NTNU – Trondheim
Norwegian University of
Science and Technology

Effects of Lichens on Seed Germination and Seedling Emergence of Vascular Plants on Dovre

Kristine Sundsdal

MSc in Biology
Submission date: May 2015
Supervisor: Bente Jessen Graae, IBI
Co-supervisor: Kristin Odden Nystuen, IBI
Richard Strimbeck, IBI

Norwegian University of Science and Technology
Department of Biology

"Those who contemplate the beauty of the earth find reserves of strength that will endure as long as life lasts."

– Rachel Carson, *The Sense of Wonder*

Definitions

Thallus *pl.* thalli	the lichen body that is not differentiated into stem and leaves and lacks true roots and a vascular system
Terricolous	growing on soil or on the ground
Fruticose	lichens having upright or pendulous thalli
Foliose	lichens having a lobed, leaf-like shape
Allelopathy	the chemical inhibition of a species by another, due to the release of substances into the environment acting as germination or growth inhibitors

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Abstract

Lichens are observed to decline when shrub covers increases due to global warming and reduced grazing in alpine and arctic areas. However, lichens are still prominent in many mountain habitats where they cover large areas. This may be due to; a) their growth structure that might inhibit vascular plant recruitment (physical structure), b) their production of secondary metabolites that may inhibit germination of vascular plants (allelopathy), or c) their ability to grow in harsh environments unsuitable for vascular plants (low environmental requirement and high stress tolerance). We sowed seeds of 12 species in an alpine common garden experiment with different species of lichen cover. We also tested the chemical effects of the lichens on germination of the species in a growth chamber experiment. Our results show that lichens promote rather than inhibit vascular plants in their early life stages. Seedling emergence was higher within the lichen cover than on bare soil for all lichen species. Except for *Cladonia stellaris* the biomass of the seedlings was in general higher within the lichens compared to the seedlings on bare soil. The physical structure of *C. stellaris* cushions seems to inhibit the establishment of the vascular plant seedlings. Whereas thickness of the lichen cover in general affected the microclimate important for the seedling establishment, it could not explain the variation in soil moisture underneath the lichens. Although an overall strong effect of allelopathy could not be seen on seed germination in the lab experiment, the chemical structure of the lichens had species-specific effects on the plant species. Altogether, the physical structure of the lichens seems to be more important than the chemical structure for seedling emergence in field.

Sammendrag

Det er observer en nedgang i lav når busker sprer seg på grunn av global oppvarming og mindre beiting i fjellet. På tross av dette er lav fortsatt utbredt i store områder i fjellet noe som kan komme av a) vekstformen som hindrer rekrutering av karplanter (fysisk struktur), b) produksjonen av sekundære metabolitter som kan hindre spiring av karplanter (allelopati) og c) lavenes tilpasning til å vokse under vanskelige forhold upassende for karplanter (lave krav til omgivelsene og høy stresstoleranse). Frø av 12 karplanter ble sådd i ulike lavarter transplantert til samme studieområde. Vi testet også hvordan kjemiske effekter av lav påvirket spiring av karplantene i et vekstkammereksperiment. Resultatene viser at lav i større grad legger til rette for enn hindrer karplanter i deres tidlige livsstadier. Spireraten var høyere inni lavmattene enn på bar jord for alle lavartene. I tillegg var biomassen av frøplantene for alle lavartene utenom i kvitkrull (*Cladonia Stellaris*) generelt høyere inni lavmattene enn på bar jord. Den tette og høye vekstformen hos *C. Stellaris* ser ut til å hindre etableringen av karplanter. Tykkelsen på lavmattene påvirket mikroklimaet generelt, men kunne ikke forklare variasjonen i markfuktighet under lavene. Negativ påvirkning fra allelopati på frøspiring var ikke veldig fremtredende, men kan sies å være artsspesifikk. Alt i alt virker det som lavens fysiske struktur er viktigere enn den kjemiske strukturen når det kommer til påvirkning på frøspiring i felt.

Introduction

To be able to persist in a changing climate species are forced to adapt to their new conditions or migrate to track the climate to which they are adapted (Jump and Penuelas 2005). Climate warming is expected to result in prolonged growing seasons and milder winter temperatures reducing the climatically harsh conditions in mountain ecosystems (Michelsen et al. 2011). This allows vascular plants to invade from lower elevations, and increase vascular plant cover (Wookey et al. 2009) especially of shrubs and dwarf shrubs (Myers-Smith et al. 2011; Rundqvist et al. 2011). Shrub encroachment in the northern hemisphere is already observed in arctic, subarctic and alpine ecosystems due to a) global warming and b) reduced grazing pressure and land-use (Myers-Smith et al. 2011; Rundqvist et al. 2011; Wookey et al. 2009). Plant succession, no longer prevented by grazing from domestic animals, may alter the landscape from open heaths and meadows to shrub and tree dominated landscapes (Bryn 2008; Bryn and Flø 2011). As a consequence, the cover of lichen and bryophyte species in arctic, subarctic and alpine ecosystems is expected to decrease (Cornelissen et al. 2001; Dawes et al. 2011; Holt et al. 2008; Joly et al. 2009). In these cold northern ecosystems terricolous lichens have an important role because of their abundance, N-fixation, contributions to nutrient cycling and the arctic carbon sink, and as a food source for herbivores such as reindeer and caribou (Cornelissen et al. 2001).

Vascular plant recruitment is low in alpine lichen heaths (Graae et al. 2011). High seedling mortality is often associated with harsh environments (Moles and Westoby 2004) such as extreme low temperatures characteristic for alpine areas (Körner 2003). The limited recruitment could therefore be related to the harsh conditions in itself. Lichens in alpine areas, however, are well adapted to harsh environments due to low environmental requirements and high stress tolerance (Krog et al. 1980). But these adaptations are thought to cause low competitiveness (Holien and Tønsberg 2006). On one hand we may expect that vascular plants colonize lichen habitats easily when the environment becomes less harsh. On the other hand, lichens have been shown to affect seed germination and seedling emergence of vascular plants through allelopathy and physical structure (Favero-Longo and Piervittori 2010; Zamfir 2000). Lichens could in that way potentially hamper the observed vascular plant expansion.

Physical structure of terricolous lichens may affect seedling establishment in several ways. First, the physical structure make them able to trap seed, in this way allow more seeds in lichen mats than on bare soil (Sedia and Ehrenfeld 2003). However, lichens may hamper seedling recruitment by a) preventing seeds to penetrate the lichen cushion (Zamfir 2000) and by b) suspend rooted seedlings during thallus expansion (Allen 1929). Second, lichen mats that cover large areas are shown to increase soil moisture, and in addition influence the temperature of the soil surface (Sedia and Ehrenfeld 2003). In this way terricolous lichens might alter microclimatic conditions that influence the microsite environment experienced by the seeds and seedlings. In alpine tundra, microsite conditions are demonstrated to have high importance for seedling recruitment (Graae et al. 2011). However, microclimatic conditions have not been thoroughly investigated for lichens (Favero-Longo and Piervittori 2010). Finally, lichen species vary greatly in physical structure (Holien and Tønsberg 2006) therefore we can expect that some species hamper seedling recruitment more than others.

