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University of
Applied Sciences

BACHELOR'S ASSIGNMENT

The response of *Vaccinium myrtillus* to simulated warming and external application of a hormonal regulator at different altitudes.

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28.05.2018

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University of Applied Sciences Bingen

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List of abbreviations

<i>V. myrtillus</i>	<i>Vaccinium myrtillus</i>
Id.	Idem
Ibid.	ibidem
Jas	Jasmonates
MeJa	methyl-jasmonate
VOC	Volatile Organic Compound
OTC	Open-top chamber
DM	Dry mass
DS	Stem diameter
H	Height
AS	Amount of shoots
GLM	Generalized linear model
GLMM	Generalized linear mixed model
DF	Degrees of freedom
F	F-value, Fisher's value
P	P – Value, Probability value
W	Water treatment
M	methyl-jasmonate treatment 30
°C	Grad Celsius
mM	millimolar
Dev	Deviance

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Abstract

Vaccinium myrtillus fulfils an essential role as a primary producer in boreal ecosystems as it provides shelter and nutritive food for several invertebrate and vertebrate species. The study investigates responses of *V. myrtillus* in a pine-bilberry ecosystem to simulated warming with open-top chambers (OTC) and the application of the hormonal regulator methyl-jasmonate (MeJa) along an elevational gradient over a period of two years (2016 – 2017). Aiming at providing additional information about the direct impacts on the plants itself and improving the understanding of associated indirect effects on other constituents in the ecosystem that may occur in the course of climate change.

Plant defences against herbivory induced by the hormonal regulator were assumed to increase the resistance against herbivores while restricting the growth and reproduction of the plants due to the reallocation of resources. Whereas simulated warming was suggested to favour the plant development and emphasizing the response to the hormonal regulator. A uniform trend of significantly reduced amount of flowers was found in 2017, when bilberry were treated with MeJa. Moreover, in consequence of MeJa application and natural grazing, a negative impact on the growth of plants at the lowest elevation was observed in 2016, since plants suffered a significant loss of leaves and were restricted in their vertical growth. Also the resistance against invertebrate herbivores increased in that case, indicating the upregulation of defence genes at the expense of growth and reproduction. The study could not confirm whether simulated warming affects the responses of bilberry to the application of MeJa.

1 Introduction

Warmer temperatures, as they are predicted in prospective climate scenarios, are likely to have complex impacts on the abundance and distribution of plant species in boreal ecosystems¹. Former studies indicate, that besides increasing temperature itself locally changing weather phenomena will also cause shifts in prevailing and dominating flora and fauna species. Some shrubs for instance are anticipated to gain more benefits from climate-induced alterations in the ecosystems compared to other plant species, as they may take advantage of shifts in nutrient availability or soil disturbances². However too little is known about the responses of shrubs and their interactions with other species to evaluate how changing climatic conditions may affect the communities and ecosystems. For example vegetal shifts have direct and indirect impacts on the vertebrate and invertebrate herbivores that rely on the plants for food³.

Thus, this study aims at improving the understanding of the dominant species *Vaccinium myrtillus* in a boreal alpine ecosystem, since it fulfils an essential role in the food chain as a primary producer. *Vaccinium myrtillus*, also known as European blueberry or bilberry, is a deciduous dwarf shrub with evergreen stems and usually reaches a height of 15 – 60 cm.⁴ Its maximum vegetative and reproductive development can be observed in low to moderately fertile woodlands⁵, especially in pine forests due to its relatively high shade-tolerance⁶.

¹ Ayres, M. P., 1993. Global change, plant defense and herbivory.: Sinauer Associates, Sunderland, MA.

² Hallinger, M., Manthey, M. and Wilmking, M., 2010. Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia, vol. 186. *New Phytologist* (4), 890–899. 10.1111/j.1469-8137.2010.03223.x.

³ Agrawal, Anurag A., Tuzun, Sadik and Bent, Elizabeth, 2000. Induced Plant Defenses Against Pathogens and Herbivores: Biochemistry, ecology, and agriculture. Minnesota: APS Press, 270, 279.

⁴ Seidel, Dankwart and Eisenreich, Wilhelm, 1985. Foto-Pflanzenführer. BLV-Bestimmungsbuch, vol. 35. München, 260.

⁵ Hegland, Stein Joar, Seldal, Tarald, Lilleeng, Marte S. and Rydgren, Knut, 2016. Can browsing by deer in winter induce defence responses in bilberry (*Vaccinium myrtillus*)?, vol. 31. *Ecol Res* (3), 441–448. 10.1007/s11284-016-1351-1. Accessed 10 April 2018.

⁶ Ritchie, J. C., 1956. *Vaccinium Myrtillus* L.: British Ecological Society. *Journal of Ecology* (Vol. 44 No. 1), 291–299. Accessed 12 April 2018.

Its early spring bloom as well as its deciduous leaves in summer are beneficial for several species within the ecosystem feeding on bilberry⁷. Moreover the berry formation 2 – 4 weeks after the pollination⁸ and the evergreen stems in winter provide essential nutrient supply for e.g. birds, mammals and invertebrates⁹. Additionally its ecological importance can be highlighted by its shelter function within a habitat (ibid.). Altogether *V. myrtillus* can be determined as a key species in boreal and alpine ecosystems and hence is well suited to represent possible intra and inter species reactions in the investigated mountain area (Hegland, Seldal, Lilleeng and Rydgren, 2016). For instance as Hegland et al. states, correlations between population sizes of invertebrate as well as vertebrate herbivores feeding on bilberry and the abundance of the plant itself have been proven in several former studies (ibid.). However only little information is available about if and to which extent warmer temperatures in combination with accompanying changes in grazing patterns may affect bilberry and its role in the ecosystem. Gaining more information about how key species, such as *V. myrtillus*, respond to those external forces is crucial to understand the effects that changing climatic conditions may have on the earth's ecosystem. Therefore this study investigates how *Vaccinium myrtillus* in a pine-bilberry ecosystem responds at different altitudes to simulated warming and external application of a hormonal regulator in order to simulate herbivory induced defence responses.

