

Norwegian University of Life Sciences

Master's Thesis 201830 ECTSFaculty of Environmental Sciences and Nature Resource Management

The effect of long-term experimental warming on lichens and vascular plants in an alpine *Dryas* heath

Åshild Hasvik Natural Resource Management

Preface

This thesis completes my master's degree in natural resource management at the Norwegian University of Life Sciences (NMBU). Working with this thesis has been both challenging and rewarding. I am thankful for the opportunity to do the field work at Finse, in fantastic weather, and to have a fellow student to work together with.

I wish to thank my supervisors, Kari Klanderud, Johan Asplund and Ruben Erik Roos, for great help through the entire process, for guidance with field work, with analyses and through the writing process.

A special thanks to Maria Skar Knutsen for cooperation with field work, and for feedback and positivity during the last couple of months.

I would also like to thank Finse research Station for hospitality during the field work.

Ås, May 2018

Åshild Hasvik

Abstract

Global warming affects species diversity and ecosystems throughout the world, and alpine and arctic plant communities are considered to be particularly sensitive. During the last decades, several studies have shown a shift in species composition and a movement of species to higher elevations. Long-term warming studies have been conducted in these areas, with the aim to better understand and predict how consequences of global warming will affect the flora in cold climate ecosystems.

In this thesis, I have collected data from an on-going, 17-year-old, warming experiment in an alpine *Dryas* heath at Finse, Norway. I wanted to analyse how warming has affected species cover and richness of lichens and vascular plants and to assess if species composition of lichens and vascular plants has changed. Furthermore, I examined the role of soil moisture and cover of the dominant dwarf shrub *Dryas octopetala* on species cover, species richness, and composition. To examine if species cover and species richness differed between warmed plots and control plots I used one-way analysis of covariance (ANCOVA) with soil moisture and cover of *D. octopetala* as covariates. To visualise community composition in relation to the warming experiment I used ordination analysis.

I hypothesised that experimental warming would lead to a decrease in lichen richness and species cover, at the expense of an increase in species richness and cover of vascular plants. I found some support for the hypothesis, however, the majority of the results showed no effect of the warming manipulation. Few significant results may indicate stability in the community at Finse, and the ability to tolerate small changes in temperature. Possible explanations for stability is the influence of the dominant dwarf shrub *D. octopetala* and climatic conditions in Norway with a high level of precipitation that could counteract the effects of warming.

Table of contents

Prefaceii
Abstractiv
Introduction
Materials and methods 3
Study area3
Study design and data collection3
Statistical analyses4
Results
Discussion
Effects of warming on cover and diversity of lichens and vascular plants
Effects of the dominant dwarf shrub D. octopetala13
Effects of soil moisture
Conclusions15
References
Appendix19

Introduction

Global climate is changing, with implications for species diversity and ecosystems worldwide. Cold climate ecosystems have been particularly sensitive to global warming, and the International Panel of Climate Change predicts that alpine systems will continue to be especially vulnerable to further change (Settele et al., 2014). Cold-adapted plant communities are expected to be vulnerable to a changing climate as they are adapted to a have high stress-tolerance, but not adapted to be strong competitors. A warmer environment in alpine and arctic areas can lead to shifts in species composition (Walker et al., 2006; Rammig et al., 2010; Burrows et al., 2011; Pauli et al., 2012) and changes in ecosystems due to global warming are already observed. For instance, it is recorded a movement of species to higher elevations (Pauli et al., 2012; Steinbauer et al., 2018) together with changes in community composition and species diversity (Klanderud & Birks, 2003; Parmesan & Yohe, 2003; Hollister et al., 2005; Walker et al., 2006; Elmendorf et al., 2012; Pauli et al., 2012; Vanneste et al., 2017).

To enable precise predictions of community responses to global warming, climate change experiments such as warming manipulations, have been conducted in various alpine and arctic vegetation sites across the world. In Norway, experimental warming has been implemented at an alpine site in the central Norwegian mountain plateau at Finse. Here, open top chambers (OTCs) have been used as a warming method since year 2000. The warming experiment at Finse did not show any significant changes in community composition after four years (Klanderud & Totland, 2005b; Klanderud, 2008). However, a meta-analysis that includes the site at Finse and 60 others found that the abundance and species richness of lichens and mosses were in decline, while graminoids and taller shrubs increased depending on region and temperature (Elmendorf et al., 2012). Furthermore, there has been a decline in lichen cover as a response to a warmer climate in several other studies (Cornelissen et al., 2001; Hollister et al., 2005; Wahren et al., 2005; Walker et al., 2006; Lang et al., 2012; Alatalo et al., 2017; Vanneste et al., 2017). Although lichens have high tolerance for environmental stress factors, they are weak competitors. The decline in lichen diversity has been explained as an indirect effect of warming where an increased cover of vascular plants and their litter has weakened light conditions for lichens (Cornelissen et al., 2001; Lang et al., 2012; Alatalo et al., 2017). Lichens are an important part of alpine vegetation and have a key role in the function of northern ecosystems (Asplund & Wardle, 2017). They contribute to the carbon balance and certain lichens incorporate nitrogen by fixation, lichens are also an important food source for animals

in arctic and alpine areas, such as reindeer and caribou (Nash, 2008). Furthermore, a decline in lichen communities in alpine and arctic areas can contribute to reducing the albedo-effect, and thus amplify global warming (Thompson et al., 2004; Stoy et al., 2012).

Alpine and arctic species are slow-growing, and long-term studies are therefore pivotal for our understanding of the responses of these habitats to environmental changes. Responses to climate change differ by the region or habitat of the system, and some habitats seem to be more resistant than other (Jónsdóttir et al., 2005; Hudson & Henry, 2010; Bokhorst et al., 2017). Better knowledge about different habitats and regions and their responses to global warming are decisive in order to more accurately predict the consequences of higher temperatures, and to detect which habitat types that are more vulnerable to climate change. At Finse, the study-system is dominated by the dwarf shrub *D. octopetala*, a long-lived species with clonal growth. It is possible that plants with such traits can contribute with stability in their habitats, as high age and clonality have shown to provide higher resistance towards climate changes because of high genetic variability and turnover (De Witte et al., 2012).