Allelopathic effects of lichens may inhibit the establishment of vascular plants with secondary metabolites and thus prevent shrub spread and expansion of vascular plants. The effects of lichen secondary metabolites exert on plants can be through inhibition of growth in roots (Hobbs 1985; Latkowska et al. 2008; Nishitoba et al. 1987; Peres et al. 2009; Pyatt 1967) and hypocotyls (Nishitoba et al. 1987; Tigre et al. 2012), in addition to effects on seed germination (Hobbs 1985; Peres et al. 2009; Sedia and Ehrenfeld 2003; Tigre et al. 2012). All the above-mentioned findings of allelopathy are results from *in vitro* experiments. Although lichens have been observed to have suppressive effects on seedling establishment in the field (Hawkes and Menges 2003), allelopathy was only suggested as a possible cause but not investigated. In natural settings allelopathy has been suggested to indirectly affect growth of seedlings by inhibition of soil-microorganisms and mycorrhizal fungi (Brown and Mikola 1974; Sedia and Ehrenfeld 2003), though this was not found by Stark and Hyvarinen (2003), Stark et al. (2007) and Kytöviita and Stark (2009). However, Favero-Longo and Piervittori (2010) argue that generalization on allelopathic effects should be avoided because they depend on the secondary metabolites and plants tested.

In subarctic mountain regions such as Dovrefjell, terricolous lichens are the dominant species in lichen heaths, covering large areas with coherent monospecific mats. In a future warmer subarctic climate seedling establishment is expected to increase (Milbau et al. 2009) and both seedling establishment and seed germination are said to limit population dynamics and expansion more than seed production *per se* (Clark et al. 2007; Körner 2003). The extent of vascular plant expansion in lichen heaths in Dovrefjell will depend on availability of both viable seeds and suitable microsites, allowing seeds to germinate and seedlings to survive. Therefore, the ability of lichens to prevent or promote seed germination and seedling emergence will influence the rate of vascular plant colonization and vegetation responses to climate warming.

The aim of this study is to investigate how different species of lichens affect seed germination and seedling emergence of vascular plants and which factors contribute to their effect on vascular plant recruitment in subarctic mountain areas. I will try to answer the following research questions by investigating physical and chemical structures of the different lichen species.

1. Is seedling emergence affected by lichen species?
2. Is seedling growth (i.e. biomass) affected by lichen species?
3. Are the microclimatic conditions affected by the thickness of lichen cover?

Because allelopathy is hard to distinguish from other factors in natural settings I also conducted a laboratory experiment to answer the following question.

4. Is seed germination affect by the chemical structure of the lichen species?

Methods and materials

Study site

The study-site was located at Kongsvoll (*c.* 930 m above sea level, 62°18'N 9°36'E) close to Kongsvoll Biological Station on the east side of Drivdalen. This part of Dovre belongs to the Trondheim field, an area that consists of nutritious, easy eroded and partly lime rich bedrocks (Rekdal, 1998). The vegetation in the study area is dominated by the heathland species *Vaccinium myrtillus, Emprium nigrum* ssp*. hermaphroditum, Betula nana* and *Salix glauca*. The lichens *Alectoria ochroleu*ca and *Flavocetraria nivalis* are dominant on the exposed ridges.

Table 1: Species of lichens and vascular plants used in the study, growth form and secondary metabolites in the lichens (Krog et al. 1980). For the vascular plants number of seeds and the absence of species in field and/or laboratory experiments are shown.

Lichens species	**Growth form**	**Secondary metabolites**		
Cladonia stellaris	Fruticose	Usnic acid and perlatolic acid		
Cladonia arbuscula	Fruticose	Usnic acid and fumar protocetraric acid		
Alectoria ochroleuca	Fruticose	Usnic acid and diffractaic acid		
Stereocaulon paschale	Fruticose	Atranorin and lobaric acid		
Cetraria islandica	Foliose	Fumar protocetraric acid and protolichesterinic acid		
Flavocetraria nivalis	Foliose	Usnic acid and protolichesterinic acid		
Vascular plants species	**Growth form**	**Nr. of seeds**	**Lack in field**	**Lack in lab**
Betula pubescens	Tree	30	**X**	**X**
Pinus sylvestris	Tree	10		
Betula nana	Shrub	30		
Salix glauca	Shrub	15		
Dryas octopetala	Dwarf shrub	30	**X**	
Vaccinium myrtillus	Dwarf shrub	30		
Empetrum nigrum	Dwarf shrub	30	**X**	**X**
Anthoxanthum nipponicum	Graminoid	30		
Luzula spicata	Graminoid	30		
Avenella flexuosa	Graminoid	30		
Silene acaulis	Forb	30		
Solidago virgaurea	Forb	30		
Bistorta vivipara	Forb	30		**X**

The Dovre Mountains have a continental climate with short mild summers and long cold winters. At the weather station Fokstugu (930 m a. s. l.) *c*. 26 km south of the study site the mean annual precipitation was 435 mm and mean annual temperature was –0.1 °C for the period 1961-1990. For the same period the warmest month was July and the coldest was January, with average monthly temperature at 9.8 °C and –8.8 °C, respectively (Michelsen et al. 2011).

In November 2013 six common lichen species and seeds of 12 vascular plants were collected at Dovre (Table 1). The *Pinus sylvestris* seeds were supplied by Skogfrøverket, and originated from Oppdal. All the plants were used in both field and laboratory experiments.

Field experiment

Plastic trays (56 x 26 x 8 cm) divided into 4 plots each were filled with commercial garden soil (1 liter of soil per plot). Each tray had holes to drain water, and the vegetation underneath the trays was removed to allow the same height of the plots as the surrounding vegetation. Eight replicate plots were made for each lichen species and randomly assigned to the trays. Two types of controls were made. One with bare soil where seeds were sown, and one with bare soil and no seeds to estimate external seed influx.

For the cushion-forming lichens (*Cladonia stellaris* and *Cladonia arbuscula*), monospecific cushions were collected near the field site and transplanted into the plots so the lichen covered the whole plot. Due to the growth structure of *Alectoria ochroleuca*, *Flavocetraria nivalis, Cetraria islandica* and *Stereocaulon paschale* the plots were filled with smaller lichen samples to fill the whole plot. A mixture of 30 seeds from each plant species (only 10 for *Pinus sylvestris* due to expected high germination percentage and 15 for *Salix glauca* because of limited number of seeds available) was sown in October 2013. String was tied in a grid over the lichens to keep them within the trays. From October to May the trays were placed in a sheltered area to reduce wind exposure. The trays were moved to a ridge in May, the typical vegetation for the lichen species used in this experiment.

In May 2014 temperature loggers (NexSens Micro-T DS1921G loggers) were placed 0.5 cm below the soil surface in each plot to measure the soil temperature. Soil moisture was measured for each plot during a rainy day (26.8.14) and a dry day (28.8.14) with a hand-held moisture meter (TRIME-PICO, IMKO GmbH, Ettlingen, Germany). In late August and early September 2014 the temperature loggers were collected and the seedlings harvested. Seedlings were identified, counted, oven dried (70°C) and weighed. The thickness of the lichen cushions and the soil depth was measured for each plot.

Biomass for the vascular plant seedlings was measured as the average weight of each plant species in a plot.

Laboratory experiment

Lichens collected in November 2013 were cleaned for debris, dried and crushed with a hand blender. Five replicates were made for each lichen species and a control, with a total of 35 Petri dishes per plant species (Figure 1). In each Petri dish 2 gram of lichen was added underneath a filter paper. Thirty seeds (except for *Pinus sylvestris* and *Salix glauca* with 10 and 15 seeds, respectively) were placed on the filter paper and 6 ml of distilled water was added. In the controls there was only filter paper and water. Every Petri dish was sealed with laboratory film and left in a cold room (3°C) for 12 weeks. The Petri dishes were checked every third week. After the cold stratification the Petri dishes were transferred to growth chambers (Percival E-36L) for 6 weeks with 20 hours daylight at 20°C, and 4 hours darkness at 10°C. Every week the Petri dishes were rotated within the chamber and 2 ml of distilled water was added. More water (1-2 ml) was added when signs of desiccation on the filter paper occurred. Germinated seeds were counted and removed from the Petri dishes.