⁷ Benevenuto, Rafael Fonseca, Hegland, Stein Joar, Töpfer, Joachim Paul, Rydgren, Knut, Moe Stein R., Rodriguez-Saona, Cesar and Seldal, Tarald. Multiannual effects of induced plant defenses: Are defended plants good or bad neighbors? (unpublished).

⁸ Mark Andrew Gillespie, 2018. Information about bilberry reproduction. Personal comment. Sogndal.

⁹ Hegland, Stein Joar, Rydgren, Knut and Seldal, Tarald, 2005. The response of *Vaccinium myrtillus* to variations in grazing intensity in a Scandinavian pine forest on the island of Svanøy, vol. 83. *Can. J. Bot.* (12), 1638–1644. 10.1139/b05-132. Accessed 13 April 2018.

Hormonal regulators in plants, such as Jasmonates (Jas) control several developmental processes (Bennett and Wallsgrave, 1994) including seed germination, root growth, flowering, fruit ripening and senescence^{10,11,12}. For instance the volatile compound methyl-jasmonate (MeJa) is not only known to regulate physiological processes but also to be involved in the signal transduction in order to activate plant defence mechanisms¹³. Those processes can be induced by external stimuli¹⁴ such as herbivore or insect-driven wounding and are expressed by a rise in the responsible compounds followed by the mobilization of various defence genes (Cheong and Choi, 2003).

Previous laboratory and field studies have shown, that the defence genes of *Vaccinium* plants are activated by the exogenous application of methyl-jasmonate (MeJa), subsequently deterring insect attacks (Benevenuto et al., in press). Thus in this study MeJa has been used to elicit bilberry defence responses, which are expected to be reflected in the plant growth and reproduction, as the hormonal regulator may also affect diverse physiological processes¹⁵, such as growth inhibition or promotion of senescence and abscission (Farmer and Ryan, 1990).

¹⁰ Koo, Yeon Jong, Yoon, Eun Sil, Seo, Jun Sung, Kim, Ju-Kon and Choi, Yang Do, 2013. Characterization of a methyl jasmonate specific esterase in arabidopsis, vol. 56. *J Korean Soc Appl Biol Chem* (1), 27–33. 10.1007/s13765-012-2201-7. Accessed 14 April 2018.

¹¹ Farmer, Edward E. and Ryan, Clarence A., 1990. Interplant communication: Airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves: (jasmonic acid/pathogen/wound-inducible genes/localized/systemic defense responses). *Botany* (Vol. 87), 7713–7716. Accessed 14 April 2018.

¹² Agrawal, Anurag A., Tuzun, Sadik and Bent, Elizabeth, 2000. *Induced Plant Defenses Against Pathogens and Herbivores: Biochemistry, ecology, and agriculture*. Minnesota: APS Press.

¹³ Cheong, Jong-Joo and Choi, Yang Do, 2003. Methyl jasmonate as a vital substance in plants, vol. 19. *Trends in Genetics* (7), 409–413. 10.1016/S0168-9525(03)00138-0. Accessed 14 April 2018.

¹⁴ Delker, C., Stenzel, I., Hause, B., Miersch, O., Feussner, I. and Wasternack, C., 2006. Jasmonate biosynthesis in *Arabidopsis thaliana*--enzymes, products, regulation, vol. 8. *Plant biology (Stuttgart, Germany)* (3), 297–306. 10.1055/s-2006-923935. Accessed 14 April 2018.

¹⁵ Bennett, R. N. and Wallsgrave, R. M., 1994. Secondary metabolites in plant defence mechanisms. Harpenden, Herts ALS 2JQ, UK. *New Phytologist* (127), 617–633. Accessed 10 April 2018.

Following the findings of previous studies, the hormonal regulator is expected to initiate defence responses and lower the plant's attractiveness to potential herbivores and concurrently negatively affect growth and reproduction indicating an allocation of the plant resources. Additionally one can assume, that simulated warming favours the plant development, since the reproductive performance of bilberry is especially closely related to temperature (Ritchie, 1956). Moreover the increase in temperature in combination with the application of methyl-jasmonate is expected to emphasize the plant responses to the hormonal regulator, since plants are expected to be more alert to react to herbivory during a warmer climate¹⁶.

Furthermore plant growth and the occurrence of reproductive traits are also anticipated to differ along altitudinal gradients, since the plant performance may vary within its habitat range as it is dependent on environmental conditions, such as local climate or nutrient availability¹⁷. In summary the investigation of *V. myrtillus* responses to climate alterations and hormonal regulation in a pine-bilberry ecosystem will improve the understanding of the direct impacts on the plant itself and the associated indirect effects on other surrounding biotic constituents.

¹⁶ Cornelissen, T., 2011. Climate change and its effects on terrestrial insects and herbivory patterns, vol. 40. *Neotrop. entomol.* (2), 155–163. 10.1590/S1519-566X2011000200001.

¹⁷ Nestby, Rolf, Percival, David, Martinussen, Inger, Opstad, Nina and Rohloff, Jens, 2011. The European Blueberry (*Vaccinium myrtillus* L.) and the Potential for Cultivation.: Global Science Books. *European Journal of Plant Science and Biotechnology* (Volume 5), 5–16. Accessed 12 April 2018.

2 Study method and equipment

The performance of a field study has been favoured, since it is likely to display more valuable information about the plant responses within the ecosystem than laboratory studies. The plants are exposed to several environmental stressors and the group of sampled species represents a broader genetical variability, when investigated within their natural habitat. However the results of a field study may be less distinct compared to a laboratory study due to its higher level of complexity (Hegland, Seldal, Lilleeng and Rydgren, 2016).

2.1 Terrain and environmental conditions

The three study sites used in this project are located within a pine-bilberry ecosystem on the south facing hillside of Storehaugfjellet near Kaupanger, Western Norway (61°9'52"N 7°8'5"E, Supplementary Map 1). The sampling locations are situated in recently cut clearings within pine forest in order to minimize variations in the micro climate, for instance caused by differing insolation and shadowing effects.

