 m), while each pair was separated from the next one 100 m approximately (500m in Skeiðarársandur).

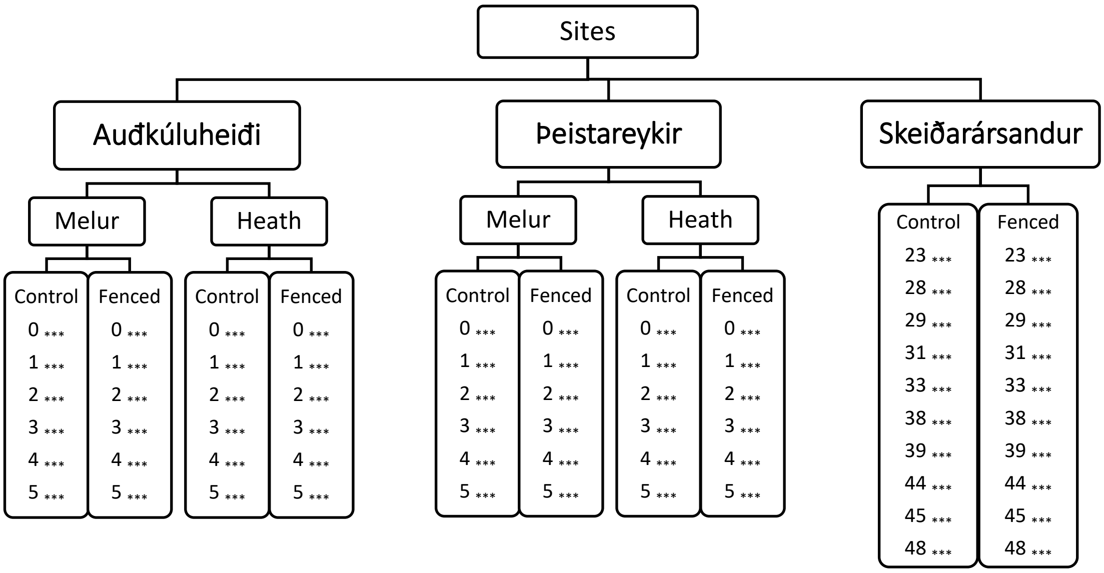


Figure 2.2 *Overview of the hierarchical experimental design. The experiment was conducted at three sites (Auðkúluheiði, Þeistareykir or Skeiðarársandur). Within Auðkúluheiði and Þeistareykir two habitats with contrasting vegetation cover were targeted (melur or heath). At each site, 6 pairs of plots (indicated by numbers; 10 pairs in Skeiðarársandur), one fenced and one unfenced (control), were established, and three seed traps were installed per plot (indicated with asterisks in the diagram).*

Towards the end August 2016, when most plants have already produced and are dispersing their seeds (Ryvarden, 1975), three seed traps were installed per plot, regularly spaced. Seed traps consisted of 15 × 30 cm mats of synthetic grass (Astroturf brand), fixed to the ground with a couple of nails in both ends. This sampling method has been effectively used to measure seed rain in tundra ecosystems (Molau & Larsson, 2000). However, it is necessary to point out that this system can underestimate the seed rain of graminoids and herbs (Larsson & Molau, 2001).

After 1 month, in late September 2016, the seed traps were recovered from the field, and individually packed in labelled plastic bags for transport back to the lab. Each seed trap was air dried and cleaned in the lab, and the content recovered from the traps was weighted. Samples were packed again into smaller air-tight plastic bags and placed in the fridge (4°C) for one month to simulate wintertime and stimulate germination.

2.3 Sampling and method trial

To estimate the number of seeds and species of plants collected by each seed trap I used 3 different methods: direct counting of seeds under a magnifier glass, flotation method to separate seeds from other soil particles, and germination. I conducted a trial to identify the main advantages and disadvantages of each method.

2.3.1 Magnifier

The simplest method I tried consisted on placing the content of the bags in a petri dish to count and identify the seeds using a magnifier. Before that, I sieved the sample to remove the particles smaller than the smallest of the seeds.

Due to the big volume of some of the samples, it was usually necessary to split them in more than one petri dish and process them in different rounds requiring around 45 min average to process each bag. Moreover, the large amount of sand and the small size of some of the seeds made it very hard to find some of the species entailing a significant risk of obtaining a biased result. Consequently, we considered this method excessively time-consuming and not precise enough to be used, so we decided to reject it.

2.3.2 Flotation

As a second option, I tried the flotation method based on the procedure described by Tsuyuzaki (1994). This method aims at separating the organic matter (seed and leaves) from the inorganic matter (mostly sand) due to their different densities. By adding a K_2CO_3 solution 5.5 molar to the samples, and through centrifugation, it is possible to separate in different phases the organic material (with a lower physical density) from the inorganic one. By casting the supernatant, after filtering and removing the solution rinsing it with water, it is easier to count the seeds once the sand has been subtracted.

In order to evaluate the suitability and effectivity of this method in our experiment, it was pertinent to perform some trials before testing with the real samples, especially due to the lack of consistency among its application in earlier studies. For these trials, we used sterile sand and a selection of some of the most representative seeds of Icelandic ecosystems (*Poa sp, Rumex sp.*, *Gallium sp.*, *Viscaria sp.*, *Silene sp.* and *Parnassia sp.*).

First of all, I replicated the processes described in previous works (Ishikawa-Goto, & Tsuyuzaki, 2004; Wahl, 2011), with minor variations in the way of shaking, the speed of centrifugation or the duration of the different phases, until the most suitable method was successfully achieved for our particular experiment.

After that, I tested the method that I had previously developed in order to evaluate its reliability. Firstly, I prepared 6 trial samples adding 72 seeds/sample in half of them and 28 seeds/sample in the other half to $25cm^3$ of sand, in order to compare the results of samples with different seed densities. After mixing the sand and the seeds I placed them in centrifuge tubes and added $25cm^3$ of K_2CO_3 solution. Samples were hand-shaken during 3 min in different directions and centrifuged at 1000 rpm during 2 min and at 3600 rpm during 8 more minutes. As a result, the supernatant phase should include the seeds of the trial sample floating on its surface. Most of these seeds could be seen at first sight and recovered with a pipette. All seeds retrieved were placed on a coffee filter and were rinsed 6 times with water to remove the solution avoiding an unwanted reduction in seed viability (Tsuyuzaki, 1993). Finally, the content of the filter was looked under a magnifier to determine species identity and all seeds were counted.

Finally, the developed methodology was tried with real samples.