After 17 years of warming experiment in the alpine *Dryas* heath at Finse, I have examined whether higher temperature has affected the heath community. I compared species cover, richness and composition of lichens and vascular plants in warmed plots versus control plots. The aim of this thesis is to increase the understanding of the effects of global warming on alpine plant communities. I used this experimental set-up to test the following hypotheses (1) Vascular plants, will respond positively to increased warming, as many of these are strong competitors. (2) Experimental warming will cause a decline in lichen coverage and diversity as a result of stronger competition from vascular plants, and in particular graminoids. I further explore how soil moisture and cover of the dominant species *D. octopetala* affect plant and lichen communities.

Materials and methods

Study area

Fieldwork was conducted at Finse, in the northern part of Hardangervidda mountain plateau in southwestern Norway. The plots are placed at a southwest facing slope at mountain Sandalsnuten (60°36059"N, 07°31023"E), 1520 meter above sea level (Olsen & Klanderud, 2014). Here, the mean monthly temperature in June, July and August are 6,3°C (Aune, 1993), in the same months mean monthly precipitation is 89 mm while annual precipitation is 1030mm (Førland, 1993). The study area is on a relatively exposed ridge where the wind speed is high and there is a low accumulation of snow (Klanderud & Totland, 2004). The bedrock of Sandalsnuten is relatively calcareous with phyllite, mica chist and some areas with layers of limestone (Klanderud & Totland, 2004). The rich bedrock at Sandalsnuten provides the basis for a species-rich heath community where the dwarf shrub *D. octopetala* is dominant (Olsen & Klanderud 2014). The area is relatively homogenous, but there are differences, some plots are on almost bare mountain ridges, some have a thicker layer of soil and a cover of various plants, while others are almost entirely covered by *D. octopetala*.

Study design and data collection

In 2000, 40 open top chambers (OTCs) and 40 control plots were established at Sandalsnuten. The chambers are made of plexiglass material with an opening at the top to let wind and rain in, they are five-sided and have an inside diameter of one meter. Inside the chambers two plots measuring 30 x 60 cm are established. To avoid edge effects the plots were put in the centre of the chambers (Klanderud & Totland, 2005b). The OTCs at Finse increase the above ground temperature (~5 cm) with 1,5°C, and the below-ground temperature (~5 cm) with 1°C (Klanderud & Totland, 2005b). OTCs have been used in several surveys to examine how higher temperatures may affect arctic and alpine communities (Hollister et al., 2005; Klanderud & Totland, 2005b; Wahren et al., 2005; Klanderud, 2008; Hudson & Henry, 2010). Analysis of overall performance of OTCs and possible biases can be found in Hollister & Webber (2000) and Marion et al. (1997).

Fieldwork with collection of species cover and richness for lichens was conducted during ten days in July 2017, while data on vascular plants were collected one year earlier, in July 2016,

by Siri Lie Olsen (unpublished). Collections of data for both vascular plants and lichens were conducted using the same method.

Prior to conducting fieldwork, a subset of 10 OTC-plots was randomly selected. In the field, prior to data collection, the plots were checked by visual judgement. One plot showed very low lichen cover (under 2%), and it was decided to reject the plot as it would not contribute with enough data, it was replaced with the next plot on the list of randomised plots. Control plots were chosen based on total cover of lichens (> 2%).

I recorded presence-absence data for all lichen species, except crustose lichens. I used a grid which covered the 30 x 60 cm plots, the grid consisted of 18 sub-plots each measuring 10 x 10 cm. Presence of all lichens was recorded for each square, and summed for each plot. Additionally, cover in percent was estimated for all lichens in each 30 x 60 cm plots, the estimation was done by visual judgement. Many lichens had a low cover, which made estimation challenging. Lichens with a cover below 1% are registered with 0.5%.

Soil moisture was measured at the end of August 2017, it was 6 °C with a 3/8 cloud cover after a clear morning. The measurements were taken with a Delta-T SM150 soil moisture kit with mineral soil settings. Eight measurements were conducted in each plot; the mean of these measurements was used in the analysis. By error, one plot was not measured (O8B). Where analyses required at number character, NA was replaced by the mean of the measurements in all OTC plots.

Statistical analyses

To visualise if species composition changed as a response to warming I performed ordination analyses, with non-metric multidimensional scaling (NMDS), using the metaMDS function in the Vegan R-package (Oksanen et al., 2017). When choosing distance both Jaccard and Bray-Curtis showed the same results, and Bray-Curtis was selected. Dimensions were set to two and three depending on stress levels (goodness of fit). In the analysis I used species cover data, all species were included, and split into the categories lichens and vascular plants. Two variables were added to the plots, soil moisture and coverage of *D. octopetala*, the latter to examine how the dominant species are related to the heath community. Envfit function in vegan package (Oksanen et al., 2017) was used to test if the environmental variables were related to the species composition. Ordielipse function was used to add a 95% confidence interval in the NMDS plots, in order to test for significant differences between OTC and control plots (Oksanen et al., 2017).

One-way analysis of covariance (ANCOVA) was performed to test for significant differences in species cover and species richness (response variables) between OTCs and control plots (explanatory variable). Response variables tested were lichens and vascular plants, and, in addition the functional types forbs, graminoids and dwarf shrubs. Soil moisture and cover of *D*. *octopetala* were covariates. When testing vascular plant cover and richness with *D*. *octopetala* as a covariate, sums of species richness and percent cover of *D*. *octopetala* were removed from the vascular plant data set. For variables with non-normal distribution, I used the package ImPerm to do permutation tests with 9999 permutations (Wheeler & Torchiano, 2016).

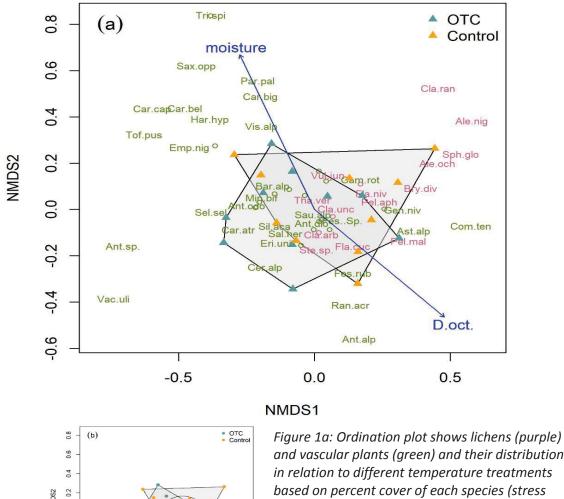
To test if there were any differences in soil moisture and cover of *D. octopetala* between OTC and control plots I performed one-way analysis of variance (ANOVA).