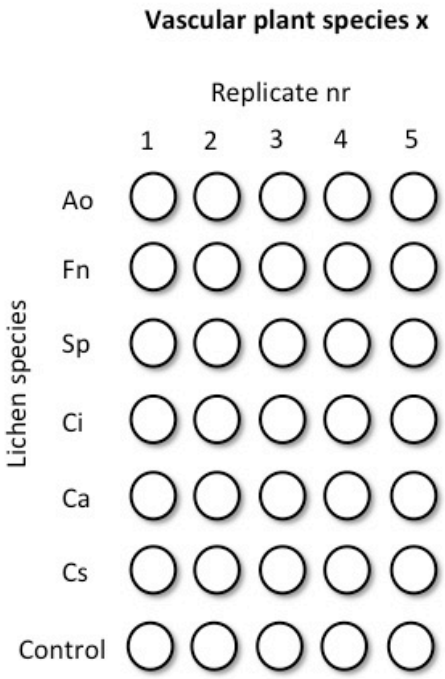

Figure 1: Experimental design for vascular plant species nr x (n=13, see Table 1). There were 5 replicates for each of the 6 lichen species. In each petri dish 30 seeds from one of the plant species were added. In addition there were 5 petri dishes with seeds, but without lichen (control), making a total of 35 petri dishes per plant species. Ao; *Alectoria ochroleuca*, Fn; *Flavocetraria nivalis*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*.

Statistical analysis

Effects of lichen treatments on seedling emergence (question 1) were investigated by fitting a mixed-effects logistic regression model (Generalized Linear Mixed-Effects Model with Binomial distributed errors and logit link-function) with proportion of seed emerged as seedlings (due to difference in the number of seeds sown between plant species) as response variable, and lichen treatments and plant species as explanatory variables. Soil depth was added as a covariate to account for variation in soil depth among the plots. Tray was treated as a random factor to account for the variation among them. To test if there was an effect of the treatments on seedling emergence, model comparisons based on the Akaike information criterion (AIC) were made between the fitted model and models without treatment included. The same procedure was used for investigating the effect of lichen treatments on seedling emergence of each vascular plant species separately. The differences among treatments were tested by a Tukey *post hoc* test from the package multcomp (Hothorn et al. 2007).

Effects of lichen treatments on seedling biomass (question 2) were investigated by fitting a linear mixed-effects model with average biomass per seedling per plot as the response variable, and lichen treatment and plant species as explanatory variable. Tray was added as a random factor. Model comparisons were done as above. The same procedure was used for investigating the effect of lichen treatments on seedling biomass of each vascular plant species separately. Because biomass was affected by the lichen treatments, a second model was fitted with the same random structure but with the thickness of lichen covers as a fixed factor.

Mixed-effects regression models were used to test if the thickness of lichen cover affected microclimatic conditions, i.e. soil moisture and soil temperature (question 3). Models were fitted for soil moisture and all the soil temperature proxies with lichen thickness as a fixed factor, soil depth as a covariate and tray as a random factor.

Effects of lichen treatments on seed germination (question 4) were investigated by fitting a mixed-effects logistic regression model (Generalized Linear Mixed-Effects Model with Binomial distributed errors and logit link-function). The model was fitted with the proportion of germinated seeds as response variable, and lichen treatment and

plant species as explanatory variables. Water was treated as a random factor, to account for the variation in total amount of water added to each Petri dish. The same procedure was used for investigating the effect of lichen treatments on seed germination of each vascular plant species separately. Model comparisons were done as above.

All statistical analyses were performed in R, version R 3.1.2 (R Core Team 2015). Mixed-effect models were fitted with the lme4 package (Bates et al. 2014). For the plant species with external seed influx (only *B. nana* and *V. myrtillus*) the mean seed influx was subtracted from the data prior to the statistical analyses.

Results

Table 2 gives an overview of the hypothesis tested, statistical models and AIC-values (see appendix A for the AIC-values for the models made for each plant species).

Table 2: Hypothesis, model parameters and statistical results showing the number of parameters (*k*) and AIC-values of mixed-models. Under model parameters the random factors are denoted (1 | random effect), soil depth is a covariate and the other parameters are fixed factors.

Hypothesis	Model parameters		*k*	AIC
Field experiment				
H1: There is an effect of lichen treatment and plant species on seedling emergence	treatment + plant + soil depth + (1 | tray)		18	1860
	plant + soil depth + (1 | tray)		12	2066
	treatment + soil depth + (1 | tray)		9	3268
	soil depth + (1 | tray)		3	3439
	constant + (1 | tray)		2	3603
H2: The biomass of the seedlings are affected by the lichen treatments	treatment + plant + soil depth + (1 | tray)		18	1054
	plant + soil depth + (1 | tray)		12	1067
	treatment + soil depth + (1 | tray)		10	1482
	soil depth + (1 | tray)		3	1492
	constant + (1 | tray)		2	1598
H3: The biomass of the seedlings are affected by the thickness of the lichen cushions	thickness + plant + soil depth + (1 | tray)		13	964
	plant + soil depth + (1 | tray)		12	1067
	thickness + soil depth + (1 | tray)		4	1392
	soil depth + (1 | tray)		3	1492
	constant + (1 | tray)		2	1598
H4: Lichen cushion thickness affect soil temperature (without control)	thickness + soil depth + (1 | tray) soil depth + (1 | tray) constant + (1 | tray)	*Minimum temperature*	5	82
			4	122
			3	120
		Maximum temperature	5	284
			4	318
			3	317
		Mean temperature	5	39
			4	58
			3	56
		Amplitude	5	293
			4	329
			3	329
H5: Lichen cushion thickness affect soil moisture (without control)	thickness + soil depth + (1 | tray)		5	254
	soil depth + (1 | tray)		4	252
	constant + (1 | tray)		3	254
H6: Lichen cushion thickness affect soil moisture (with control)	thickness + soil depth + (1 | tray)		5	243
	soil depth + (1 | tray)		4	291
	constant + (1 | tray)		3	306
Laboratory experiment				
H7: There is an effect of lichen treatment and plant species on seed germination	treatment + plant + (1 | water)		17	1955
	plant + (1 | water)		11	1999
	treatment + (1 | water)		8	5399
	constant + (1 | water)		2	5422

Field experiment – seedling emergence

The rate of seedling emergence was affected by the lichen treatments (Table 2, H2). Seedling emergence was in general low, although there was a significant difference between the control and all the lichen treatments (Tukey *post-hoc* test, Table 3). The highest estimated emergence rate was found in *S. paschale* (10.2 %) and the lowest in *C. stellaris* (4.3 %). All the plant species, except *B. nana* and *B. vivipara,* were affected by the lichen treatments whereby the lichens in general increased the seedling emergence (Table 4). There were also some differences among the lichen treatments (Figure 2). The effect of the lichens on the seedlings was species-specific.

Table 3: Model estimates of the overall seedling emergence rate. Soil depth (cm) was included in the models as a covariate. The letters (a-d) indicates significant differences detected by Tukey *post hoc* test. Model estimates for plant species are not shown.

	Seedling emergence			
Treatment	**Estimate ± SE**	**Z value**	***Estimates %**	**Tukey test**
Control (Bare soil)	-4.34 ±0.31	-13.917	1.3	D
Flavocetraria nivalis	-3.06±0.27	-11.489	4.5	C
Alectoria ochroleuca	-2.32±0.29	-7.948	8.9	A
Stereocaulon paschale	-2.18±0.28	-7.660	10.2	A
Cetraria islandica	-2.75±0.28	-9.691	6.0	BC
Cladonia arbuscula	-2.52±0.28	-8.935	7.5	AB
Cladonia stellaris	-3.11±0.29	-10.559	4.3	C
Soil depth (cm)	0.10±0.11	0.606	0.5	

* Back-transformed estimates of the logit transformed estimates of the model

Table 4: Percentage seedling emergence for each plant species in the different lichen treatments. The * indicate significance values from a GLM with binomial errors. The numbers shown are back-transformed from the logit transformed model estimates (see appendix B). *Betula nana* and *B. vivipara* did not show any difference among treatments and are not included. Significant codes; *** P<0.001, ** P<0.01, * P<0.05, ’P<0.1 are shown for estimates significant different from the control.