As depicted in the Supplementary Figure 1, the study sites are established at three different altitudes (~100 m, 450 m and 900 m) to achieve a range of temperature and snow melt timing regimes. Furthermore these altitudes are likely to represent the elevational range of the focal plant species, *Vaccinium myrtillus*, with the 450m site providing optimal growing conditions and the lower and upper sites at the edges of the range. These sites will be referred to as Low, Medium and High throughout this thesis.

2.2 Experimental design and treatments

In May 2016, six experimental blocks were established at each of the three different elevated locations in order to consider the impact of altitude on plant processes during the study. They are placed within relatively homogenous vegetation ensuring a good representation of the target plant *V. myrtillus*. At the low (100 masl) and middle (450 masl) sites the blocks measured 10 x 10 m and were at least 10 m apart from each other.

In the four corners of each block, 2 x 2 m grids of 16 squares (50 x 50 cm) were marked out and then one square was randomly selected using a random number generator. Each chosen square became an established treatment plot (2.5 m²) if it contained a good cover of *V. myrtillus*. If this could not be ensured, for example due to a tree stump or bare rock, an adjacent plot was selected. This selection procedure was conducted to provide semi-random selection of plots within blocks and to ensure that plots were at least 4 m apart. The square block design was not possible at the high site due to the sparsity of vegetation, hence the plots were most often arranged linearly.

In order to prevent the activation of defence mechanism through plant communication, each plot was at least 4 m away from its nearest neighbour, based on the findings of Benevenuto et al. (in press). Each plot within the study blocks was randomly assigned to one of the four different plant treatments:

- 1) Ambient temperature and water application (Control)
- 2) Ambient temperature and methyl jasmonate application
- 3) Elevated temperature and water application
- 4) Elevated temperature and methyl jasmonate application

Water and MeJa (10mM), based on the study of Benevenuto et al. (in press), were sprayed on assigned plots with a 5 liter knapsack sprayer three times during the summer 2016 (Low site: 26 May, 3 and 14 June; Middle site: 2, 10 and 19 June; High site: 10, 19 and 30 June). Each application involved steadily spraying the liquid over the plot twice to ensure complete coverage. In this study, the exogenous application of MeJa has been favoured over the clipping method, which attempts to simulate herbivory related stress by imitating the grazing process. Even though the latter might evoke defence responses as well, it is known that herbivore specific cues, transmitted by their saliva, are involved and required to fully activate the activation of defence mechanisms (Agrawal, Tuzun and Bent, 2000, 126–127; Hegland, Seldal, Lilleeng and Rydgren, 2016). The chemical method using MeJa may generate plant defence responses, yet this method is not able to differ between specific herbivory types as invertebrates or vertebrates (ibid.).

In order to increase the temperature and simulate a warmer climate open-top chambers (OTCs) were installed on the same day as the first exogenous water and MeJa applications in 2016. Previous studies revealed, that the hexagonal miniature greenhouses, constructed of transparent polycarbonate panels, elevate the temperature on plots by average of 1°C¹⁸. The OTCs were removed at the end of the growing seasons (28 October 2016 and 11 October 2017) and replaced in spring the subsequent year to prevent the accumulation of snow during the winter. Open-top chambers were preferred over other simulated warming techniques, such as soil heating cables or infrared heaters, in order to minimize costs and effort regarding the study set-up.

Four ramets of *V. myrtillus* were selected within each plot by placing a metal quadrat (50 x 50 cm) featuring strings to create a grid of 16 squares (12.5 x 12.5 cm) over the plot. Marker sticks were then inserted into the soil at the grid cross-points closest to the four corners. The nearest *V. myrtillus* ramet to each stick was then marked with a cable tie and small coloured bead, so that the same ramets could be measured repeatedly.

¹⁸ MARION, G. M., HENRY, G.H.R., FRECKMAN, D. W., JOHNSTONE, J., JONES, G., JONES, M. H., LÉVESQUE, E., MOLAU, U., MØLGAARD, P., PARSONS, A. N., SVOBODA, J. and VIRGINIA, R. A., 1997. Open-top designs for manipulating field temperature in high-latitude ecosystems, vol. 3. *Global Change Biology* (S1), 20–32. 10.1111/j.1365-2486.1997.gcb136.x.

2.3 Sampling procedure and plant measurements

In advance of the first spraying (26 May 2016 (Low), 2 June 2016 (Medium) and 10 June 2016 (High)), growth and herbivory impact on the four individual ramets in each plot were recorded. Each ramet was measured for 1) stem diameter at surface level (using digital calipers), 2) ramet height, 3) number of leaves, 4) number of annual shoots, 5) number of leaves grazed by insects, 6) number of shoots browsed by deer.

Approximately 8 – 9 weeks after the initial recording, when *V. myrtillus* was assumed to have ceased growing for the season, the measurements were repeated (Low: 17 July 2016, Medium: 25 July 2016, High: 1 August 2016). In 2017 the measurements were conducted in the same way, first on 22 May 2017 (Low), 5 June 2017 (Medium) and 26 June 2017 (High), and then on 29 July 2017 (Low), 3 August 2017 (Medium) and 24 August 2017 (High). Additionally the dry mass data was calculated with the equation from Hegland et al. as non-destructive estimation¹⁹:

$$\log_2(DM) = 1.41700 \times \log_2(DS) + 0.97104 \times \log_2(H) + 0.44153 \\ \times \log_2(AS + 1) - 7.52070$$

Since this model exclusively uses the stem diameter (DS), height (H) measurements and the number of annual shoots (AS) for its calculation, it allows the estimation of biomass data without detaching the whole plant from its habitat. The differences in measurements between the two measuring dates for each parameter, are used as response variables in the subsequent analysis.

Furthermore in 2017, the number of flowers occurring in each plot was counted every week during the flowering season as a measure of reproductive effort. The maximum number of flowers per plot was then used as a response variable in the analysis.

¹⁹ Hegland, Stein Joar, Jongejans, Eelke and Rydgren, Knut, 2010. Investigating the interaction between ungulate grazing and resource effects on *Vaccinium myrtillus* populations with integral projection models, vol. 163. *Oecologia* (3), 695–706. 10.1007/s00442-010-1616-2.