All analysis was performed with R 3.4.2 (R Core Team, 2017).

Results

The 95 % confidence intervals of the OTC and control plots in the NMDS overlapped, meaning that the species composition was not significantly different between the two treatments. This was the case both for total species composition, composition of lichens, and composition of vascular plants (Fig 1-3).

For total species composition, there are no significant relationships between the environmental variables soil moisture ($R^2 = 0.22$, P = 0.132) and cover of *D. octopetala* ($R^2 = 0.26$, P = 0.098) (Fig. 1a). The analysis shows that lichens are slightly clustered along an axis, but does not seem to be related to OTC/control or environmental variables (Fig. 1a).



0.5

and vascular plants (green) and their distribution in relation to different temperature treatments based on percent cover of each species (stress level = 0.13). Arrows show the environmental variables moisture and percent cover of D. octopetala and their relation to the species data. The length of the arrow represents the strength of the interaction, proportionally. Figure 1b show 95% confidence interval symbolized by circles, overlapping circles indicate no significance.

NMDS2

0.0

-0.2

-0.4

-0.6

-0.5

0.0 NMDS1

NMDS analysis with lichens show no significant relationship between composition of lichens and the environmental variables soil moisture ($R^2 = 0.07$, P = 0.524) and cover of *D. octopetala* ($R^2 = 0.01$, P = 0.906) (figure 2a).

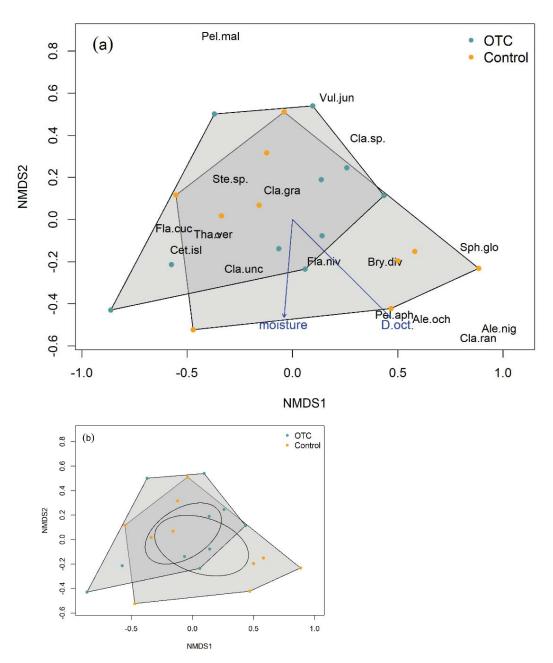
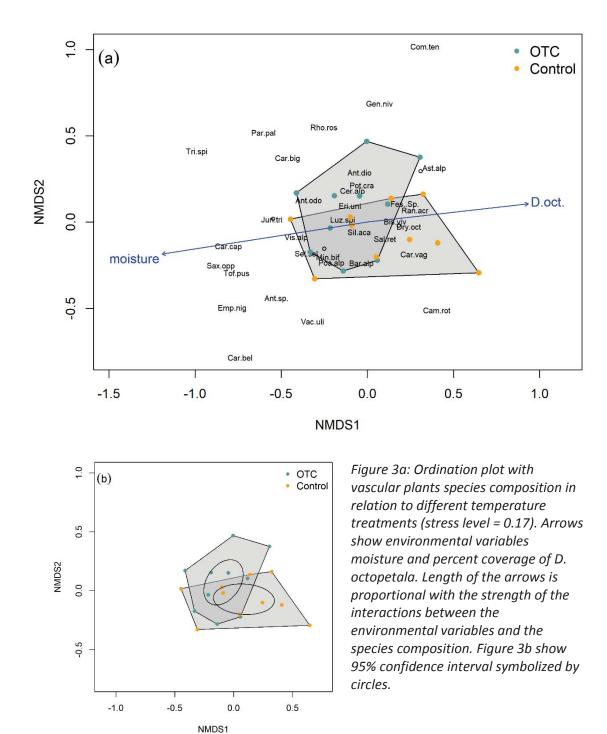


Figure 2a: Ordination plot shows how lichen composition is related to different temperature treatments based on percent cover of each species (stress level = 0.17). Arrows show the environmental variables moisture and percent cover of D. octopetala and their relation to the species data. The length of the arrow represents the strength of the interaction, proportionally. Figure 2b show 95% confidence interval symbolized by circles, overlapping circles indicate no significance.

NMDS analysis for vascular plants shows a significant relationship between cover of *D*. *octopetala* ($R^2 = 0.3$, P = 0.049) and species composition of other vascular plants. Soil moisture do not have a significant relationship with the composition of vascular plants ($R^2 = 0.14$, P = 0.28) (figure 3a).



Average cover of lichens in control plots are (15.9%), and in OTC plots (11.75%), for vascular plants, average cover in control plots are (85.3%), and in OTC plots (85.1%) (appendix table 1). The ANCOVA analysis showed a significant difference between OTCs and control plots for species richness of lichens, (Fig. 4a, mean values: OTC = 10.6, control = 12, SD = 2.386). Also species richness of forbs was significant related with higher temperature (Fig. 4e, mean values: OTC = 22.2, control = 20.5, SD = 2.305). There were no significant effects of OTCs on species cover in either functional groups (Fig 4a, c) (appendix table 2).