	Lichen treatments						
Plant species	Control	*F. nivalis*	*A. ochroleuca*	*S. paschale*	*C. islandica*	*C. arbuscula*	*C. stellaris*
P. sylvestris	31.4	65.0***	70.1***	65.5***	61.8***	66.6***	45.7´
S. glauca	0.5	8.7**	4.5´	8.7**	0	7.1*	8.5*
V. myrtillus	0.9	2.3	4.5**	3.9**	1.6	4.1**	3.8**
A. nipponicum	0.8	5.0***	3.4*	6.4***	4.0**	8.3***	2.8*
A. flexuosa	0.7	6.3*	5.6*	10.3**	7.3*	5.0´	12.8**
S. acaulis	2.2	3.9	17.7***	9.8**	16.5***	4.8	2.8
S. virgaurea	0.1	1.7**	5.2***	9.5***	3.0**	3.8***	1.9**
L. spicata	-	1.9	4.2	19.1	0.9	12.3	6.6

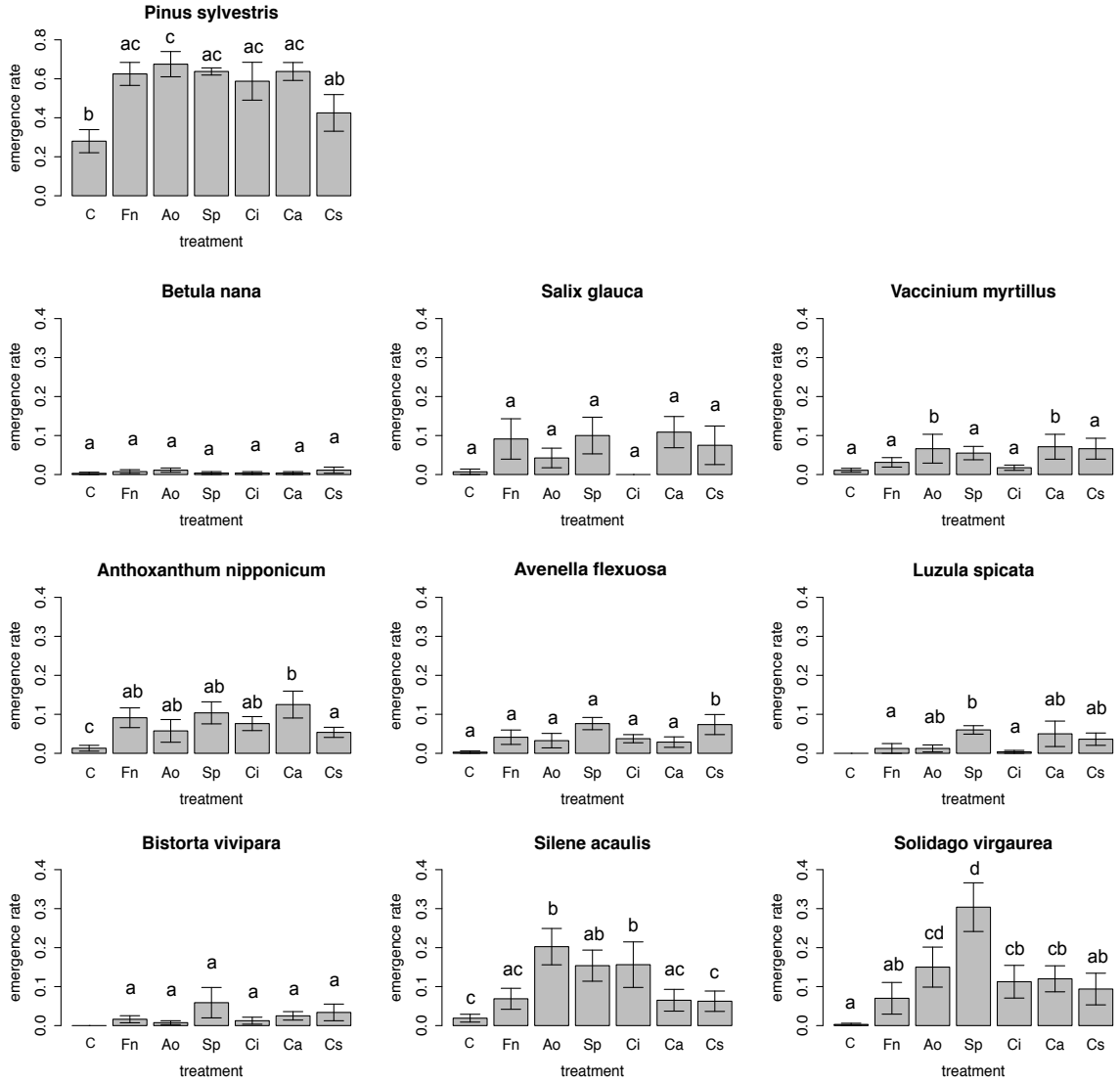

Figure 2: Seedling emergence rate of each plant species in field. Except for *P. sylvestris* all plant species had seedling emergence under 40 %. The letters (a-d) indicates significant differences detected by Tukey *post hoc* test of the model; seedling emergence ~ treatments +(1|tray) for each plant species. C; Control, Ao; *Alectoria ochroleuca*, Fn; *Flavocetraria nivalis*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*.

Field experiment – seedling biomass

The biomass of the seedlings was affected both by lichen treatments (Table 2, H2) and thickness of the lichen cover (Table 2, H3). The biomass of the seedlings decreased (slope; –0.22±0.05) with increased thickness of lichen cover.

Differences in seedling biomass were found for some treatments (Tukey *post hoc* test, Table 5). Seedlings emerging within *C. stellaris* had significantly lower biomass compared to seedlings in all other lichen treatments but not compared to the bare soil control. In *S. paschale* the seedlings had a higher biomass than those in the control and in *C. stellaris*, but not when compared to the other lichen species.

Table 5: Model estimates for effects of lichen treatments on seedling biomass. Soil depth (cm) was included in the models as a covariate. The letters (a-c) indicate significant differences detected by Tukey *post hoc* test. Model estimates for plant species are not shown.

Seedling biomass (mg)				
Treatment	**Estimate ± SE**	**df**	**T value**	**Tukey test**
Control (bare soil)	0.53±0.56	266	0.95	AB
Flavocetraria nivalis	1.27±0.50	266	2.57	BC
Alectoria ochroleuca	1.24±0.52	266	2.40	BC
Stereocaulon paschale	1.74±0.51	266	3.43	C
Cetraria islandica	1.17±0.52	266	2.25	BC
Cladonia arbuscula	1.25±0.51	266	2.46	BC
Cladonia stellaris	0.21±0.52	266	0.40	A
Soil depth (cm)	0.35±0.20	266	1.79	

Field experiment – microclimatic conditions

Soil temperature was affected by the thickness of the lichen cushions (Table 2, H4). Thickness could not explain the variation in soil moisture between lichens, but the presence of the lichens had an effect on soil moisture when compared to controls (Table 2, H5 and H6).

The average thickness of the lichen layers was greatest in *C. stellaris*, followed by *C. arbuscula* (Figure 3 a) and the temperature fluctuation (Figure 3 e) was least in these two lichen species. The bare soil control plots had the most extreme values for both minimum and maximum soil temperature and thus the highest temperature amplitude (Figure 3 c-f). The control plots had in addition the largest variation in soil moisture (Figure 3 f) with a large difference between dry and moist soil conditions.