3 Statistical data analysis

The statistical analysis was performed using the software programme R, Version 3.4.3 (2017-11-30)²⁰ in order to test the impacts of the different treatment combinations on the plant responses. Predominately linear mixed effect models were chosen to compare the treatment plots with the untreated control ramets due to the block design of the experiment.

3.1 Data set

The compacted data set comprises the explanatory variables 1) block, 2) site (Low, Medium, High), 3) temperature (Ambient, OTC), and 4) treatment (Water or MeJa), with the effects emanating from the three latter are of most interest. Therefore the modelling considered the impact of these variables on all of the response variables listed below.

- Stem
- Height
- Leaves
- Grazed leaves
- Shoots
- Grazed shoots
- Dry mass (calculated)
- Total amount of flowers (only in 2017)

Each response variable (except for flowers) describes the difference between the initial and the second recording in each year, as described in the prior chapter (3.3). To simplify the analysis, the values of the four sampled ramets in each plot are averaged to gain a single value for each plot, rather than four non-independent values. The response variables were initially inspected visually for their distribution and it was found that all approximate a normal distribution except for the flower data, which approximately displays a Poisson distribution.

²⁰ R Core Team, 2017. A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

3.2 Methods of analysis

Initially maximal linear mixed effects models²¹ were fitted for all response variables with the three categorical (id., 411) explanatory variables 1) site (three levels), 2) temperature (two levels), 3) treatment (two levels) and all two-way interactions as fixed effects and block as a random effect (id., 682) to take into account the block design of the study. After simplifying the models by stepwise deletion of non-significant variables, the minimal adequate model was checked for validity by visual inspection for constancy of variance and normality of residuals. There were no validity issues, except that the removal of outliers was performed for the models of the number of leaves (removal of one outlier) and shoots (removal of two outliers) for 2016 in order to gain normally distributed residuals. The removal of outliers did not qualitatively affect the results of the analysis, and the results presented here are from models with the outliers excluded.

The model for grazed leaves for the same year (2016) also contained four outliers, but in this case, a log transformation of the data was favoured over the removal of the outliers in order to avoid diluting the data set. Due to the presence of negative values in this variable, the transformation was achieved by adding the absolute value of the smallest number and adding the constant 1 to all values to guarantee a valid logarithmic transformation all values. This method was not applicable for the previous mentioned variables, because the log transformation caused a non-normal distribution of the data. The flower data from 2017 represents count data and hence requires the use of a generalized linear model (GLM) with poisson distributed errors. The initial and final models for this response variable suffered from overdispersion²², so this was taken into account by specifying “quasipoisson” errors (id., 561). In order to operate a valid analysis the cover data of the corresponding year (2017) was also included in that model, since the coverage ratio of *V. myrtillus* is likely to have an impact on the total amount of flowers in the equivalent plot.

²¹ Crawley, Michael J., 2013. The R book, second edition, 2nd edn. Chichester, West Sussex, U.K.: John Wiley & Sons, 684.

²² If the residual deviance is greater than the residual degrees of freedom in the minimal adequate model, it is called overdispersion. Since this is contravening the assumptions of the model it is necessary to correct this by specifying the errors, as mentioned above (Crawley, Michael J., 2013).

The cover of bilberry within each plot was estimated by visual judgement. The blocking design was not taken into account in the analysis of the flower data, since this would require the specification of a generalized linear mixed model (GLMM, beyond the scope of this study). However, in previous work, the blocking factor was found to have a negligible effect on this variable²³.

²³ Mark Andrew Gillespie, 2018. Statistical analysis. Personal comment. Sogndal.

4 Results

Table 1: Overview of statistical responses after running the maximal linear mixed effect models fitted for all response variables including the three explanatory variables (site, temperature, treatment) and all two-way interactions.²⁴ (Part 1)

Response	Treatment	DF	2016		2017	
			F	P	F	P
Dry mass	Treatment	1	2.394	0.129	1.365	0.248
	Temperature	1	0.367	0.548	4.503	0.039
	Site	2	1.780	0.180	3.243	0.047
	Site:Treatment	2	1.515	0.230	0.099	0.906
	Site:Temperature	2	2.266	0.115	6.747	0.003
	Temperature:Treatment	1	2.043	0.160	0.807	0.373
Leaves	Treatment	1	40.855	< 0,0001	2.372	0.129
	Temperature	1	0.017	0.897	1.625	0.208
	Site	2	2.430	0.097	0.766	0.470
	Site:Treatment	2	2.932	0.062	0.417	0.661
	Site:Temperature	2	0.034	0.966	1.680	0.196
	Temperature:Treatment	1	0.087	0.769	1.250	0.268
Grazed leaves	Treatment	1	1.024	0.316	0.115	0.736
	Temperature	1	1.139	0.290	2.277	0.137
	Site	2	11.771	1.00E-04	3.497	0.037
	Site:Treatment	2	4.726	0.013	2.578	0.085
	Site:Temperature	2	0.096	0.908	4.077	0.022
	Temperature:Treatment	1	0.809	0.372	0.076	0.784
Grazed shoots	Treatment	1	0.196	0.660	2.372	0.129
	Temperature	1	0.400	0.530	1.625	0.208
	Site	2	1.898	0.159	0.766	0.470
	Site:Treatment	2	1.012	0.370	0.417	0.661
	Site:Temperature	2	0.595	0.555	1.680	0.196
	Temperature:Treatment	1	0.021	0.885	1.250	0.268

²⁴ The minimal model p-values can be found in the supplementary table 2, whereas some differ slightly from the maximal model p-values displayed in this table. The interaction of the site and MeJa treatment for the amount of leaves variable was found to be significant after model simplification, whereas in the maximal model only the single MeJa treatment caused a significant response.