Statistical analysis

The data gathered using artificial trial samples were analyzed statistically. The total percentage of seeds recovered from each tube was calculated dividing the number of seeds counted in a tube by the known number of seeds present.

The effect of species and seed density were explored using Generalized Linear Mixed effects Models (GLMM), where the number of seeds retrieved was our response variable, and sample identity was included as a random factor. A Poisson error structure was used in the models because the response variable was counts of number of seeds (Zuur et al., 2009).

In the first case, the effect of species was investigated by comparing 2 models, with and without species as a fixed effect; in the second case, the 2 models included (or not) seed density as a fixed effect.

2.3.3 Germination

Germination methods have limitations (Thompson, & Grime 1979), as they will only provide information about the readily germinable fraction of the seeds and not the total number of them. Therefore, this method is likely to underestimate the seed rain leaving out the species that have specific germination requirements and all the non-viable ones (Roberts, 1981). However, we decided to try it because it is a generally accepted method to estimate the viable seed rain and it is relatively simple to conduct (Gross, 1990).

To carry out the germination experiment, we placed the material contained in the seed traps on trays with sterile soil and let them grow in the greenhouse under a 16:8 D:N cycle, at 16ºC. We watered them every other day and monitored germination writing down and removing from the tray the species that were sufficiently developed to be identified. Total germination was assessed by counting and identifying seedlings after 6 weeks, when most species should have germinated.

Statistical analysis

For the statistical analysis, we used GLMM because of the non-normal distribution of the response variable and the hierarchical structure of the experimental design that includes possible interactions between the variables (Zuur et al., 2009).

Due to the different approach of the experiment in Auðkúluheiði and Þeistareykir compared to Skeiðarársandur it was necessary to perform two separate analyses. In both of them, the effect of the treatment (sheep grazing) was included as a fixed effect. However, the other factors of interest (habitat and site) had to be analyzed with a different approach. On one side, to analyze the effect of site variability in germination, we included the data gathered at the 3 sites. On the other side, when aiming to study the effect of the habitat, we did not take into account the data obtained in Skeiðarársandur since the habitat differentiation (melur and heath) was not clear there.

In both analyses, models with different structures were compared and the discrimination was based on the philosophical foundations of the design, supported by their AIC and the p-values of the different terms. A Poisson error structure was used in the models because the response variable was counts of number of seeds (Zuur et al., 2009).

In the same vein, the effect of plot nested within pair was in both studies included as a random factor in congruence with the experiment design. This model structure was also supported by the lowest AIC value compared to models that include each factor separately. The fixed component however included different factors depending on the approach.

For the analysis that focusses on site effect, the model generated included as a fixed factor, the interaction between the effect of site (Auðkúluheiði, Þeistareykir or Skeiðarársandur) and treatment (fenced or not fenced).

For the analysis that focusses on habitat effect I included as fixed factors the interactive effects of the treatment (fenced or not) with habitat (melur or heath), and the separate effect of site (Auðkúluheiði, Þeistareykir). In this case, the sample size conditioned the complexity that the model structure could support, which was no more than one interaction as a fixed effect. The interaction between treatment and habitat was supported by the sample size and coherent with our experiment design and therefore we included it in the comparison of all the possible models with different fixed effect combinations.

2.3.4 Estimation of aeolian deposition

In order to estimate the different levels of aeolian deposition in each of the sites and habitats I used the data obtained from weighting the total amount of material collected by each seed trap (i.e. sand and seeds).

Statistical analysis

In accordance with the previous analyses and following the experimental design, we analyzed the data with 2 different approaches, one of them focused on the different sites including all the data and the other considering the different habitats and therefore only including Auðkúluheiði and Þeistareykir. I used 2 Linear Mixed Effect Models (LMM) to assess the effect of the variables treatment, habitat and site, and their interactions, on the amount of material trapped by the seed traps. Plot identity nested within pair was included as random effect in both studies.

All statistical analyses were conducted using the software R (Zuur et al., 2009) with the packages lattice, lme4 and lmerTest.

3 Results

3.1 Flotation method

In our preliminary trial, 91.1 ± 2.0 % of seeds were retrieved on average using the flotation method.

From the Generalized Linear Mixed effects Model we concluded that neither species identity (GLMM, Chisq=5.414, df=5, p=0.367) nor seed density (GLMM, Chisq=0.888, df=1, p=0.346) were significantly associated with the number of seeds retrieved. However, in spite of those encouraging results, when I first tried to apply it to the real samples from our study sites, the outcome was quite different. Since it was a natural soil, the amount of organic material was greater than in the trial samples. Together with the thinner size of the soil particles, this resulted in a more diffuse differentiation between the two phases, making the extraction of the organic material difficult, either with the pipette or by casting it. In addition, the frequent washing and transferring of soil required could likely result in considerable loss of the sample material (Gross, 1990). This, together with the possibility of damaging the seeds as a consequence of prolonged immersion in K_2CO_3 solution and the excessive time required in the process, drove the decision of dismissing this method.

3.2 Germination method

3.2.1 Site and treatment analysis:

In the analyses including all sites, the effect of fences on the number of seeds germinated depended on the site (*Table 1*). That is, the interaction between treatment and site was significant (LRT: Chisq=6.433, DF=2, p=0.040; appendix A). The lowest AIC value corresponded also with the model including the interaction and therefore we decided to keep it in our model.

***Table 1**. Factors affecting the number of germinated seeds according to the GLMM model for all three sites.*

Fixed effects:	*Estimate*	*Std. Error*	*t value*	*Pr(>|z|)*
(Intercept)	0.6602	0.3770	1.751	0.0799 .
fTTMF	0.2335	0.2542	0.918	0.3583
fSITES	-0.3896	0.5726	-0.680	0.4963
fSITET	-0.8889	0.5507	-1.614	0.1065
fTTMF:fSITES	-0.9934	0.4310	-2.305	0.0212 *
fTTMF:fSITET	0.1012	0.3970	0.255	0.7988

The effects of treatment (fenced or unfenced plots; fTTM) and site (fSITE). Baseline levels for treatment and site are unfenced plots and Auðkúluheiði, respectively. According to the hierarchical experimental design, plot identity nested within pair was included as a random effect in the model. ('.'=0.1, '*'=0.05) Model definition: seed.nr ~ fTTM + fSITE + (1|fPAIR/fPLOT)

This interaction was most likely driven by the patterns observed at one of the sites, Skeiðarársandur (*Figure 3.2.1)* where germination was larger in the control plots than in the fenced plots. In Þeistareykir and Auðkúluheiði the number of germinated seeds tended to be higher in the plots protected from sheep grazing (fenced).