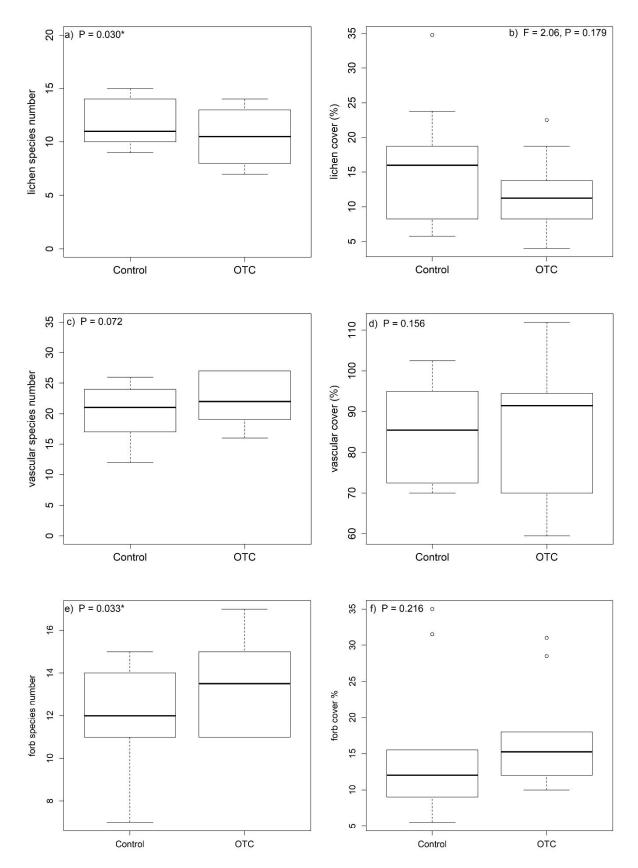


Figure 4: Cover and species number for lichens and vascular plants in OTCs and control plots. The box plots show species richness and cover of respectively lichens (a, b), vascular plants (c, d) and forbs (e, f). F- and P-values from the ANCOVA analyses. Significant values are marked with *. Figure c and d shows F- and P-values from the analyses where D. octopetala is omitted from the species data. The boxplots show the median and the interquartile range. (NB: Various y-axis).

Soil moisture varies significantly for species richness of vascular plants when cover of *D*. *octopetala* is omitted as co-variable (P = 0.036). In addition, soil moisture is close to significant for dwarf shrub cover (F = 4.46, P = 0.052). There are no differences in soil moisture between control and OTC when tested with ANOVA (Fig. 5a).

Cover of *D. octopetala* has a significant relationship with cover of vascular plants (P = 0.010). There are no differences in cover of *D. octopetala* between control and OTC when tested with ANOVA (Fig. 5b).

The analysis showed significant interactions between co-variables and temperature treatment for species richness of lichens, where it was a significant interaction between temperature treatment, cover of *D. octopetala* and soil moisture (P = 0.029). Other than this there were no significant interactions (appendix table 2).

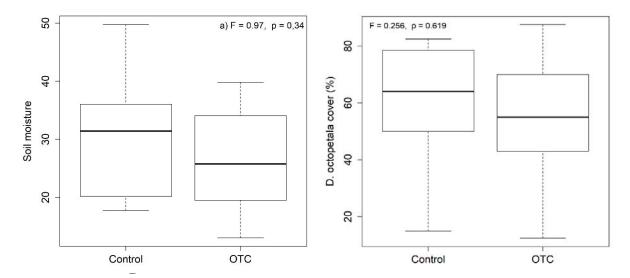


Figure 5a: Differences in soil moisture between OTCs and control plots. Figure 5b: Cover of Dryas Octopetala in OTCs and control plots. F- and P-values are obtained from ANOVA-analysis. *The boxplots show the median and the interquartile range.*

Discussion

The objective of my study was to examine if 17 years of experimental warming in an alpine *Dryas* heath at Finse has affected species richness, cover, or species composition. I found few significant differences as a result of warming, only species richness of lichens and forbs varied between OTCs and control plots, and in the ordination analysis species composition between OTCs and control plots showed no difference. Even though this is a long-term experiment there are few effects of warming, which may indicate that the community at Finse is robust and able to resist small increases in temperature. Long life cycles of the dominant shrub *D. octopetala* and other alpine plants could be a possible explanation of stability.

Effects of warming on cover and diversity of lichens and vascular plants

The results show that species richness of lichens was negatively affected by warming while forbs were positively affected. These results support my hypothesis that experimental warming with OTCs increases species richness of vascular plants at the expense of species richness of lichens. The results are also in line with several warming manipulation experiments and resurvey studies along elevational gradients, which report that lichen as a group are in decline because of higher temperatures (Elmendorf et al., 2012; Lang et al., 2012; Vanneste et al., 2017; Vuorinen et al., 2017). Interestingly, species cover does not seem to be affected by warming for neither of the functional types, in addition, ordination analysis did not show any differences in species composition between OTCs and control plots. Stability in the community could explain few significant responses after experimental warming. Effects of global warming on species richness and composition are likely to vary between different regions and habitats and other conditions like species diversity, the presence of dominant species and abiotic conditions like soil and climate (Van Wijk et al., 2004; Jónsdóttir et al., 2005). In the Norwegian Scandes, the loss of habitats as a consequence of climate change is predicted to be lower compared with mountains in southern Europe, due to an expected increase in rainfall while the rise in temperature is predicted to be less pronounced (Engler et al., 2011). In the study system at Finse, a high precipitation rate could counteract the effects of warming from the OTCs, as a release from drought stress might help the species to cope with higher temperatures.

Alpine vegetation is slow growing, and it is proposed that alpine communities respond slowly to climate warming (Cotto et al., 2017; Alexander et al., 2018). Epstein et al. (2004) found that some arctic systems needed up to 20 years and more before responses to an increase in 12

temperature of 3°C got evident. The increase in temperature at Finse is ~1.5°C above ground, Delayed responses could explain few differences between OTCs and control plots in this study. To further continue the experiment is important to assess if responses will occur after a prolonged time-period.

Effects of the dominant dwarf shrub D. octopetala

Cover of *D. octopetala* do not seem to be affected by warming, but, the ANCOVA analysis shows a significant effect of *D. octopetala* on species cover of vascular plants. A high percentage cover of *D. octopetala* will automatically lead to less space for other plants to grow, and it is not clear what the importance of these result is. The results could indicate that *D. octopetala* is an important species in this community, and it is possible that the presence of *D. octopetala* has masked the effect of the temperature treatments, explaining the low degree of significant differences between warmed plots and control plots in the results. Ordination analysis shows that the distribution of vascular plants in the ordination plots is significantly affected by the cover of *D. octopetala*. However, *D. octopetala* are not omitted from the species analysed, as a consequence this interaction may have a statistical bias because of autocorrelation.