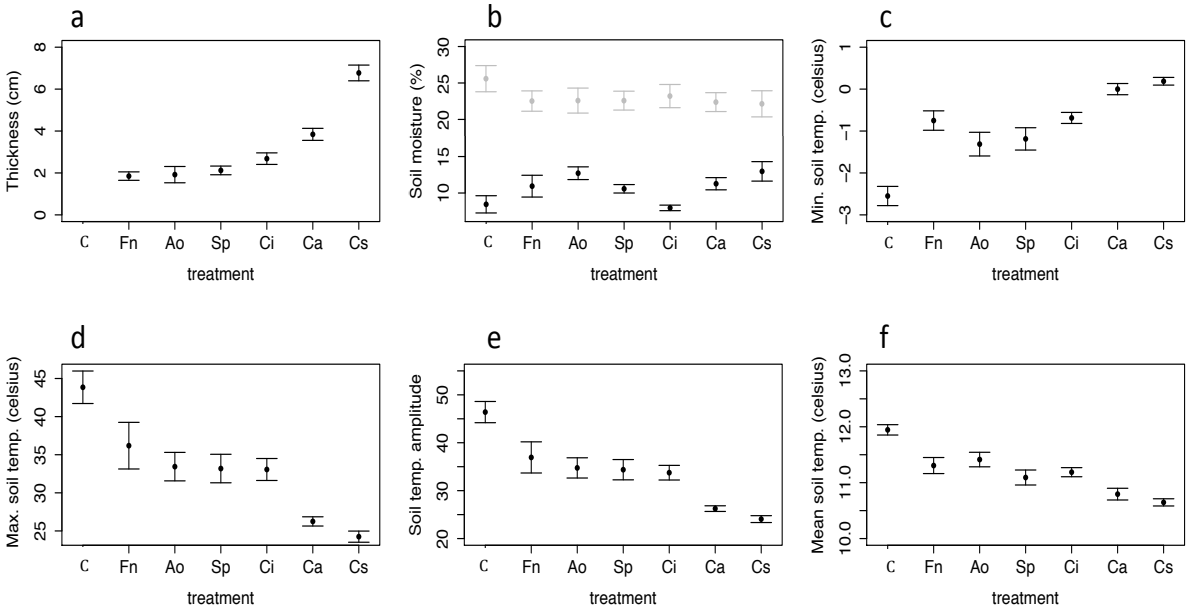

Figure 3. Lichen thickness (a) and microclimatic conditions (b-f) shown with mean and standard error for each lichen treatment; b) soil moisture, gray bars = rainy day, black = sunny day; c) minimum soil temperature; d) maximum soil temperature; e) soil temperature amplitude; f) mean soil temperature. C; Control, Ao; *Alectoria ochroleuca*, Fn; *Flavocetraria nivalis*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*.

Laboratory experiment – seed germination

The germination rate of seeds of the vascular plants in the petri dishes was affected by the lichen treatments (Table 2, H7), and the lichen treatments affected the vascular plants differently (Table 7). Only *P. sylvestris*, *D. octopetala* and *L. spicata* were not affected by the lichen treatments (Table 8, Figure 4).

Germination rates of vascular plants were lower when sown in *A. ochroleuca* and *F. nivalis* than in the control (Table 7), but not solely negative considering each plant species (Table 8). *Avenella flexuosa* germinated better in the lichen treatments but only significantly different from the control in two of the lichen treatments. The germination percentage of *B. nana*, *S. glauca* and *V. myrtillus* was significantly reduced by at least two of the lichen treatments. The germination percentage was both positively and negatively affected by the lichen species. When seed germination was significantly reduced by the lichen treatment (Table 8), the difference between the control and lichen treatment varied from – 6.6 % (*S. glauca* in *C. stellaris*) to – 28 % (*S. glauca* in *F. nivalis*).

Table 7: Model estimates for effects of lichen treatments on germination rate in the lab experiment. Only estimates for the lichen treatments are shown. The letters (a-d) indicates significant differences detected by Tukey *post hoc* test of the model; germination rate ~ treatments + plant species + (1| water).

Germination rate				
Treatment	Estimate ± std. error	Z value	*Estimate %	Tukey test
Control	-1.79±0.12	-15.56	14.3	C
Flavocetraria nivalis	-2.13±0.12	-17.96	10.7	AB
Alectoria ochroleuca	-2.28±0.12	-18.99	9.3	A
Stereocaulon paschale	-1.60±0.11	-14.07	16.8	C
Cetraria islandica	-1.76±0.12	-15.31	14.7	C
Cladonia arbuscula	-2.03±0.12	-17.28	11.6	BC
Cladonia stellaris	-1.87±0.12	-16.12	13.4	BC

* Back-converted estimates of the logit transformed estimates of the model

Table 8: Percentage germination for each plant species in the different lichen treatments in the lab experiment. The * indicate significance values from a GLM with binomial errors. The numbers shown are back-transformed from the logit transformed model estimates (Actual germination percentage is shown for *S. acaulis,* see appendix C.). *Pinus sylvestris, D. octopetala* and *L. spicata* did not show any difference among treatments and are not included. Significant codes; *** P<0.001, ** P<0.01, * P<0.05, 'P<0.1 are shown for estimates significant different from the control.

Plant species	**Lichen treatments**						
	Control	*F. nivalis*	*A. ochroleuca*	*S. paschale*	*C. islandica*	*C. arbuscula*	*C. stellaris*
B. nana	20.2	13.2	12.8	15.2	5.6***	12.4	11.4*
S. glauca	29.4	1.4***	14.8***	13.6***	38.6	17.2***	22.8***
V. myrtillus	75.4	83.4	54.8***	70.0	77.4	56.8***	63.4*
A. nipponicum	6.0	4.2	3.4	8.1	3.4	10.7'	4.8
A. flexuosa	18.8	23.3	34.0**	21.3	24.2	26.7	31.3*
S. acaulis	10.8	0.0	0.6	40.4	32.8	2.0	20.2
S. virgaurea	78.0	63.8**	66.6*	81.4	74.8	84.0	75.8