Table 2: Overview of statistical responses after running the maximal linear mixed effect models fitted for all response variables including the three explanatory variables (site, temperature, treatment) and all two-way interactions. (Part 2)

Response	Treatment	DF	2016		2017	
			Dev	P	Dev	P
Total amount of flowers	Treatment	1	-	-	1,094.490	< 2,2E-16
	Cover	1	-	-	229.330	3.09E-07
	Site	2	-	-	14.100	0.483
	Temperature	1	-	-	37.690	0.038
	Treatment:Cover	1	-	-	11.670	0.200
	Treatment:Site	2	-	-	67.370	0.033
	Treatment:Temperature	1	-	-	11.610	0.250
	Cover:Site	2	-	-	1.630	0.912
	Cover:Temperature	1	-	-	0.590	0.795
	Site:Temperature	2	-	-	30.810	0.172

The statistically significant effects differ in the two study years, yet the comprehensive data set allows to subdivide the results into detected impact on plant growth, herbivory and reproduction. The stem diameter, plant height, amount of leaves and new shoots, as well as the resultant dry mass data represent the progress of growth. In terms of simplification the single variables height, stem diameter and new shoots are not listed and discussed explicitly below, because they are integrated in the dry mass estimation. However they can be found in the appendix (Supplementary Table 1, Supplementary Table 2). The impact of herbivory is supposed to be demonstrated by the amount of leaves attacked by insects and the number of shoots grazed by deer.

Table 1 and Table 2 display the responses of the tested variables after running the maximum model and compares both study years. The red coloured values highlight statistically significant values ($p < 0.05$). A similar structured table, exclusively including significant responses after model simplification can be found in the appendix (Supplementary Table 2).

4.1 Growth

4.1.1 Effect of simulated warming

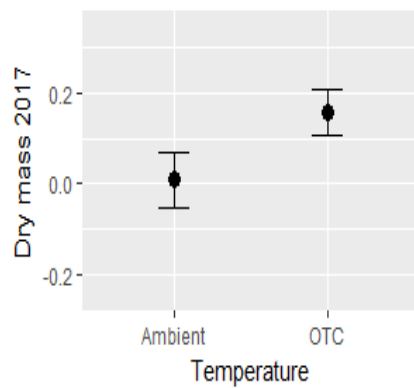


Figure 1: Significant impact on the gain in dry mass in 2017 by the temperature treatment (ambient, OTC)

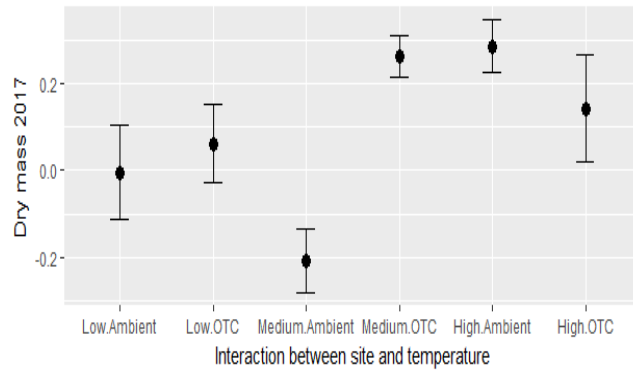


Figure 2: Significant impact on the gain in dry mass in 2017 by the interaction between site (low, medium, high) and temperature (ambient, OTC)

The response of dry mass in 2017 demonstrates accelerated growth within the tested period for plots equipped with open-top chambers (Figure 1). However this phenomenon cannot be supported by the data of the previous year. Even though the ramets in 2016 show a positive impact of simulated warming on plant growth of *V. myrtillus* at high altitude (Supplementary Figure 5), this effect is not visible in the calculated dry mass data. This may be due to the lack of significant impacts on the variables stem and shoots.

Considering the interaction between site and temperature and its influence on the gain in dry mass, a distinct difference between the temperature treatments can neither be detected at low site nor at the high site. At the middle site though, the gain in dry mass is significantly higher within plots exposed to simulated warming compared to ramets grown at ambient temperature (Figure 2).

4.1.2 Effect of MeJa

The amount of leaves of plants treated with MeJa drastically reduced within the sampling period, whereas the plants sprayed with water were not affected by this defoliation process (Figure 3)²⁵. This impact is visible at all study sites, while it is most pronounced in the lower and higher altitudes than at the medium site, where no significant p-value could be registered in the statistical testing (Figure 4).

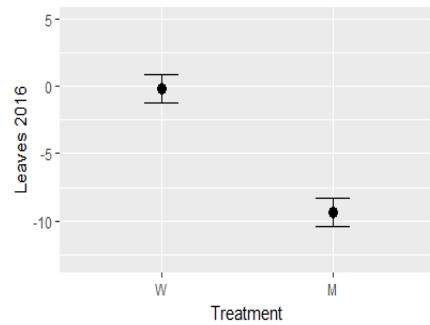


Figure 3: Significant impact on the increase of the amount of leaves in 2016 by the treatment with MeJa or water

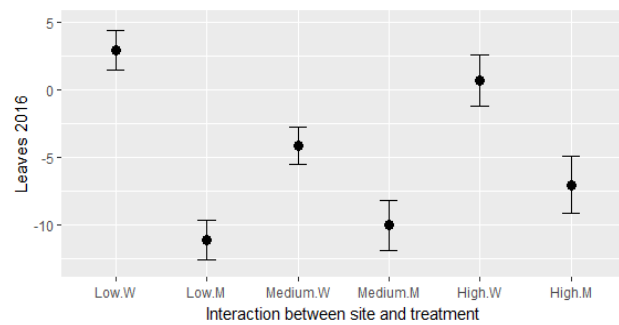


Figure 4: Significant impact on the increase of the amount of leaves in 2016 by the interaction between site (low, medium, high) and treatment (MeJa, water)

The responses of other growth variables to the methyl-jasmonate treatment are limited in both study years. The data set of 2016 exhibits significantly reduced vertical growth of plants at the low site, when treated with MeJa compared to plants sprayed with water. However no similar effects can be detected for the medium or high site during the same growing period (Supplementary Figure 6).

Controversial are the results for the same response variable height in the second year (2017), regarding to the MeJa impact on *V. myrtillus*. Opposite to the expectations, the sampled ramets experienced an increased growth when treated with MeJa in the second year of the study (1 year after MeJa application, Supplementary Figure 7). Since no other statistically significant impact on growth variables could be proven during the modelling, it is challenging to gain information about the influence of the methyl-jasmonate application on the plant development from the data.

²⁵ The term “treatment” in the figures and their captions refers to the application of either water or methyl jasmonate.