Earlier removal experiments at Finse have shown how *D. octopetala* is an essential species with considerable influence on its surroundings. The effects of removing *D. octopetala* around two target species: *Thalictrum alpinum* and *Carex vaginata* were studied and compared with removal of all neighbouring vegetation in another experiment. The removal was conducted together with environmental manipulations (warming with OTC and nutrient addition) and showed a higher response on plant growth for the two target species after removal of *D. octopetala* than after removal of all neighbouring vegetation (Klanderud, 2005; Klanderud & Totland, 2005a).

Similar experimental studies with *Salix* spp. has shown that the shrub can influence soil temperature by trapping snow in winter season which isolates the soil, particularly in areas where the snow gets redistributed by the wind. In addition, shading in the summer season lowers the soil temperature. The combined effect of the shrubs is lower fluctuations in temperature through the year (Myers-Smith, 2011). The experiment was conducted with willow species, with a canopy height of 30-100 cm, so it is not clear if the results would account for the dwarf shrub *D. octopetala* as well, but it is conceivable that it could have a similar impact on its

habitat. Such temperature control from the dominant dwarf shrub could help explaining why *D*. *octopetala* seem to be essential for the species community at Finse.

D. octopetala is a long-lived, conservative species. De Witte et al. (2012) found that clonal diversity, genet size structure and genet longevity in populations of four arctic-alpine clonal plants has old genets and that they have survived previous climatic oscillations. The study looked into the diversity, structure, and age of *Carex curvula, Salix herbacea, Vaccinium uliginosum* and *D. octopetala*, and related it to community stability, and ecosystem resilience towards climate change (De Witte et al., 2012). This study supports the notion that *D. octopetala* could contribute with stability and higher persistence to global warming. Stability in dwarf shrub communities is also observed in other studies with experimental warming. Jonsdottir et al. (unpublished results), found a *Dryas* heath at Iceland and Svalbard to be stable towards higher temperatures and Henry and Hudson (2010) found that an evergreen shrub heath in the high arctic was resistant after 15 years of experimental warming. Also, in the Falkland Islands, 12 years of experimental warming in an *Empetrum rubrum* community with OTCs did not show any changes in cover, biomass or species richness (Bokhorst et al., 2017).

Effects of soil moisture

Only species richness of vascular plants had significant effects of soil moisture while species cover of dwarf shrubs had a close to significant effect. Besides, experience from the fieldwork was that the conditions were drier in OTCs compared to control plots (personal observations). This experience was also observed in fieldwork conducted in the same area one year earlier, where the result of the study found higher decomposition rates in control plots, supporting the observations that these plots may be more moist than OTCs (Haakonsen Karr, 2017). Other studies have shown that OTCs affect soil moisture negatively (Marion et al., 1997; Aronson & McNulty, 2009, Jónsdóttir (unpublished)), and it is possible that drier conditions inside OTCs counteract a positive effect of warming. However, since the measurements of soil moisture were conducted during one day, it is likely that my results do not sufficiently reflect the long-term conditions, and it is uncertain whether the significant and close to significant effects are valid. To measure soil moisture over an extended period, and in addition to measure humidity above ground, would give a better insight into the actual moisture regimes at Finse. The latter is an environmental variable worth investigating in order to understand lichen cover and richness since lichen absorbs moisture from surrounding air.

Conclusions

To conclude, this thesis points out that long-term experimental warming in a Dryas heat at Finse to some extent supports the hypothesis that lichens decline while vascular plants show positive responses to warming. In this case, there were differences between OTCs and control plots in species richness; lichens decreased, while forbs were positively affected by warming. However, it seems as the system here is stable, and able resist increased warming as the majority of my results showed no difference between warmed OTCs and control plots.

I suggest that *D. octopetala* may contribute to a stable system and hence masks the effects of warming. Other studies have also found stability against warming in dwarf shrub communities (Jónsdóttir et al. 2005, Jónsdóttir (unpublished), Hudson & Henry, 2010), and research pointing on shrubs and clonal plants as stabilizing (Myers-Smith, 2011; De Witte et al., 2012) supports the notion that *D. octopetala* contributes with stability in the heath community at Finse.

Soil moisture does not seem to be affected by warming, however, personal observations from the field are that the soil inside the OTCs is drier than in the control plots. Measurements of soil moisture were conducted during one day, and it is unclear how reliable they are.

Alpine vegetation is slow-growing, and changes in species composition, species diversity, and species abundance might occur slowly, or with a time-lag, this underlines the importance of continuing the warming experiment in the future. Some thoughts for future research is to conduct soil measurements over a longer time frame and to look closer in to whether dwarf shrubs and in this case, *D. octopetala*, has a stabilising effect on the alpine community.