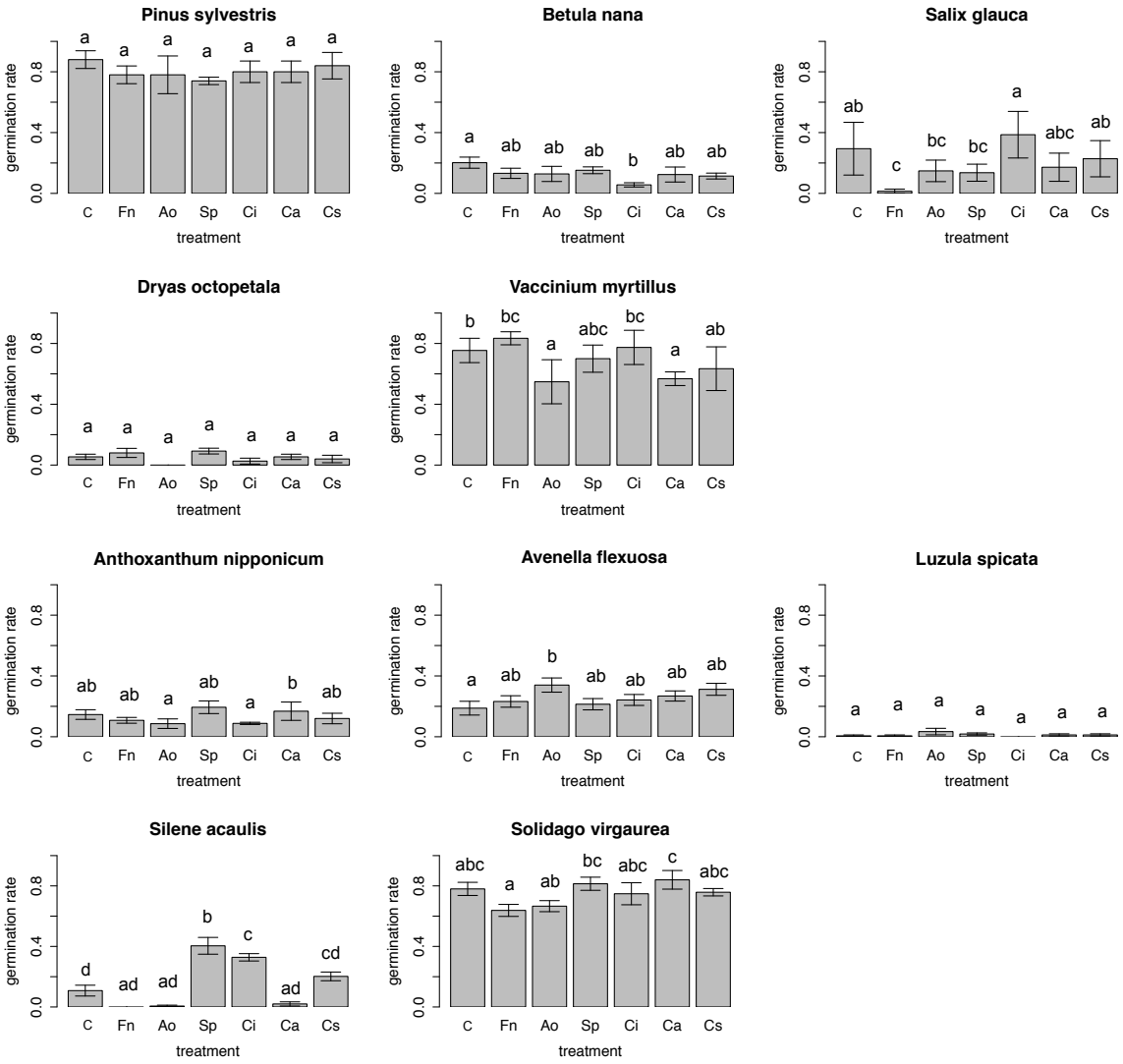

Figure 4: Germination rate of seeds for each plant species in the laboratory. The germination rates were highest for *P. sylvestris*, *V. myrtillus* and *S. virgaurea*. The letters (a-d) indicates significant differences detected by Tukey *post hoc* test of the model; germination rate ~ treatments +(1|tray) for each plant species. C; Control, Ao; *Alectoria ochroleuca*, Fn; *Flavocetraria nivalis*, Sp; *Stereocaulon paschale*, Ci; *Cetraria islandica*, Ca; *Cladonia arbuscula* and Cs; *Cladonia stellaris*.

Discussion

This study showed that lichens rather facilitate than prevent seedling recruitment and that the important effects of the lichens is more related to structure than to chemistry. The lichens prevent high temperature fluctuations and this may have caused the increased emergence, growth and survival we observed in lichen mats compared to on bare soil in our experiment. For lichens with very thick mats however, the facilitative effect was replaced by restrained recruitment and growth conditions.

Lichens as vascular plant facilitators

In the field the presence of lichens increased the seedling emergence in comparison to emergence on bare soil for all the plant species except *B. nana*, which had a very low seedling emergence in all treatments. This demonstrates the importance of the sheltering effect the lichens provide. On the exposed ridges where lichens dominate and the vegetation is otherwise sparse the shelter of lichens might be an advantage for other species. This is in agreement with the Stress Gradient Hypothesis, which predicts more facilitation under stressful conditions (Brooker et al. 2008). However, our findings were surprising because we were expecting an overall stronger negative effect of growth structure and allelopathy of the lichens in agreement to the observations of Sedia and Ehrenfeld (2003) and Hawkes and Menges (2003). However, these experiments were conducted on lower altitudes and in more benign environments. The negative effect of lichens on vascular plants does not seem to be large enough to counterbalance the facilitating effect of lichens observed on ridges.

The control plots had larger diurnal temperature fluctuations with higher temperature extremes, and a dryer environment compared to the plots with lichen cover. These conditions might be favorable for seed germination but not for seedling emergence and survival, hence reflect the conflicting requirements of different regenerative phases of plant recruitment (Welling 2002). The limited emergence on bare soil is in agreement with the findings of Schlag and Erschbamer (2000) and Bell and Bliss (1980). In addition, relationships between soil surface characteristics and seed morphological attributes often determine the microsites of seed entrapment and influence patterns of seedling establishment on exposed soils (Chambers 1995). Light seeds are less likely to germinate on wind-exposed sites, while large seeds are more exposed to seed predators

in open sites (Fenner and Thompson 2005) potentially reducing the amount of seeds on bare soil. However, the seedling emergence and survival in contrast to seed entrapment and retention depended on the ability of different soils to meet the requirements of the plant species (Chambers 1995). Lichens therefore seem to provide better microsites than bare soil regarding the abiotic conditions in the plots and in this way lichens may facilitate vascular plants. Thus differences in seedling emergence found among lichens might imply that some lichen species constitute more resistance to colonization than others.

Physical structure of lichens

Physical structure of lichens seems to increase the amount of seeds within lichens. In contrast to bare soil, the structure of the lichens traps seeds (Sedia and Ehrenfeld 2003), which can explain the observed difference between soil and lichen cover. The variation in seedling emergence among lichens is more complex. The seedling emergence in the two foliose lichens was lower compared to seedling emergence in all the fruticose lichens except *C. stellaris,* which forms substantially thicker mats than the other lichens. The difference in growth structure between foliose and fruticose lichens might explain some of the variation observed. Foliose lichens have flat leaf-like thalli (Holien and Tønsberg 2006), which might prevent more seeds from entering the soil. Although there is more variation in growth structure among fruticose lichens, their thalli are generally tread-like whereas their structure is bush like (Holien and Tønsberg 2006), allowing more seeds to penetrate their vertical growth pattern. Furthermore, seeds captured in lichens might be suspended in air and not able to reach the soil (Zamfir 2000). When the thickness increases, more seeds might be suspended and reduce the seedling emergence. In contrast, low thickness enables more seeds to reach the ground. Thus the cushion thickness of *C. stellaris* might contribute to prevent seedling emergence as efficient as the foliose lichens. Chambers (1995) found that seed size, the presence or absence of specialized appendages or seed coats, and the nature of the appendages or seed coat influenced the numbers of seeds trapped and the seed distribution in different soils. The microsite of seed entrapment within lichens might somewhat be determined in a similar manner, depending on the seed morphology and the growth structure of the lichens. In addition, variation among plant species depending on species-specific requirements for germination and growth (Baskin 2001) is likely to increase the variation in seedling emergence as well.

The thickness of the lichen cushions influences the biomass of the seedlings. In the thickest lichen cushions the biomass was reduced in comparison to the thinner ones. In contrast to the other lichen treatments where the average thickness varied between 2 cm and 4 cm, the *C. stellaris* cushions were on average 7 cm. This large difference in thickness may play an important role in the establishment of seedlings. Although seedlings in general seem to have higher seedling biomass in the lichen cushions than on soil, a certain thickness of cushion reduces the advantage of establishment within lichens. The physical structure of lichens will also influence the microclimatic conditions underneath the lichens.