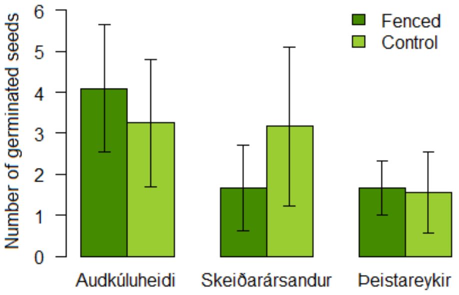


Figure 3.2.1. Bar plot representing the number of seeds germinated per site in fenced (dark green) and unfenced plots (light green). Error bars show standard errors.

3.2.2 Habitat, site and treatment analysis:

From the model comparison, we have noticed how the three-way interaction of the variables (treatment, habitat and site) is not significant (Pr(>Chisq)= 0.1044). Moreover, this model structure has a similar AIC value than the two-way interaction model, having both almost the same explanatory power (appendix A). Therefore, we procced to realize a two-way interactions comparison finding that the interactions between treatment and habitat and treatment and site are neither significant. We can conclude from the analysis, that the only truly significant interaction is between site and habitat (LRT: Chisq=6.6316, D F=1, p=0.01002; appendix A) and consequently that is the only one we have kept in the final model. However, we found problems to converge the model and therefore the specific results of the model are not displayed in the report.

In *Figure 3.2.2*, it is shown a significantly larger number of germinated seeds in the melur than in the heath. The difference between fenced and control plots was not significant. In *Figure 3.2.3*, we observe a significantly higher number of germinated seeds in Auðkúluheiði than in Þeistareykir. Moreover, germination in the heath is quite similar in both sites, while in the Melur the difference in germination is huge being that the reason for the significance of the interaction between site and habitat.

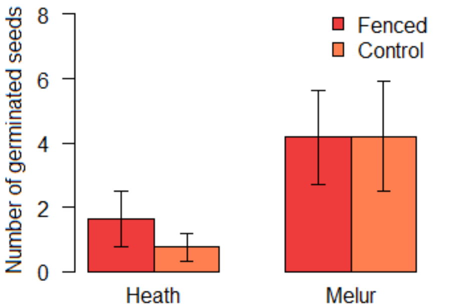


Figure 3.2.2. Bar plot representing the number of seeds germinated in each habitat in fenced (dark pink) and control (light pink) plots. Error bars show standard errors.

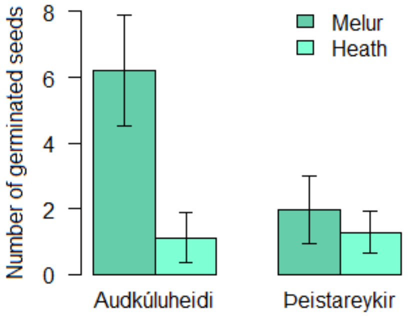


Figure 3.2.3. Bar plot representing the number of seeds germinated in each site in different habitats: melur (dark blue) and heath (light blue) plots. Error bars show standard errors

3.3 Aeolian deposition analysis

3.3.1 Site and treatment analysis:

After the comparison of the three sites, and the development of the most suitable model, we observed that the effect of the interaction between treatment and site was not significant (LRT Chisq= 0.2921 DF=2 p=0.8641) and it generated the less explanatory model with the largest AIC so we decided to drop it from the model.

Table 2. *Factors affecting the aeolian deposition resulting from the model LMMsp2 for all sites*

Fixed effects:	*Estimate*	*Std. Error*	*DF*	*t value*	*Pr(>|t|)*
(Intercept)	10.087	7.148	33.580	1.411	0.16739
fTTMF	-2.333	2.239	32.970	-1.042	0.30493
fSITES	36.573	10.239	32.360	3.572	0.001**
fSITET	-3.712	9.988	32.040	-0.372	0.71262

The table shows the effects of treatment (fenced or unfenced plots; fTTM) and site (fSITE). Baseline levels for treatment and site are unfenced plots and Auðkúluheiði, respectively. According to the hierarchical experimental design, plot identity nested within pair was included as a random effect in the model. ('*'=0.05 '**'=0.005) Model definition: weight ~ fTTM + fSITE + (1|fPAIR/fPLOT)

From the summary of the final model (*Table 2*), we can point out that aeolian deposition was significantly greater in Skeiðarársandur respect to Auðkúluheiði (estimate=36.57±10.24, p=0.001). In Þeistareykir we recovered a lower amount of sand than in Auðkúluheiði but the difference was not significant (-3.712 p=0.71262). In the same vein, fenced plots showed a non-significant trend to collect lower aeolian deposition than the control ones (-2.333 p=0.30493). The aeolian deposition in each site is showed in *Figure 3.3.1*.

3.3.2 Habitat, site and treatment analysis:

When we included the effect of habitat, we observed how the effects of the interactions between the variables treatment and site (LRT Chisq=3.559, DF= p=0.287), treatment and habitat (LRT Chisq=2.4713, DF=1, p=0.1159) and site and habitat (LRT Chisq=3.5709, DF=1, p=0.059) were not significant (appendix A). Consequently, the final model included the separate effects of the treatment, habitat and site, being also the more explanatory one.

Table 3. *Factors affecting the aeolian deposition obtained from the model LMMtsh*

Fixed effects:	*Estimate*	*Std. Error*	*DF*	*t value*	*Pr(>|t|)*
(Intercept)	3.322	2.179	24.815	1.525	0.140
fTTMF	-2.078	1.312	23.347	-1.584	0.127
fHABM	13.273	2.405	20.901	5.519	1.81e-05 ***
fSITET	-3.722	2.405	20.901	-1.548	0.137

Table 3 shows the effects of treatment (fenced or unfenced plots; fTTM) and site (fSITE). Baseline levels for treatment and site are unfenced plots and Auðkúluheiði, respectively. According to the hierarchical experimental design, plot identity nested within pair was included as a random effect in the model. ('***'=0.05) Model definition: weight ~ fTTM + fSITE + fHAB + (1 | fPAIR / fPLOT)

The only significant effect was in this case that of the habitat, since we found a bigger amount of depositions in the melur with respect to the heath (13.273 p=1.81e-05 ***). We observed a smaller amount of sand recovered in the fenced plots with regard to the unfenced ones but this difference was non-significant (-2.0701 p=0.1272). Regarding the site its influence was neither significant but aeolian deposition was marginally lower in Þeistareykir in comparison with Auðkúluheiði (-3.722 p=0.137) (*Table 3*).