References

- Alatalo, J. M., Jägerbrand, A. K., Chen, S. & Molau, U. (2017). Responses of lichen communities to 18 years of natural and experimental warming. *Annals of Botany*, 120 (1): 159-170. doi: 10.1093/aob/mcx053.
- Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S. *et al.* (2018). Lags in the response of mountain plant communities to climate change. *Global Change Biology*, 24 (2): 563-579. doi: 10.1111/gcb.13976.
- Aronson, E. L. & McNulty, S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, 149 (11): 1791-1799.
- Asplund, J. & Wardle, D. A. (2017). How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews*, 92 (3): 1720-1738.
- Aune, B. (1993). *Temperaturnormaler : normalperiode 1961-1990 = Air temperature normals : normal period 1961-1990*, vol. 02/93. Oslo: Det Norske meteorologiske institutt.
- Bokhorst, S., Convey, P., Huiskes, A. & Aerts, R. (2017). Dwarf shrub and grass vegetation resistant to long-term experimental warming while microarthropod abundance declines on the Falkland Islands. *Austral Ecology*, 42 (8): 984-994. doi: 10.1111/aec.12527.
- Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M. *et al.* (2011). The Pace of Shifting Climate in Marine and Terrestrial Ecosystems. *Science*, 334 (6056): 652-655. doi: 10.1126/science.1210288.
- Cornelissen, J. H. C., Callaghan, T. V., Alatalo, J., Michelsen, A., Graglia, E., Hartley, A. *et al.* (2001). Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, 89 (6): 984-994.
- Cotto, O., Wessely, J., Georges, D., Klonner, G., Schmid, M., Dullinger, S. *et al.* (2017). A dynamic ecoevolutionary model predicts slow response of alpine plants to climate warming. *Nature communications*, 8: 15399.
- De Witte, L., Armbruster, G. F., Gielly, L., Taberlet, P. & Stoeclin, J. (2012). AFLP markers reveal high clonal diversity and extreme longevity in four key arctic-alpine species. *Molecular Ecology*, 21 (5): 1081-1097.
- Elmendorf, S. C., Henry, G. H., Hollister, R. D., Björk, R. G., Bjorkman, A. D., Callaghan, T. V. *et al.* (2012). Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology letters*, 15 (2): 164-175.
- Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araújo, M. B. *et al.* (2011).
 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17 (7): 2330-2341. doi: 10.1111/j.1365-2486.2010.02393.x.
- Epstein, H. E., Calef, M. P., Walker, M. D., Stuart Chapin, F. & Starfield, A. M. (2004). Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology*, 10 (8): 1325-1334.
- Førland, E. J. (1993). Nedbørnormaler : normalperiode 1961-1990 = Precipitation normals : normal period 1961-1990. Precipitation normals normal period 1961-1990, vol. nr 39/93. Oslo: Det Norske Meteorologiske Institutt.
- Haakonsen Karr, E. (2017). *En studie av klimaendringenes påvirkning på nedbrytning av plantemateriale i et alpint miljø*. A study of climate change effects on decomposition of plant litter in an alpine environment: Norwegian University of Life Sciences, Ås.
- Hollister, R. D. & Webber, P. J. (2000). Biotic validation of small open-top chambers in a tundra ecosystem. *Global Change Biology*, 6 (7): 835-842. doi: 10.1046/j.1365-2486.2000.00363.x.

- Hollister, R. D., Webber, P. J. & Tweedie, C. E. (2005). The response of Alaskan arctic tundra to experimental warming: Differences between short-and long-term responses. *Global Change Biology*, 11 (4): 525-536.
- Hudson, J. M. G. & Henry, G. H. R. (2010). High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology*, 98 (5): 1035-1041. doi: 10.1111/j.1365-2745.2010.01690.x.
- 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. doi: 10.1111/j.1365-2486.2005.00928.x.
- Klanderud, K. & Birks, H. J. B. (2003). Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, 13 (1): 1-6. doi: 10.1191/0959683603hl589ft.
- Klanderud, K. & Totland, Ø. (2004). Habitat dependent nurse effects of the dwarf-shrub Dryas octopetala on alpine and arctic plant community structure. *Ecoscience*, 11 (4): 410-420.
- Klanderud, K. (2005). Climate change effects on species interactions in an alpine plant community. *Journal of Ecology*, 93 (1): 127-137.
- Klanderud, K. & Totland, Ø. (2005a). The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, 93 (3): 493-501.
- Klanderud, K. & Totland, Ø. (2005b). Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86 (8): 2047-2054.
- Klanderud, K. (2008). Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science*, 19 (3): 363-372.
- Lang, S. I., Cornelissen, J. H., Shaver, G. R., Ahrens, M., Callaghan, T. V., Molau, U. *et al.* (2012). Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology*, 18 (3): 1096-1107.
- Marion, G. M., Henry, G. H. R., Freckman, D. W., Johnstone, J., Jones, G., Jones, M. H. *et al.* (1997). Open-top designs for manipulating field temperature in high-latitude ecosystems. *Global Change Biology*, 3 (S1): 20-32. doi: 10.1111/j.1365-2486.1997.gcb136.x.
- Myers-Smith, I. H. (2011). *Shrub encroachment in arctic and alpine tundra: Patterns of expansion and ecosystem impacts*. PhD. Edmonton, Alberta: University of Alberta.
- Nash, T. H. (2008). Nutrients, elemental accumulation, and mineral cycling. In Nash, T. H. (ed.) *Lichen Biology*, pp. 234-251: Cambridge University Press.
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. *et al.* (2017). *Vegan: Community Ecology Package*. Available at: <u>https://CRAN.R-project.org/package=vegan</u>.
- Olsen, S. L. & Klanderud, K. (2014). Exclusion of herbivores slows down recovery after experimental warming and nutrient addition in an alpine plant community. *Journal of Ecology*, 102 (5): 1129-1137.
- Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, 421: 37. doi: 10.1038/nature01286

https://www.nature.com/articles/nature01286#supplementary-information.

- Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Alonso, J. L. B. *et al.* (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. *Science*, 336 (6079): 353-355. doi: 10.1126/science.1219033.
- R Core Team. (2017). *R: A Language and Environment for Statistical Computing*. Vienna, Austria,: R Foundation for Statistical Computing,. Available at: <u>https://www.R-project.org/</u>.
- Rammig, A., Jonas, T., Zimmermann, N. E. & Rixen, C. (2010). Changes in alpine plant growth under future climate conditions. *Biogeosciences*, 7 (6): 2013-2024. doi: 10.5194/bg-7-2013-2010.
- Settele, J., Scholes, R., Betts, R. A., Bunn, S., Leadley, P., Nepstad, D. *et al.* (2014). Terrestrial and inland water systems,. In *Climate Change 2014 Impacts, Adaptation and Vulnerability: Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovermental Panel on Climate Change*: Cambridge University Press.