Microclimate underneath lichens

Although the presence of a lichen cover seems to have an effect on soil moisture, we did not find that thickness could explain the variation in soil moisture among lichens. It could be that the soil moisture data was less accurate because it was not measured continuously as temperature was. However, the water absorbing and retaining abilities depend on lichen morphology (Larson 1981) such as thallus size (Gauslaa and Solhaug 1998) and vary among species (Larson 1979). Because the growth structure, hence morphology of the lichens in this experiment varied a lot, thickness of lichen cover is probably not a sufficient measure to explain variation in soil moisture among species. However, soil temperature was affected by the thickness of lichen cover. Lichens absorb and retain moisture from fog and dew and ameliorate extremely dry or hot soil conditions (Hawkes and Menges 2003), and so influence the microclimatic conditions. Sedia and Ehrenfeld (2003) found that lichen mats covering large areas increased soil moisture and influence the temperature of the soil surface. Our results support these findings though on a smaller scale.

The variation in soil temperature among lichen species varied with the thickness of the lichen cushions. The soil temperature underneath lichen species with the thinnest lichen cover had higher temperature amplitudes than the two thickest lichens and could contribute to lower germination in these two lichen species. Especially for small-seeded species with low competition ability fluctuations in soil temperature may be important for germination (Fenner and Thompson 2005) indicating gaps or shallow burial. However, the pattern of seedling emergence did not simply follow the thickness of

lichen cover, implying that several factors work together to influence seedling emergence.

Lichen allelopathy on higher plants

Despite of generally low germination percentage in the laboratory experiment our results show that the vascular plants were both negatively and positively affected by the lichen species as compared to the control. There was also a difference among plant species if several or only a few lichen treatments affected the germination. Among lichens species, secondary metabolites differ in composition, concentration and effect (Latkowska et al. 2008; Nishitoba et al. 1987; Tigre et al. 2012). The allelopathic action of certain metabolites can vary to a great extent between different plant species (Peres et al. 2009). In addition, adaptations between species of plants and lichens might further complicate the picture regarding allelopathy. It is therefore not surprising to find variation in plant species reaction to different lichen species, or that some plant species is more affected than others by the same lichen species.

Because the secondary metabolites that cause inhibition are not distinguished from other chemicals in this study we cannot say for sure what chemicals reduced germination. However, pure lichen acids are not likely to be present in nature alone, especially not in such high concentration that some times has been tested in laboratory experiments (Nishitoba et al. 1987; Tigre et al. 2012). Neither are secondary metabolites isolated from other chemicals or other influencing factors in nature whereby the allelophatic effect may first be obtained or have a stronger effect when acting synergetically (Tigre et al. 2012). In addition, pH is known to influence germination (Baskin 2001) and the water solubility of secondary metabolites might vary with pH (Stark et al. 2007). In the laboratory a rough test with pH-indicator paper showed that *S. paschale* did have a higher pH than the rest of the lichens. Although not representative for all plant species this could have contributed to the difference in germination between *S. paschale* and the other treatments. It would be interesting to know if lichens in natural conditions alter pH in the same way as observed in the laboratory experiment.

In summary, allelopathy seems to only have a minor effect on the vascular plants in this experiment considering that three plant species did not respond to the lichen treatments, while the responses of the other plant species to the treatments were to

complex and inconsistent to get a clear view of their effects. Neither did the plant species affected by lichen treatments in the laboratory experiment show similar patterns of reduction compared to the seedling emergence in field.

Implication on vegetation dynamics

In conclusion our study showed that lichens are preferable microhabitats for vascular plants and do not seem to prevent seedling establishment except in the case of *C. stellaris*. However, species-specific interactions between vascular plants and lichens might influence the colonization of lichen dominated vegetation. Recruitment of vascular plants not inhibited by lichens or hampered by lichen growth structure, are then more limited by the plants ability to produce and disperse seeds and by the abiotic environment. In subarctic plant communities regeneration by seeds can have major impacts on the dynamics and structure of vegetation (Welling and Laine 2002). In a future warmer climate with more seedling establishment (Milbau et al. 2009) lichens will probably not hamper the expected vascular plant expansion. We might therefore expect the observed facilitative effect of lichens to influence succession by rather increase the speed of change in vegetation structure than decrease it. On the other hand, lichen heaths of *C. stellaris* might offer some resistance to colonization by vascular plants.

Acknowledgements

I like to thank my supervisors Bente, Kristin and Rick for your guidance through this master providing me with advice, technical skills, field work assistance and cookies, Rozi for helping me out on the lab, Øystein for your statistical guidance, the ECOSHRUB-gang for letting me be a part of your team, Kamal for lending out laboratory equipment, Skogfrøverket for providing us with seeds, NTNU Vitenskapsmuseet for access to Kongsvoll Research Station, Tommy Prestø for your advices on study-site and Maja for proofreading and sharing wisdom from your own master experience. I also like to thank the lovely girls in Primærprodusentene and my fellow students in TKSF for social support and motivation through the master study.

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Appendix A

Table 9: Model parameters and statistical results for A) seedling emergence A1) with and without A2) control, B) seedling biomass and C) seed germination. Number of parameters (*k*) and AIC-values are given for each plant species. Under model parameters the random factors are denoted (1 | random factor), soil depth is a covariate and the other parameters are fixed factors. The lowest AIC-values are shown with bold font if treatments are included in the model.

FIELD	**A1) Seedling emergence - with control included**																	
	Pinus		*Salix*		*Betula*		*Vaccinium*		*Anthoxanthum*		*Avenella*		*Luzula*		*Bistorta*		*Silene*		*Solidago*	
Model parameters	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC
Treatments + soil depth +(1|trays)	9	**251**	9	**156**	8	71	9	**226**	9	**227**	9	**167**	9	**-**	9	**-**	9	**254**	9	**279**
Soil depth+(1|trays)	2	280	2	180	2	71	2	275	2	288	2	198	2	-	2	-	2	343	3	406
Constant +(1|trays)	1	292	1	209	1	102	1	293	1	316	1	239	1	-	1	-	1	369	2	440

	A2) Seedling emergence - without control																	
	Pinus		*Salix*		*Betula*		*Vaccinium*		*Anthoxanthum*		*Avenella*		*Luzula*		*Bistorta*		*Silene*		*Solidago*	
Model parameters	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC
Treatments + soil depth +(1|trays)	8	**224**	8	**182**	8	**223**	8	**188**	8	**261**	8	**308**	8	**122**	8	**115**	8	**185**	8	**184**
Soil depth+(1|trays)	2	258	2	220	2	332	2	327	2	324	2	369	2	149	2	117	2	265	2	286
Constant +(1|trays)	1	262	1	243	1	373	1	330	1	346	1	401	1	187	1	148	1	281	1	292

	B) Biomass of seedlings (with control included)																	
	Pinus		*Betula*		*Vaccinuim*		*Anthoxanthum*		*Avenella*		*Luzula*		*Bistorta*		*Silene*		*Solidago*	
Model parameters	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC
Treatments + soil depth +(1|trays)	10	**224**	8	11	10	54	10	**120**	10	77	9	**71**	9	**57**	10	51	10	**129**
Soil depth+(1|trays)	4	257	4	14	4	44	4	125	4	72	4	76	4	64	4	38	4	133
Constant +(1|trays)	3	265	3	11	3	49	3	127	3	71	3	77	3	67	3	34	3	138

LABORATORY	**C) Seed germination (with control included)**																	
	Pinus		*Salix*		*Betula*		*Vaccinium*		*Dryas*		*Anthoxanthum*		*Avenella*		*Luzula*		*Silene*		*Solidago*	
Model parameters	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC	k	AIC
Treatments +(1|water)	7	138	8	**229**	8	**163**	8	**351**	8	65	8	**157**	8	**175**	8	65	8	**120**	8	**197**
Constant +(1|water)	1	130	1	268	1	182	1	396	1	70	1	168	1	187	1	70	1	326	1	218

Appendix B

Table 10: Model estimates of the seedling emergence rate for each plant species. Soil depth (cm) was included in the models as a covariate. The estimates of *B. nana, B. vivipara* and *L. spicata* were made without the controls.