4.2 Grazing

4.2.1 Leaf grazing insects

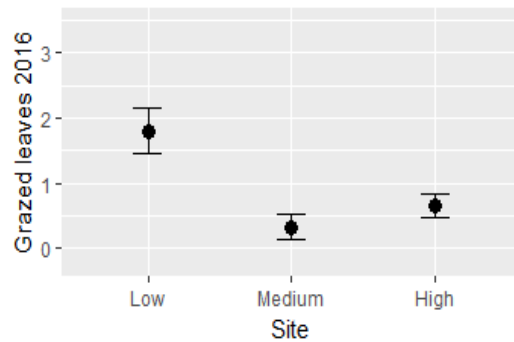


Figure 5: Significant impact on the increase of grazed leaves in 2016 by site (low, medium, high)

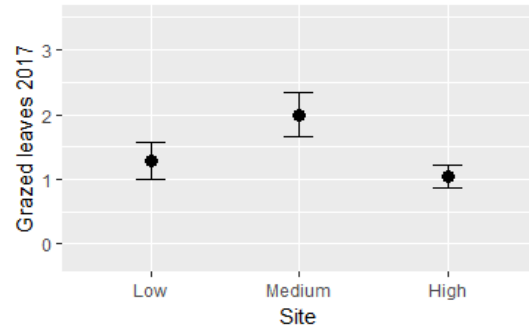


Figure 6: Significant impact on the increase of grazed leaves in 2017 by site (low, medium, high)

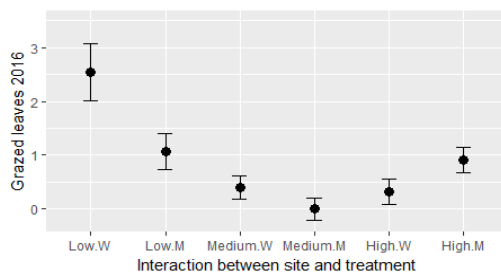


Figure 7: Significant impact on the increase of grazed leaves in 2016 by the interaction between site (low, medium, high) and treatment (MeJa, water)

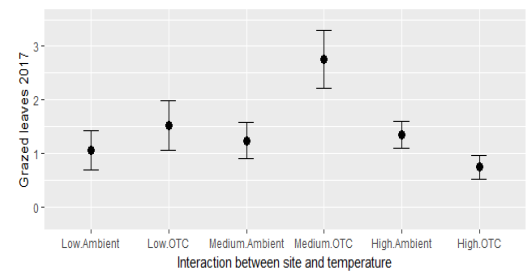


Figure 8: Significant impact on the increase of grazed leaves in 2017 by the interaction between site (low, medium, high) and temperature (ambient, OTC)

Figure 5²⁶ displays significantly more grazing at the low site during the study period in 2016 compared to both other sites, independently from temperature (ambient or OTC). Whereas in 2017 grazing pressure was most intense at the medium site (Figure 6) with significantly higher grazing levels compared to the high site. The tendency at the lowest location however, was decreasing after grazing was most dominantly there the previous year (2016), especially within water treated plots (Figure 7).

²⁶ The statistical testing of the grazed leaves variable (2016) is based on a logarithmic transformation after addition of a constant to the raw data values in order to valid the modelling. However the depicted graphs display the values before transformation to simplify comparison and ensure a better understanding.

Furthermore the low site is the only site demonstrating a significant difference between its MeJa and water treated plots in 2016, because the data exhibits significantly reduced grazing for the MeJa applied plots. While the graph demonstrates a similar tendency at medium site, the grazing at high site even appears to be slightly increased after MeJa application. Nevertheless none of the latter trends provide significant differences between water and MeJa treated plots based on the change in insect herbivory.

Little variation between the different temperature treatments can be detected in 2017. However significantly more insect grazed leaves can be found inside OTCs at medium site, underlining the tendency of increased grazing (Figure 8). Additionally less grazing (compared to OTC plots at the medium site) was found at the low site grown at ambient temperature reflecting the trend of decreasing grazing at that location during the second year of the study (2017).

4.2.2 Shoot grazing by deer

There were no significant differences in grazed shoots for any of the explanatory variables.

4.3 Reproduction

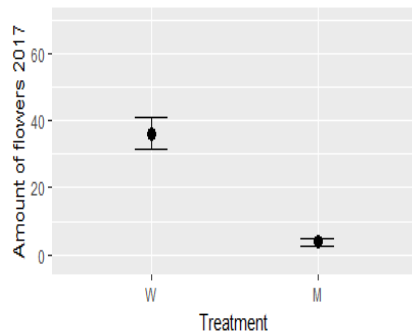


Figure 9: Significant impact on the total amount of flowers in 2017 by the treatment with MeJa or water

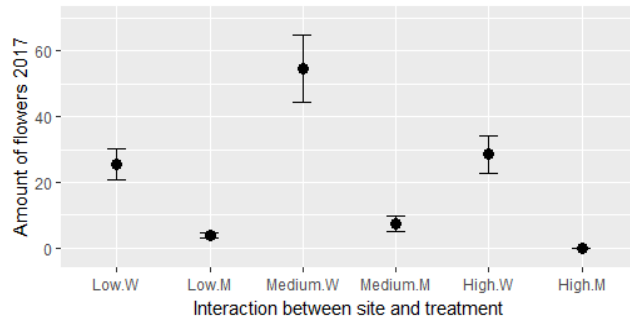


Figure 10: Significant impact on the total amount of flowers in 2017 by the interaction between site (low, medium, high) and treatment (MeJa, water)

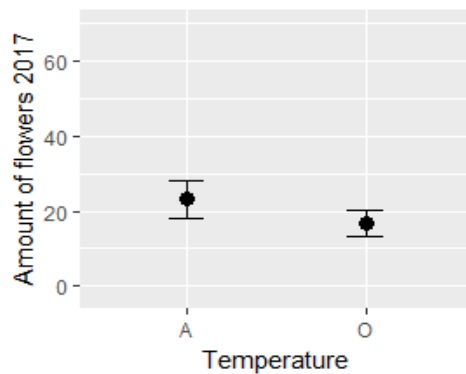


Figure 11: Significant impact on the total amount of flowers in 2017 by temperature (ambient, OTC)