- Steinbauer, M. J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H. *et al.* (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556 (7700): 231-234. doi: 10.1038/s41586-018-0005-6.
- Stoy, P. C., Street, L. E., Johnson, A. V., Prieto-Blanco, A. & Ewing, S. A. (2012). Temperature, heat flux, and reflectance of common subarctic mosses and lichens under field conditions: might changes to community composition impact climate-relevant surface fluxes? *Arctic, antarctic, and alpine research,* 44 (4): 500-508.
- Thompson, C., Beringer, J., Chapin III, F. & McGuire, A. (2004). Structural complexity and land-surface energy exchange along a gradient from arctic tundra to boreal forest. *Journal of Vegetation Science*, 15 (3): 397-406.
- Van Wijk, M. T., Clemmensen, K. E., Shaver, G. R., Williams, M., Callaghan, T. V., Chapin, F. S. *et al.* (2004). Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology*, 10 (1): 105-123. doi: 10.1111/j.1365-2486.2003.00719.x.
- Vanneste, T., Michelsen, O., Graae, B. J., Kyrkjeeide, M. O., Holien, H., Hassel, K. *et al.* (2017). Impact of climate change on alpine vegetation of mountain summits in Norway. *Ecological Research*, 32 (4): 579-593. doi: 10.1007/s11284-017-1472-1.
- Vuorinen, K. E., Oksanen, L., Oksanen, T., Pyykönen, A., Olofsson, J. & Virtanen, R. (2017). Open tundra persist, but arctic features decline—Vegetation changes in the warming Fennoscandian tundra. *Global change biology*, 23 (9): 3794-3807.
- Wahren, C. H., Walker, M. & Bret-Harte, M. (2005). Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, 11 (4): 537-552.
- Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H., Ahlquist, L. E., Alatalo, J. M. *et al.* (2006). Plant community responses to experimental warming across the tundra biome. *Proceedings* of the National Academy of Sciences, 103 (5): 1342-1346.
- Wheeler, B. & Torchiano, M. (2016). *ImPerm:Permutation Tests for Linear Models*.

Appendix

Functional groups		Cover (%) control	Cover (%) OTC
Lichens		15.9	11.75
Vascular plants		85.3	86.1
Forbs		15.5	17.25
Graminoids		6.65	7.9
Dwarf shrubs		63.15	60.95
Species	Abbreviations	Cover (%) control	Cover (%) OTC
Lichens			
Flavocetraria nivalis,	Fla.niv	4.08	3.05
Cetraria islandica	Cet.isl	3.40	2.83
Flavocetraria cucullata	Fla.cuc	1.50	0.63
Cladonia arbuscula	Cla.arb	1.40	1.38
Peltigera aphthosa	Pel.aph	1.08	0.48
Stereocaulon sp.	Ste.sp.	0.68	0.23
Cladonia uncialis	Cla.unc	0.63	0.60
Thamnolia vermicularis	Tha.ver	0.58	0.63
Cladonia gracilis	Cla.gra	0.50	0.50
Bryocaulon divergens	Bry.div	0.43	0.13
Peltigera malacea	Pel.mal	0.33	0.55
Alectoria ochroleuca	Ale.och	0.30	0.08
Sphaerophorus globosus	Sph.glo	0.28	0.13
Cladonia sp.	Cla.sp.	0.25	0.35
Alectoria nigricans	Ale.nig	0.18	0.03
Vulpicidia juniperinus	Vul.jun	0.13	0.15
Cladonia rangiferina	Cla.ran	0.10	0.05

Table 1: Average cover (%) of lichens and vascular plants in control plots and OTCs. Below average cover in OTCs and control plots of all lichens and vascular plants divided into functional groups. Abbreviation matches those used in the NMDS-analyses.

Forbs

10105			
Silene acalis	Sil.aca	5.6	5.7
Bistorta vivipara	Bis.viv	1.5	2
Saussurea alpina	Sau.alp	1.4	1.45
Thalictrum alpinum	Tha.alp	1	1
Bartsia alpina	Bar.alp	0.6	0.85
Euphrasia wettsteinii	Eup.wet	0.55	0.5
Potentilla crantzii	Pot.cra	0.55	0.8
Erigeron uniflorus	Eri.uni	0.5	0.65
Minuartia biflora	Min.bif	0.5	0.25
Ranunculus acris	Ran.acr	0.45	0.2
Selaginella selaginoides	Sel.sel	0.45	0.5
Campanula rotundifolia	Cam.rot	0.4	0.2
Oxytropis lapponica	Oxy.lap	0.4	0.6
Antennaria dioica	Ant.dio	0.35	0.5
Viscaria alpina	Vis.alp	0.35	0.2
Astragalus alpinus	Ast.alp	0.2	0.15
Huperzia selago	Hup.sel	0.2	0.05
Tofieldia pusilla	Tof.pus	0.15	0.1
Antennaria alpina	Ant.alp	0.1	0.05
Cerastium alpinum	<i>Cer.alp</i>	0.1	0.4
Cardamine bellidifolia	Car.bel	0.05	0
Parnassia palustris	Par.pal	0.05	0.25
Saxifraga oppositifolia	Sax.opp	0.05	0.05
Antennaria sp.	Ant.sp.	0	0.25
Comastoma tenellum	<i>Com.ten</i>	0	0.15
Gentiana nivalis	Gen.niv	0	0.2
Leontodon autumnalis	Leo.aut	0	0.05
Rhodiola rosea	Rho.ros	0	0.1
Saxifraga aizoides	Sax.aiz	0	0.05

Graminoids

Carex vaginata	Car.vag	2	1.7
Festuca sp.	Fes.sp.	1.2	1.75
Carex rupestris	Car.rup	1.1	1.85
Luzula spicata	Luz.spi	0.7	0.7
Juncus trifidus	Jun.tri	0.5	0.4
Carex atrata	Car.atr	0.45	0.35
Festuca rubra	Fes.rub	0.35	0.2
Poa alpina	Poa.alp	0.15	0.35
Anthoxanthum odoratum	Ant.odo	0.1	0.4
Carex capillaris	Car.cap	0.1	0.1
Carex bigelowii	Car.big	0	0.05
Trisetum spicatum	Tri.spi	0	0.05

Dwarf shrubs				
Dryas octopetala	Dry.oct	59.95	55	
Salix reticulata	Sal.ret	1.2	1.15	
Salix herbacea	Sal.her	0.9	0.55	
Harrimanella hypnoides	Har.hyp	0.85	0.05	
Empetrum nigrum	Emp.nig	0.2	3	
Vaccinium uliginosum	Vac.uli	0.05	1.2	

Table 2: ANCOVA test. All tests are performed with temperature treatment as the explanatory variable, Soil moisture and cover of D. octopetala are co-variables. Significant results in bold. For variables with non-normal distribution I used the package ImPerm to do permutation tests with 9999 permutations (†).