We represented in *Figure 3.3.2* the combined effect of site and habitat to visualize the interaction showing that the difference in aeolian deposition between melur and heath was bigger in Auðkúluheiði than in Þeistareykir.

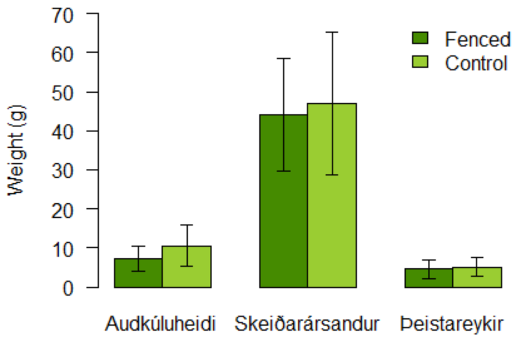


Figure 3.3.1 Bar plot representing the relation between the weights of the sand samples recovered from the seed traps in fenced (dark green) and control (light green) plots and the variable site. Error bars show standard errors

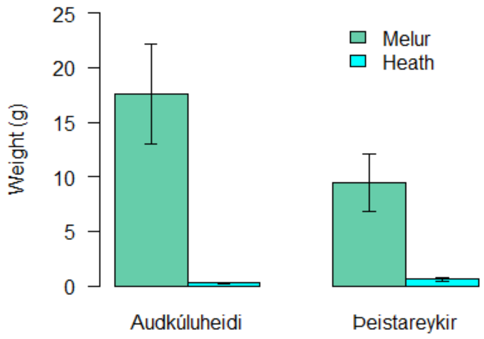


Figure 3.3.2 Bar plot representing the weight of the sand recovered from the seed traps in each site in the melur (dark blue) and heath (light blue) plots. Error bars show standard errors.

4 Discussion

Soil erosion is one of the greatest environmental problems in Iceland, if not the worst. It is mainly caused by sheep grazing, severe climate and volcanic activity. Thus, the underlying motivation of this study was to assess to some extent, the impact of sheep grazing on soil erosion in Iceland, specifically the influence on seed rain in summer rangelands. For this purpose, we have studied the seed rain and the aeolian depositions in plots with and without grazing pressure.

4.1 Flotation

Although we tough that counting the seeds with the magnifier will provide us the most complete results, we rejected it because they were likely to be biased. The small size of some of the seeds and the large amount of particles with similar size made very difficult to find them compared with the bigger ones. Moreover, the time needed on the process exceed our expectations and was excessive. Due to the big volume of some of the samples we were forced to split them and count the seeds on different rounds per sample.

We also rejected the flotation method due to several reasons. First of all its inefficiency in organic soils (Roberts, 1981) from which it was very difficult for us to extract the seeds. Secondly, the risk of losing sample material as a result of the frequent washing and transferring of soil needed (Gross, 1990), along with the possibility of damaging the seeds because of the immersion in K_2CO_3 solution. On third place, some studies point out that floatability varies with the size and hydrophobicity of the seeds (Trahar, 1981). Finally, the process takes more time than desirable and was not sufficiently efficient with our samples. However, this method has the advantage that the results are not influenced by differences on germination requirements.

Therefore, we decided to use the germination method that was a generally accepted system to estimate seed rain and relatively simple to conduct (Gross, 1990). It needs less sample processing and it was the faster method. However, it only serves to estimate the viable seeds but not the dead or the dormant ones. Therefore, it is pertinent to keep in mind that some seeds could need additional time, scarification processes or two winter periods to be ready for the germination (Bliss, 1958). Thus, it would be interesting to extend the method during a longer period and submit the samples after that for a second cold phase and germination round, to obtain more representative and less biased results.

4.2 Germination

The effect of the treatment (fenced versus not fenced) was not significant in the Site-treatment analysis but we found a slightly higher seed rain in the fenced plots than in the control ones meeting our expectations. However, we were surprised that this trend was only valid for Auðkúluheiði and Þeistareykir. In Skeiðarársandur a larger seed rain in the control than in the fenced plots occurs. For this reason, the model shows a significant interaction between site and treatment. It would be advisable to perform a long-term study of seed germination on the fenced plots because the effect of grazing is presumably very difficult to detect in a short-term study like this one. The effect of reducing grazing depends on the capability of re-establishment of plants that is usually low in eroded ecosystems and needs of time to be perceptible (Olofsson, 2006). Moreover, the proximity between fenced and unfenced plots could distort the difference in seed rain in both of them. Although most of the seeds trapped were most likely originated in the plot in which the seed traps were located, there may also be seed flow between plots. If the fenced plots were producing higher number of seeds as we hypothesized, part of them could end in the seed traps of the unfenced plots mitigating the differences on seed rain. It would be advisable to explore that possibility on future studies.

Across the three sites with different soil erosion degree, germination seemed to be larger in Auðkúluheiði than in Skeiðarársandur and in Skeiðarársandur bigger than in Þeistareykir but the differences were not significant. Moreover, when comparing Auðkúluheiði with Þeistareykir only, the germination was significantly bigger in Auðkúluheiði. These results differ from what we expected being the ecosystems with lower vegetation cover the ones with larger germination measured. We believe that those differences on seed germination were most likely related with the ecological variation between sites, but it would be advisable to characterize the specific factors involved in next studies.

Regarding the Site-Treatment-Habitat analysis, we found that on average, the melur (which has the lower vegetation cover) received a significantly greater seed rain than the heath, opposite to our initial hypothesis. Moreover, there was an unexpected significant interaction between site and habitat. Germination in the melur was significantly different between Auðkúluheiði and Þeistareykir while in the heath the number of germinated seeds was quite similar. This it's most likely related with the distinct successional stages and vegetation composition in both habitats and sites. Different types of plants have different reproductive strategies and are not equally prolific, producing distinct number of seeds. Therefore, the total number of seeds recovered from each habitat cannot be directly related with the effect of erosion. In our experiment, sample size was not big enough to realize a statistical analysis comparing among the number of seeds of every specie germinated. However, I did a preliminary review of our data and it showed that in accordance with that hypothesis, there were a few genera like Silene, Thymus, Festuca, Rumex or Polygonum, that were very determinant on our results because of the great amount of seeds germinated from them. In particular, in Auðkúluheiði, Thymus was especially decisive in the melur, producing almost half of the seeds that we recovered. In this way, it would be interesting to analyze statistically the seeds recovered per specie in further investigations and to relate it with the abundance of those species in the vegetation.

4.3 Aeolian deposition:

Although the effect of the treatment was not significant in this study, we found more aeolian deposition in the control plots than in the fenced ones and that matches with our initial hypothesis. Again, it would be recommendable to perform a long-term study**,** because the impact of grazing may only be perceived after a longer period of time.