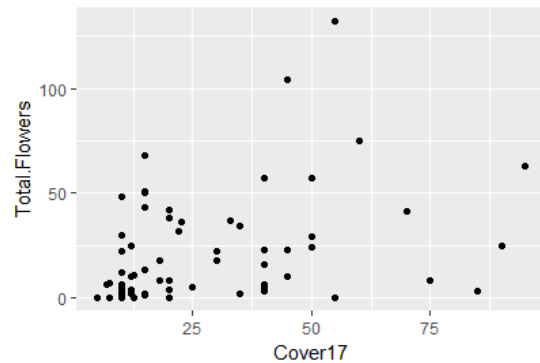


Figure 12: Significant impact on the total amount of flowers in 2017 by the bilberry coverage

The most distinct effect on the amount of flowers as a measure for the reproductive effort, can be assigned to the treatment with the hormonal regulator (MeJa). The number of flowers is significantly reduced within the plots treated with methyl-jasmonate (Figure 9). In addition the effect can clearly be seen for all three sites ($p < 0.05$), with the biggest difference at the medium site, (Figure 10). It should also be noted, that not a single flower could be found at the high site within the plots where methyl-jasmonate has been applied. Additionally a positive correlation could be found for the amount of flowers and the coverage of bilberry in the study plots.

Hence Figure 12 demonstrates, that with an increasing percentage cover of *V. myrtillus*, the number of flowers tends to increase as well. Less distinct but still significant were the responses towards the temperature treatments. On average, slightly less flowers could be counted inside OTC plots compared to plots without the simulated temperature increase, but this was only weakly significant ($p=0.035$) (Figure 11).

4.4 Weather data of 2016 and 2017

Due to the likely importance of weather in interpreting the results from the two years, weather data for monthly precipitation, temperature and the snow depth were collected from the Norwegian Meteorological Institute. The average temperatures of both years differ only slightly, yet the data reports higher monthly average values for 2016 in the study period (Beginning of May – End of July). In particular in June 2016, the mean temperature exceeds that of 2017. Moreover the average temperature reached in March 2016 was already a positive value, but still below zero in 2017, indicating a warmer spring in 2016.

The precipitation was generally higher in 2017 and the monthly values exceed the generally expected amount of precipitation in every month of the study period. The data for May and June 2016 are close to the estimated standards, while July of that year was affected by increased rainfall. (Supplementary Table 3) Low precipitation values in October and November 2016 are reflected in the low snow depth values of the following winter (Supplementary Figure 2).²⁷

²⁷ The Norwegian Meteorological Institute (MET Norway). Accessed 11 May 2018.

5 Discussion

The results of this study are relatively heterogenic, leading to accept some of the previous stated hypotheses and reject others. Some observed plant reactions may affirm the predictions regarding an inhibiting effect on growth and reproduction initiated by the application of MeJa, as well as the positive effect of simulated warming on plant growth. Moreover only in 2016 a uniform trend was found at low site regarding to responses of the growth variables and the insect grazing after MeJa application. However the data does not provide consistent information about the combined impact of simulated warming and MeJa application on bilberry. Varying responses of bilberry were found for interactions between the temperature or MeJa treatment and the site, suggesting that the sensibility of the plants to the different treatments varies along an elevational gradient.

5.1 Influence of MeJa application

5.1.1 Reproduction

The most distinct responses of wild bilberries under natural environment to the methyl-jasmonate application can be found, when considering the total amount of flowers in the different treatment plots. The data provides a strongly negative effect between the MeJa treatment and the amount of flowers in the second study year and hence supports the statement of constrained reproduction of *V. myrtillus*. This phenomenon may be explained by the hypothesis of resource allocation, which suggests, that the costs associated with the activation of defence mechanism restrict the available resources for other plant functions such as reproduction²⁸. Considering the combined impact of the MeJa treatment and the site, all studied sites provide the uniform trend of reduced flower development of ramets applied with MeJa. This leads to the conclusion that the statement of hormonal triggered restriction of reproductive mechanisms can be reached.

²⁸ Gómez, Sara, Ferrieri, Richard A., Schueller, Michael and Orians, Colin M., 2010. Methyl jasmonate elicits rapid changes in carbon and nitrogen dynamics in tomato, vol. 188. *The New phytologist* (3), 835–844. 10.1111/j.1469-8137.2010.03414.x.

Generally, growth favouring conditions at the medium site, as it is suggested to be the optimal habitat for bilberry (Ritchie, 1956; Pato and Obeso, 2012), may be the reason why the highest amount of flowers could be found there within the control plots. Since this value is exceeding the number of flowers of the water treated ramets at both other sites, the most pronounced difference can be observed at medium altitude. Contrariwise Pato et al. (2012) observed the reproductive maximum at higher elevation and refers to the required cold temperatures to successfully initiate the formation of floral buds. However, the benefit of cold conditions for bilberry flowering may be counteracted by the increasing severity of abiotic forces, such as reduced air temperature and atmospheric pressure or intensified solar radiation²⁹ and the necessity of warmth in spring to initiate the actual flowering³⁰. Besides those climatic factors, the nutrient limitation in the highlands (Pato and Obeso, 2012) may be a reason for the inhibition of the flower development of MeJa treated plants at the high site. Fabbro and Körner (2004) found that at high elevation the reallocation of biomass to reproductive structures, such as the development of flowers, is prioritised over maximisation of growth in order to compensate reduced pollinator diversity and abundance³¹. Consequently the resources attributed to the plant growth may already be minimized and the investment in defence mechanisms restricts the available amount of resources, which can be devoted to reproductive traits.

The similar effect on low site may also be attributed to external forces, whereas there especially moisture is a limiting factor due to lower precipitation (Pato and Obeso, 2012). However during the study period in 2017, the amount of rain even exceeded the expected average values and hence is unlikely to be responsible for the reproductive restriction (Supplementary Table 3).