Variables	F	Pr (> F)	Variables	Р
Lichen cover			Lichen species number	
Temptreat (T)	2.06	0.179	Temptreat (T)	0.030
D. octopetala cover (D)	1.10	0.318	D. octopetala cover (D)	0.182
Soil moisture (S)	1.47	0.251	Soil moisture (S)	0.789
ТхD	3.50	0.088	ТхD	0.208
T x S	1.96	0.189	ТхS	0.599
T x D x S	0.35	0.568	T x D x S	0.029
Vascular plant cover without dryas†			Vascular plant species number without dryas †	
Temptreat (T)		0.156	Temptreat (T)	0.072
<i>D. octopetala</i> cover (D)		0.010	<i>D. octopetala</i> cover (D)	0.430
Soil moisture (S)		1.000	Soil moisture (S)	0.277
T x D		0.865	ТхD	0.653
T x S		0.577	ТхS	0.209
T x D x S		0.605	T x D x S	0.167
Vascular plant cover †			Vascular plant cover †	
Temptreat (T)		0.886	Temptreat (T)	0.140
Soil moisture (S)		0.208	Soil moisture (S)	0.036
T x S		1.000	ТхS	0.449

Response variables and covariables	F	Pr (> F)	Response variables P and covariables	
Forb plant cover †			Forb species number †	
Temptreat (T)		0.216	Temptreat (T)	0.033
D. octopetala cover (D)		0.479	<i>D. octopetala</i> cover (D)	0.456
Soil moisture (S)		0.900	Soil moisture (S)	0.141
ТхD		0.213	T x D	0.835
ТхS		0.372	T x S	0.300
T x D x S		0.121	T x D x S	0.425
Graminoid cover †			Graminoid species number	
Temptreat (T)		0.622	Temptreat (T)	0.243
D. octopetala cover (D)		0.151	<i>D. octopetala</i> cover (D)	0.471
Soil moisture (S)		0.131	Soil moisture (S)	0.509
ТхD		0.875	ТхD	0.468
T x S		0.399	T x S	0.405
T x D x S		0.131	T x D x S	0.255
Dwarf shrub cover			Dwarf shrub species number †	
Temptreat (T)	0.29	0.597	Temptreat (T)	0.789
Soil moisture (S)	4.46	0.052	Soil moisture (S)	0.480
ТхS	0.55	0.471	ТхS	0.359

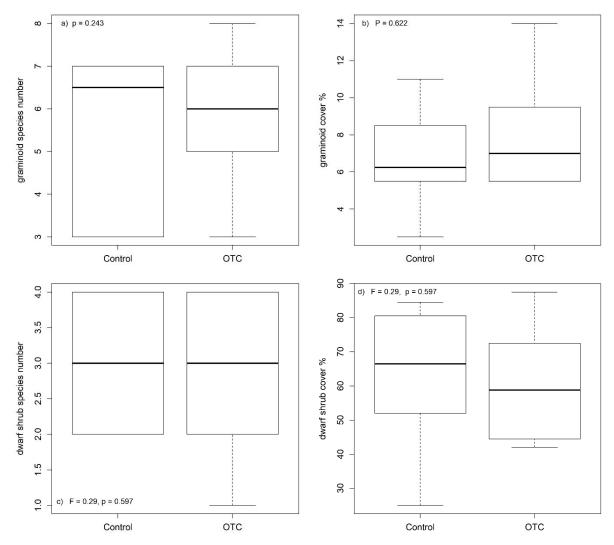


Figure 2: Box plots shows difference in species richness and cover between OTC and control plots for graminoids (a and b) and dwarf shrubs (c and d). The boxplots present the median, and the boxes define the interquartile range. (NB: Various y-axis).

Table 3: Plot list with soil moisture, percent cover and species number of various functional groups. Plots with the first letter O is a warmed plot, while plots with the first letter C is control plots. (Continue on next page).

Vascular cover % without D. octopetala	30	21	57.5	16.5	19.5	20.5	36	56	38	20	39.5	14	19	43.5	24.5	22.5	22.5	16	24.5	23.5
D. octopetala cover % witho	72.5	56.5	12.5	82.5	60	82	55	15	54	50	55	77.5	40.5	36	70	50	43	78.5	87.5	71.5
Dwarf shrub cover %	85.5	60.5	44	83.5	60.5	84.5	59	25	55.5	53	58.5	80.5	42	39.5	72.5	52	44.5	80.5	87.5	72.5
Forb cover%	11.5	11.5	16.5	5.5	10	12.5	18	35	31	6	28.5	8.5	12	31.5	15.5	15	15	11	14.5	15.5
Graminoid cover %	5.5	5.5	9.5	10	6	5.5	14	11	5.5	8	7.5	2.5	5.5	8.5	6.5	5.5	9	æ	10	7
Lichen cover % Vascular cover %	102.5	77.5	70	66	79.5	102.5	91	71	92	70	94.5	91.5	59.5	79.5	94.5	72.5	65.5	94.5	112	95
	4	8.25	13.25	34.75	5.75	7	8.25	5.75	13.25	10.25	13.75	23.75	18.75	16.75	9.25	15.25	22.5	18.75	8.75	18.5
Soil moisture	19.51	36.66	25.51	33.11	25.78	17.75	39.81	36.04	13.04	20.20	35.08	19.54	28.91	49.75	34.08	32.86	NA	29.98	13.78	27.91
plot	02A	K8D	02D	K10D	03A	K6A	04B	K1C	05B	K10A	06A	K10C	07A	K1A	07B	K5D	O 8B	K3D	010C	K3C

	Lichen	Vascular plant	Dwarf shrub	Forbs	Graminoid
Plot	species number				
02A	7	22	4	11	7
K8D	11	24	4	14	6
02D	13	27	4	15	8
K10D	15	12	2	7	3
03A	8	19	2	11	6
K6A	10	24	4	12	7
O4B	10	27	4	15	8
K1C	9	26	4	15	7
O5B	10	19	3	11	5
K10A	14	17	3	9	5
06A	8	22	3	13	6
K10C	10	17	3	11	3
07A	12	21	2	14	5
K1A	11	24	3	14	7
O7B	11	27	3	17	7
K5D	15	21	2	12	7
O8B	13	22	3	14	5
K3D	11	19	4	12	3
O10C	14	16	1	12	3
K3C	14	21	2	12	7



Norges miljø- og biovitenskapelige universitet Noregs miljø- og biovitskapelege universitet Norwegian University of Life Sciences

Postboks 5003 NO-1432 Ås Norway