Within the three sites aeolian deposition was significantly greater in Skeiðarársandur than Auðkúluheiði and in Auðkúluheiði slightly bigger than in Þeistareykir (the difference is not significant between those two last sites). The large amount of sand recovered from Skeiðarársandur is probably related with its situation on the outwash plain of the glacier and near Grímsvötn, a volcano capped with a glacier that erupted on 2011. This type of volcano produces the most explosive form of eruptions due to the mixing of hot lava and cold water. Large quantities of volcanic ash are generated as a consequence. Moreover, the glacial meltwater that occurs during eruptions can result in extraordinary voluminous floods that bring down heavy sediment loads (Arnalds, 2015f). Poorly consolidated volcanic materials and tephra layers that are prone to erosion, usually form these glaciofluvial floodplains that serve as a source of aeolian materials.

When including the habitat in the analysis, comparing Auðkúluheiði with Þeistareykir, we recovered significantly more sand from the melur than from the heath. This difference on aeolian deposition was especially remarkable in Auðkúluheiði. That is in accordance with our hypothesis that the habitats with lower vegetation cover would receive more aeolian deposition. In relation with that, the melur constitute a sandy lag-gravel formed on glacial till or alluvial surfaces that often-accumulated large amounts of aeolian sand and volcanic tephra trapped by the fragments on the surface (Arnalds, 2015g). However, contrary to what we initially thought, aeolian deposition did not seem to be hindering seed dispersal since the habitats with higher aeolian deposition are the ones with higher number of germinated seeds.

Aditionally, the fact that there is more sand accumulated on the seed traps in the melur than in the heath, could maybe explain in part why more seeds were found in the melur. Seeds there could be trapped by the sediments while in the heath may be more exposed to the wind and more easily dragged out of the traps. However, vegetation in the heath could also protect the seed traps from the wind but in the same way it could also prevent their access to them.

Addressing the effect of grazing on seed dispersal and aeolian deposition is a very complex challenge that will need of longer term and more specific studies. In general aeolian deposition and germination were higher in the habitats with lower vegetation cover. That trend of germination together with the significant difference on germination in the melur depending on the site need of further investigation to better understand their causes. The number of germinated seeds could not be very representative of the development or health of the ecosystem due to differences in prolificacy of the plants. In that vein, it would be interesting to investigate the number of germinated seeds in relation with the species to address this issue. Within the different sites, Skeiðarársandur was noticeable because it had the highest aeolian deposition rate and the effect of the treatment was opposite to the other sites. It would be interesting to investigate this distinct dynamic.

References

1. **Arnalds O (2000).** The Icelandic 'rofabard' soil erosion features. Earth Surface Processes and Landforms, 25 (1), 17-28.

2. **Arnalds, A. (1987).** Ecosystem disturbance in Iceland. Arctic and Alpine Research, 508-513.

3. **Arnalds, O. (2004).** Icelandic volcanic soils. O. Arnalds and H. Oskarsson, 27.

4. **Arnalds, O. (2015a).** Physical Characteristics. In: The soils of Iceland by Arnalds O, pp. page 77-90. World Soil Series, Springer.

5. **Arnalds, O. (2015b).** Collapse, erosion, condition, and restoration. In: The soils of Iceland by Arnalds O, pp. 153–180. World Soil Series, Springer.

6. **Arnalds, O. (2015c).** The Volcanic Aeolian Environments of Iceland. In: The soils of Iceland by Arnalds O, pp. 153–180. World Soil Series, Springer.

7. **Arnalds, O. (2015d).** Chemical Characteristics. In: The soils of Iceland by Arnalds O, pp. page 91-107. World Soil Series, Springer.

8. **Arnalds, O. (2015e).** Classification and the Main Soil Types. In: The soils of Iceland by Arnalds O, pp. page 55-70. World Soil Series, Springer.

9. **Arnalds, O. (2015f).** Geology. In: The soils of Iceland by Arnalds O, pp. page 31-48. World Soil Series, Springer.

10. **Arnalds, O. (2015g).** The Volcanic Aeolian Environments of Iceland. In: The soils of Iceland by Arnalds O, pp. page 139-152. World Soil Series, Springer.

11. **Arnalds, O., & Barkarson, B. H. (2003).** Soil erosion and land use policy in Iceland in relation to sheep grazing and government subsidies. Environmental Science & Policy, 6(1), 105-113.

12. **Arnalds, O., & Kimble, J. (2001).** Andisols of deserts in Iceland. Soil Science Society of America Journal, 65(6), 1778-1786.

13. **Arnalds, O., & Kimble, J. (2001).** Andisols of deserts in Iceland. Soil Science Society of America Journal, 65(6), 1778-1786.

14. **Arnalds, O., Thorarinsdottir, E.Fl., Metusalemsson, S., Jonsson, A., Gretarsson, E., Arnason, A., (2001).** Soil erosion in Iceland. Soil Conservation Service and the Agricultural Research Institute, Reykjavik Iceland, 1997 (Translated from Icelandic Version).

15. **Bliss, L. C. (1958).** Seed germination in arctic and alpine species. Arctic, 11(3), 180-188.

16. **Elmarsdóttir, Á., Vilmundardóttir, O. K., & Magnússon, S. H. (2015).** Vegetation of high-temperature geothermal areas in Iceland. In Proceedings of the World Geothermal Congress.

17. **Forbes, B. C., Ebersole, J. J., & Strandberg, B. (2001).** Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. Conservation Biology, 15(4), 954-969.

18. **Gross, K. L. (1990).** A comparison of methods for estimating seed numbers in the soil. The Journal of Ecology, 1079-1093.

19. **Hiedl, M. M., Þórhallsdóttir, Þ. E., & Svavarsdóttir, K. (2014).** Colonization of mountain birch (*Betula pubescens*)

20. **Howe, H. F., & Smallwood, J. (1982).** Ecology of seed dispersal. Annual review of ecology and systematics, 13(1), 201-228.

21. Icelandic Meteorological Office 2007, Fagurhólsmýri station.

22. **Ishikawa-Goto, M., & Tsuyuzaki, S. (2004).** Methods of estimating seed banks with reference to long-term seed burial. Journal of Plant Research, 117(3), 245-248.

23. **Jónsdóttir, I. S. (1991).** Effects of grazing on tiller size and population dynamics in a clonal sedge (Carex bigelowii). Oikos, 177-188.