	Seedling emergence rate					
Treatment	**Estimate**	**Std. error**	**Z value**	**Estimate**	**Std. error**	**Z value**
	Pinus sylvestris			*Salix glauca*		
Control	-0.77923	0.45494	-1.713	-5.3182	1.4192	-3.747
Alectoria ochroleuca	0.85382	0.46235	1.847	-3.0581	1.1349	-2.695
Cladonia arbuscula	0.68826	0.46146	1.492	-2.5646	1.0360	-2.476
Cetraria islandica	0.48119	0.46927	1.025	-14.5160	109.1636	-0.133
Cladonia stellaris	-0.17095	0.47922	-0.357	-2.6095	1.0994	-2.374
Flavocetraria nivalis	0.62222	0.42703	1.457	-2.3789	1.0494	-2.267
Stereocaulon paschale	0.64263	0.44967	1.429	-2.3566	1.0916	-2.159
Soil depth (cm)	-0.06221	0.20028	-0.311	-0.2012	0.4872	-0.413
	Vaccinium myrtillus			*Avenella flexulosa*		
Control	-4.7261	0.6956	-6.795	-4.9622	1.1460	-4.330
Alectoria ochroleuca	-3.0442	0.5837	-5.215	-2.8306	0.7150	-3.959
Cladonia arbuscula	-3.1535	0.5844	-5.396	-2.9360	0.7030	-4.177
Cetraria islandica	-4.1217	0.6427	-6.413	-2.5350	0.6757	-3.751
Cladonia stellaris	-3.2298	0.6315	-5.114	-1.9156	0.6569	-2.916
Flavocetraria nivalis	-3.7342	0.5992	-6.232	-2.6919	0.6331	-4.252
Stereocaulon paschale	-3.1963	0.5829	-5.483	-2.1605	0.6265	-3.449
Soil depth (cm)	0.3516	0.2598	1.353	-0.3194	0.2895	-1.103
	Silene acaulis			*Solidago virgaurea*		
Control	-3.78585	0.74638	-5.072	-6.8020	1.1373	-5.981
Alectoria ochroleuca	2.24958	0.46270	4.862	-2.8952	0.6042	-4.792
Cladonia arbuscula	0.79537	0.50559	1.573	-3.2213	0.6043	-5.331
Cetraria islandica	2.16222	0.46543	4.646	-3.4691	0.5913	-5.867
Cladonia stellaris	0.23578	0.52717	0.447	-3.9510	0.6617	-5.971
Flavocetraria nivalis	0.59199	0.53004	1.117	-4.0748	0.5767	-7.066
Stereocaulon paschale	1.56458	0.47838	3.271	-2.2541	0.5810	-3.880
Soil depth (cm)	0.08548	0.29335	0.291	0.6365	0.2672	2.382
	Antoxhantum nipponicum			*Betula nana*		
Control	-4.7973	0.6994	-6.859	-	-	-
Alectoria ochroleuca	-3.3375	0.5814	-5.740	-3.70779	0.81303	-4.560
Cladonia arbuscula	-2.4050	0.5298	-4.540	-2.47792	0.73245	-3.383
Cetraria islandica	-3.1721	0.5634	-5.631	-2.97870	0.73249	-4.067
Cladonia stellaris	-3.5351	0.6041	-5.852	-4.30776	0.97273	-4.429
Flavocetraria nivalis	-2.9361	0.5276	-5.565	0.10424	0.80105	0.130
Stereocaulon paschale	-2.6830	0.5341	-5.023	0.03209	0.76847	0.042
Soil depth (cm)	0.2778	0.2406	1.154	0.31963	0.34529	0.926
	Bistorta vivipara			*Luzula spicata*		
Control	-	-	-	-	-	-
Alectoria ochroleuca	-4.2092	1.0146	-4.149	-3.8132	1.0493	-3.634
Cladonia arbuscula	-5.2860	0.9501	-5.564	-1.6387	0.8265	-1.983
Cetraria islandica	-5.0541	0.9437	-5.356	-3.8052	0.9667	-3.936
Cladonia stellaris	-4.3830	0.7455	-5.879	-2.4593	0.9564	-2.571
Flavocetraria nivalis	-3.6388	0.7493	-4.856	-3.1314	0.8314	-3.766
Stereocaulon paschale	-0.2742	0.8681	-0.316	-2.4531	0.7434	-3.300
Soil depth (cm)	0.5461	0.3758	1.453	-0.1247	0.3861	-0.323

Appendix C

Table 11: Model estimates of the germination rate for each plant species with the lowest AIC-values. Estimates are only made for the models with a difference in AIC-value ≥10. Estimates of *S. acaulis* are made with lmer of the model; number of seedlings ~ lichen treatments + (1|water).

	Germination rate					
Treatment	**Estimate**	**Std. error**	**Z value**	**Estimate**	**Std. error**	**Z value**
	Antoxhantum nipponicum			*Salix glauca*		
Control	-2.7590	0.8685	-3.177	-0.8792	0.2536	-3.467
Alectoria ochroleuca	-3.3536	0.8860	-3.785	-1.7610	0.3264	-5.395
Cladonia arbuscula	-2.1184	0.8301	-2.552	-1.5622	0.3050	-5.121
Cetraria islandica	-3.3536	0.8860	-3.785	-0.4613	0.2371	-1.946
Cladonia stellaris	-2.9907	0.8741	-3.421	-1.2272	0.2758	-4.450
Flavocetraria nivalis	-3.1236	0.8780	-3.558	-4.3041	1.0067	-4.275
Stereocaulon paschale	-2.4261	0.8624	-2.813	-1.8718	0.3397	-5.510
	Vaccinium myrtillus			*Avenella flexulosa*		
Control	1.1165	0.1894	5.894	-1.4718	0.2095	-7.024
Alectoria ochroleuca	0.1872	0.1640	1.141	-0.6633	0.1724	-3.848
Cladonia arbuscula	0.2683	0.1648	1.628	-1.0116	0.1846	-5.479
Cetraria islandica	1.2272	0.1950	6.293	-1.1527	0.1912	-6.029
Cladonia stellaris	0.5465	0.1694	3.226	-0.7846	0.1760	-4.457
Flavocetraria nivalis	1.6094	0.2191	7.346	-1.1896	0.1930	-6.162
Stereocaulon paschale	0.8473	0.1782	4.755	-1.3049	0.1993	-6.547
	Betula nana			*Solidago virgaurea*		
Control	-1.3863	0.2041	-6.791	1.2657	0.1971	6.421
Alectoria ochroleuca	-1.9308	0.2455	-7.865	0.6931	0.1732	4.002
Cladonia arbuscula	-1.9308	0.2455	-7.865	1.6582	0.2227	7.445
Cetraria islandica	-2.8764	0.3634	-7.916	1.0809	0.1877	5.758
Cladonia stellaris	-2.0571	0.2576	-7.987	1.1527	0.1912	6.029
Flavocetraria nivalis	-1.8718	0.2402	-7.793	0.5754	0.1701	3.382
Stereocaulon paschale	-1.7087	0.2266	-7.540	1.4718	0.2095	7.024

Treatment	**Estimate**	**Std. error**	**t value**
	Silene acaulis		
Control	2.80448	1.15747	2.423
Alectoria ochroleuca	-0.04902	1.20353	-0.041
Cladonia arbuscula	0.03832	1.07944	0.035
Cetraria islandica	9.44138	1.14836	8.222
Cladonia stellaris	5.75098	1.20353	4.778
Flavocetraria nivalis	-0.37760	1.10408	-0.342
Stereocaulon paschale	12.14195	1.09586	11.080