24. **Jónsdóttir, I. S., Magnússon, B., Gudmundsson, J., Elmarsdóttir, Á., & Hjartarson, H., (2005).** Variable sensitivity of plant communities in Iceland to experimental warming. Global Change Biology, 11(4), 553-563

25. **Jónsdóttir, I.S. (1984).** Á hrif beitar á gróður Auðkúluheiðar (Effects of grazing on the vegetation of Auðkúluheiði heathlands. In Icelandic with English summary). Náttúrufræðingurinn 53: 19–40.

26. **Larsson, E. L., & Molau, U. (2001).** Snowbeds trapping seed rain—a comparison of methods. *Nordic Journal of Botany*, *21*(4), 385-392.

27. **Magnússon, S. H. (1997).** Restoration of eroded areas in Iceland. Restoration ecology and sustainable development, 188-211.

28. **Marteinsdóttir B (2014).** Seed rain and seed bank reveal that seed limitation strongly influences plant community assembly in grasslands. PLoS One, 9 (7).

29. **Marteinsdottir, B. (2007).** Small scale spatial patterns and colonization proccesses in early successional environment. MSc thesis, University of Iceland, Reykjavík, IS.

30. **Marteinsdóttir, B., Svavarsdóttir, K., & Thórhallsdóttir, T. E. (2010).** Development of vegetation patterns in early primary succession. Journal of Vegetation Science, 21(3), 531-540.

31. **Marteinsdóttir, B., Svavarsdóttir, K., & Thórhallsdóttir, T. E. (2010).** Development of vegetation patterns in early primary succession. Journal of Vegetation Science, 21(3), 531-540.

32. **Marteinsdóttir, B., Thórhallsdóttir, T. E., & Svavarsdóttir, K. (2013).** An experimental test of the relationship between small scale topography and seedling establishment in primary succession. *Plant ecology*, *214*(8), 1007-1015.

33. **McDaniel PA, Lowe DJ, Arnalds O, Ping C-L (2012)** Andisols. In: Huang PM,YuncongL, SumnerME (eds) Handbook of soil sciences. Properties and processes, 2nd edn. CRC Press, Boca Raton, pp 33-29–33-48

34. **Molau, U., & Larsson, E. L. (2000).** Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany*, *78*(6), 728-747.

35. **Olofsson, J. (2006).** Short-and long-term effects of changes in reindeer grazing pressure on tundra heath vegetation. Journal of Ecology, 94(2), 431-440.

36. **Oom, S. P., Sibbald, A. M., Hester, A. J., Miller, D. R., & Legg, C. J. (2008).** Impacts of sheep grazing a complex vegetation mosaic: relating behaviour to vegetation change. Agriculture, ecosystems & environment, 124(3), 219-228.

37. **Roberts, H. A. (1981).** Seed banks in soils. *Advances in applied biology*, *6*, 1-55.

38. **Ross, L. C., Austrheim, G., Asheim, L. J., Bjarnason, G., Feilberg, J., Fosaa, A. M., ... & Mysterud, A. (2016).** Sheep grazing in the North Atlantic region: A long-term perspective on environmental sustainability. Ambio, 45(5), 551-566.

39. **Ryvarden, L. (1975).** Studies in seed dispersal. II. Winter-dispersed species at Finse, Norway. Nytt magasin for NYTT MAGASIN BOTANIKK.

40. **Sigbjarnarson, G. (1969).** Afok og uppblastur (The Loessial Soil Formation and the Soil Erosion on Haukadalsheidi). Natturufraedingurinn, 39, 49-128.

41. **Thompson, K., & Grime, J. P. (1979).** Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *The Journal of Ecology*, 893-921.

42. **Thorarinsson, S. (1961).** Wind erosion in Iceland. A tephrochronological study. Icelandic, extended English summary). Icelandic Forestry Society Yearbook, 17-54.

43. **Tsuyuzaki, S. (1993).** Seed viability after immersion in K2CO3 solution. Seed science and technology, 21(2), 479-481

44. **Tsuyuzaki, S. (1994).** Rapid seed extraction from soils by a flotation method. Weed Research, 34(6), 433-436.

45. **Wahl, V. (2011).** Seed in relation to a successional gradient: An approach on the glacier foreland of Skaftafellsjökull glacier. MSc, University of Iceland.

46. **Wood, D. M., & Del Moral, R. (2000).** Seed rain during early primary succession on Mount St. Helens, Washington. *Madrono*, 1-9.

47. **Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009).** Mixed effects models and extensions in ecology with R (pp. 101-142, 209-236, 323-339). Springer New York.

Appendix A

Signif. codes: '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

4.4 Germination

4.4.1 Site and treatment analysis:

Random component selection:

MODEL	df	AIC
GLMMpr *<- glmer(seed.nr~fTTM*fSITE +(1|fPAIR), family = poisson, data=data)*	7	905.6197
GLMMpt *<- glmer(seed.nr~fTTM*fSITE +(1|fPLOT), family = poisson, data=data)*	7	913.8537
GLMMprpt *<- glmer(seed.nr~fTTM*fSITE +(1|fPAIR/fPLOT), family = poisson, data=data)*	8	893.4203

Fixed component selection:

MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
GLMMts *seed.nr ~ fTTM * fSITE + (1 | fPAIR/fPLOT)*	893.42	919.85			
GLMMt.s *seed.nr ~ fTTM* **+** *fSITE + (1 | fPAIR/fPLOT)*	895.85	915.67	6.4326	2	0.0401*

4.4.2 Habitat site and treatment analysis:

Random component selection:

MODEL	df	AIC
GLMMr *<- glmer(seed.nr~fTTM*fHAB*fSITE +(1|fPAIR), family = poisson, data=dataAT)*	9	633.6362
GLMMt *<- glmer(seed.nr~fTTM*fHAB*fSITE +(1|fPLOT), family = poisson, data=dataAT)*	9	631.9073
GLMMrt *<- glmer(seed.nr~fTTM*fHAB*fSITE +(1|fPAIR/fPLOT), family = poisson, data=dataAT)*	10	630.1148

Fixed component selection:

MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
GLMMa: *fTTM*fHAB*fSITE + (1|fPAIR/fPLOT)*	630.11	659.60			
GLMMb: *fTTM*fHAB + fTTM*fSITE + fSITE*fHAB + (1| fPAIR/fPLOT)*	630.75	657.29	2.6373	1	0.1044

MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
GLMMb: *fTTM*fHAB + fTTM*fSITE + fSITE*fHAB + (1| fPAIR/fPLOT)*	630.75	657.29			
GLMMtssh*: fTTM*fSITE + fSITE*fHAB +(1|fPAIR/fPLOT)*	631.55	655.14	2.7998	1	0.09428
GLMMthsh: *fTTM*fHAB + fSITE*fHAB +(1|fPAIR/fPLOT)*	628.76	652.35	0.0044	1	0.947

MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
GLMMthsh: *fTTM*fHAB + fSITE*fHAB + (1|fPAIR/fPLOT)*	630.75	657.29			
GLMMt.sh*: fTTM + fSITE*fHAB + (1|fPAIR/fPLOT)*	629.61	650.25	2.8542	1	0.09113 .
GLMMth.s: *fTTM*fHAB + fSITE + (1|fPAIR/fPLOT)*	633.39	654.03	6.6316	1	0.01002 *

4.5 Aeolian deposition

4.5.1 Site and treatment analysis:

Random component selection:

MODEL	df	AIC
*LMMs<- lmer(weight~fTTM*fSITE +(1|fPAIR), data=data)*	8	1667.305
*LMMp<- lmer(weight~fTTM*fSITE +(1|fPLOT), data=data)*	8	1702.459
*LMMsp<- lmer(weight~fTTM*fSITE +(1|fPAIR/fPLOT), data=data)*	9	1661.685

Fixed component selection:

MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
LMMps1 *weight ~ fTTM*SITE + (1 | fPAIR/fPLOT)*	1692.6	1712.0			
LMMsp1 *weight ~ fTTM + fSITE + (1 | fPAIR/fPLOT)*	1688.9	1722.3	0.2921	2	0.8641

4.5.2 Site treatment and habitat analysis:

Random component selection:

MODEL	df	AIC
*LMMa<- lmer(weight~fTTM*fHAB*fSITE +(1|fPAIR), data=data)*	10	946.7768
*LMMb<- lmer(weight~ fTTM*fHAB*fSITE +(1|fPLOT), data=data)*	10	952.2368
*LMMab<- lmer(weight~ fTTM*fHAB*fSITE +(1|fPAIR/fPLOT), data=data)*	11	947.5487

Fixed component selection:

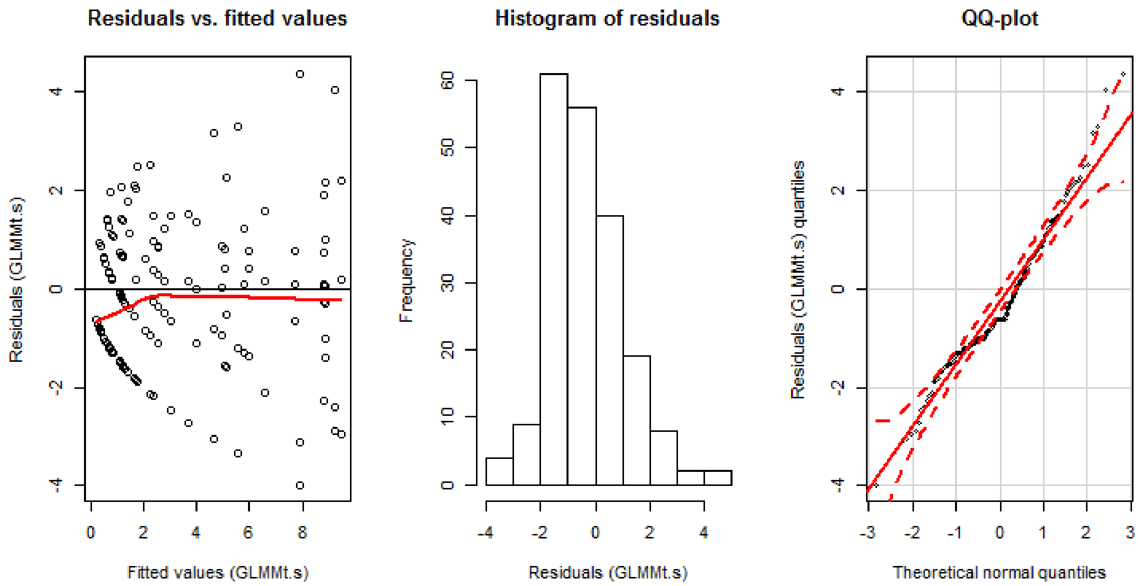
MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
LMMab2 *fTTM*fHAB + fTTM*fSITE + fSITE*fHAB + (1|fPAIR/fPLOT)*	974.90	1004.4			
LMMab3 *fTTM + fHAB* **+** *fTTM*fSITE* **+** *fSITE*fHAB + (1|fPAIR/fPLOT)*	975.42	1002.0	2.524	1	0.1121
LMMab4 *fTTM*fHAB* **+** *fTTM* **+** *fSITE* **+** *fSITE*fHAB + (1 fPAIR/fPLOT)*	974.03	1000.6	1.1315	1	0.2874
LMMab5 *fTTM*fHAB* **+** *fTTM*fSITE* **+** *fSITE* **+** *fHAB + (1 fPAIR/fPLOT)*	976.48	1003.0	3.5812	1	0.05844

MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
LMMab4 *fTTM*fHAB* **+** *fTTM* **+** *fSITE* **+** *fSITE*fHAB + (1|fPAIR/fPLOT)*	974.03	1000.6			
LMMt.sh *fTTM* **+** *fSITE*fHAB + (1|fPAIR/fPLOT)*	974.50	998.09	2.4713	1	0.1159
LMMth.s *fTTM*fHAB* **+** *fSITE + (1|fPAIR/fPLOT)*	975.59	999.18	3.5593	1	0.05921

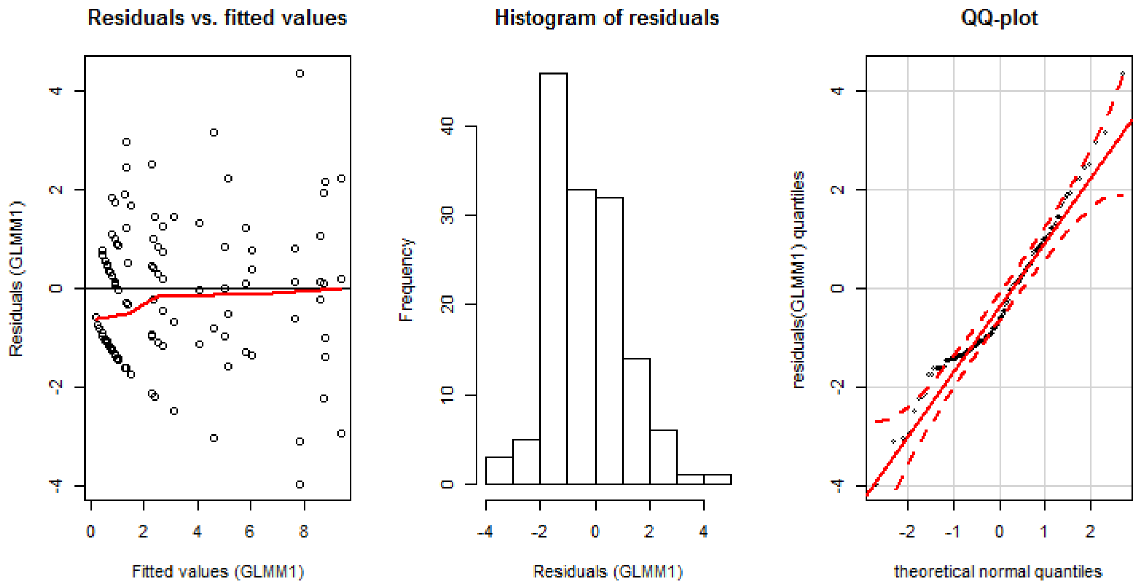
MODEL	AIC	BIC	Chisq	Df	Pr(>Chisq)
LMMt.sh *weight ~ fTTM* **+** *fSITE*fHAB + (1 | fPAIR/fPLOT)*	974.50	998.09			
LMMths *weight ~ fTTM* **+** *fHAB* **+** *fSITE + (1 | fPAIR/fPLOT)*	976.07	996.71	3.5709	1	0.0588
LMMnt *weight ~ fSITE*fHAB + (1 | fPAIR/fPLOT)*	974.98	995.62	2.4761	1	0.1156

Appendix B

4.6 Germination

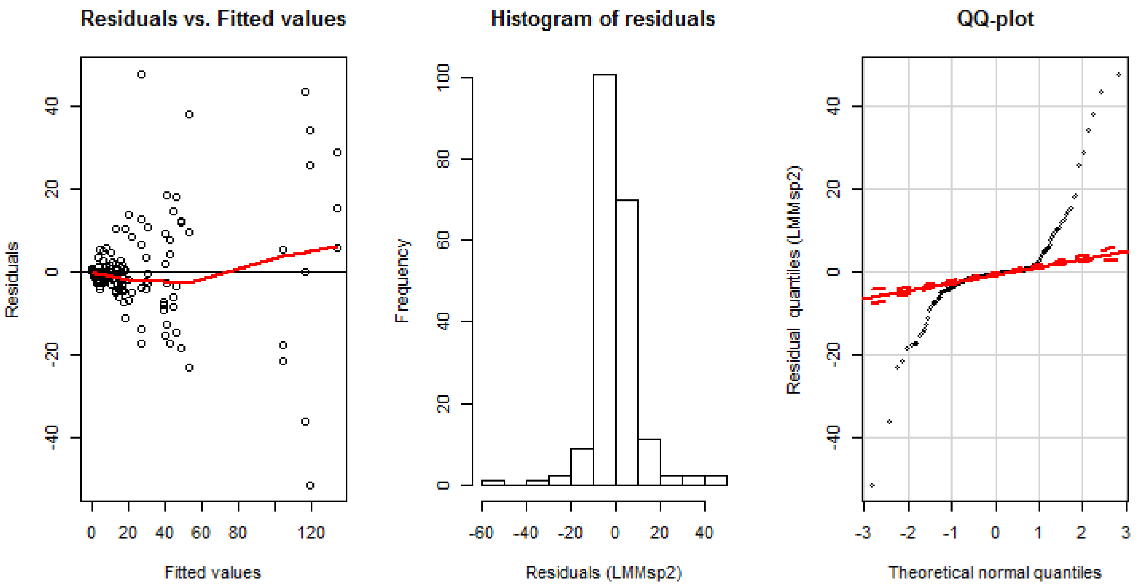


Residual graphics of the model:
*GLMMts <– glmer(seed.nr ~ fTTM*fSITE + (1 | fPAIR/fPLOT), family=poisson, data=data).*

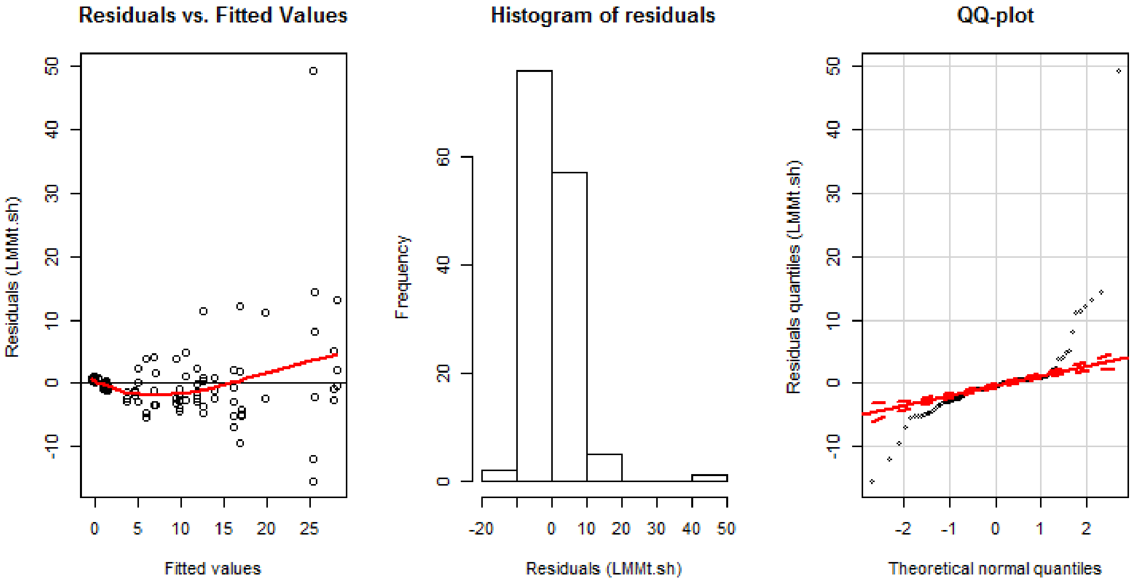


Residual graphics of the model:
*GLMM1<- glmer(seed.nr~fTTM * fHAB + fSITE +(1|fPAIR/fPLOT), family=poisson, data=data).*

4.7 Aeolian deposition



Residual graphics of the model:
LMMsp2<– lmer(weight~fTTM + fSITE + (1|fPAIR/fPLOT), data=data).



Residual graphics of the model:
*LMMt.sh <– lmer (weight~fTTM + fSITE*fHAB +(1|fPAIR/fPLOT), data=dataAT)*