²⁹ Körner, Christian, 2007. The use of 'altitude' in ecological research, vol. 22. *Trends in ecology & evolution* (11), 569–574. 10.1016/j.tree.2007.09.006.

³⁰ Jung, Christian and Müller, Andreas E., 2009. Flowering time control and applications in plant breeding, vol. 14. *Trends in plant science* (10), 563–573. 10.1016/j.tplants.2009.07.005.

³¹ Fabbro, Thomas and Körner, Christian, 2004. Altitudinal differences in flower traits and reproductive allocation, vol. 199: elsevier. *Flora* (199 // 1), 70–81. 10.1078/0367-2530-00128.

In fact Selås claims, that some species, such as bilberry, require a period of cold temperatures to initiate the successful development of floral buds³². Regarding to that, the relatively mild winter in advance of the growing period in 2017 may have inhibited the vernalization at low site. This would conform to the findings of Selås, which demonstrate a correlation between the depression of bilberry reproduction and high temperatures in winters with thin snow cover. Hence, in this study, the effort of upregulating defence genes (Cheong and Choi, 2003) induced by MeJa affects particularly already resource restricted plants dealing with challenging environmental conditions.

5.1.2 Grazing

In general, one can expect variations in herbivory sort and intensity along altitudinal gradients³³, since the diversity of faunal species is strongly correlated to vegetal distribution due to their mutual dependency, as e.g. plant-pollinator³⁴ or food chain correlations. This study found a relatively little increase in attacked leaves at high elevation, whereas the invertebrate grazing was most dominant in 2016 at the low site while this peak shifted to the middle site in the subsequent year. Generally, the abundance and diversity of species decreases with increasing elevation or peaks at intermediate altitudinal level Speed et al. (2013), since vertical distribution of insects currently is limited by temperature and the length of the growing season³⁵, which both declines along an altitudinal gradient (Hallinger, Manthey and Wilmking, 2010).

³² Selås, Vidar, 2000. Seed production of a masting dwarf shrub, *Vaccinium myrtillus* in relation to previous reproduction and weather, vol. 78. *Can. J. Bot.* (4), 423–429. 10.1139/b00-017.

³³ Speed, James D. M., Austrheim, Gunnar and Mysterud, Atle, 2013. The response of plant diversity to grazing varies along an elevational gradient, vol. 101. *J Ecol* (5), 1225–1236. 10.1111/1365-2745.12133.

³⁴ Ollerton, Jeff, Winfree, Rachael and Tarrant, Sam, 2011. How many flowering plants are pollinated by animals?, vol. 120. *Oikos* (3), 321–326. 10.1111/j.1600-0706.2010.18644.x. Accessed 13 April 2018.

³⁵ Descombes, Patrice, Marchon, Jérémy, Pradervand, Jean-Nicolas, Bilat, Julia, Guisan, Antoine, Rasmann, Sergio and Pellissier, Loïc, 2017. Community-level plant palatability increases with elevation as insect herbivore abundance declines, vol. 105. *J Ecol* (1), 142–151. 10.1111/1365-2745.12664.

Moreover, according to White (1984)³⁶, weather stressed plant may accumulate an increased amount of nitrogen in their tissues, which consequently provide nutritious food for invertebrates. Based on this theory, potentially drought stressed plants at the low site affected by the warm and relatively dry weather in 2016, could be responsible for the attraction of invertebrate herbivores there³⁷, since their population dynamics are highly dependent on the food palatability³⁸. Also the deer grazing was most dominant at low site in 2016, even though the variations in ungulate shoot grazing along the elevational gradient were not statistically significant. Hegland et al. (2005) found that ungulate grazing may have a negative impact on invertebrate population dynamics due to the reduced biomass and degraded food quality. Since according to the plant vigour hypothesis (Price, 1991) herbivore species tend to prefer the most nutritive plants, mammal herbivory at the low site in 2016 may have influenced the shift in insect grazing peak.

Moreover the grazing pressure at the low site in 2016 may have contributed to the activation of induced plant defences, as bilberry are known to accumulate secondary metabolites in terms of resistance against herbivory³⁹. Since only at that site MeJa treated plants showed an increased resistance against insect herbivory, conforming to findings of former studies, which indicate that methyl-jasmonate can lower the attraction of the plant to herbivores (Agrawal, Tuzun and Bent, 2000, 323). In contrast plants at high site exhibit even an opposite trend (yet not significant), which may be attributed to measurement errors. Additionally the absent resistance against herbivores, may be due to stronger winds at the less sheltered site and lower air pressure due to increased altitude.

³⁶ White, T. C. R., 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants: Springer-Verlag. *Oecologia* (63), 90–105. Accessed 22 May 2018.

³⁷ Khaliq, A., Javed, M., Sohail, M. and Sagheer, Muhammad, 2014. Environmental effects on insects and their population dynamics. *Journal of Entomology and Zoology Studies* (2 (2)), 1–7. Accessed 22 May 2018.

³⁸ Cornelissen, T., 2011. Climate change and its effects on terrestrial insects and herbivory patterns, vol. 40. *Neotrop. entomol.* (2), 155–163. 10.1590/S1519-566X2011000200001.

³⁹ Koski, Tuuli-Marjaana, Kalpio, Marika, Laaksonen, Toni, Sirkiä, Päivi M., Kallio, Heikki P., Yang, Baoru, Linderborg, Kaisa M. and Klemola, Tero, 2017. Effects of Insect Herbivory on Bilberry Production and Removal of Berries by Frugivores, vol. 43. *Journal of chemical ecology* (4), 422–432. 10.1007/s10886-017-0838-8.

Those conditions favour evaporation and thus may lower the concentration of methyl-jasmonate⁴⁰. However the sparsity of responses in the subsequent year (2017) does not allow to determine a pattern of insect grazing patterns in MeJa treated plots. Especially because the defence mechanisms may be expected to be the strongest in 2017 based on the findings of Benevenuto et al. (in press). They found the strongest resistance of bilberry against insect grazing one year after MeJa application due to delayed responses of the relatively slow growing perennial and deciduous shrub (ibid.). The study of Benevenuto et al. (in press) included a different technique to apply the MeJa to the plants, as cotton wool soaked with MeJa was attached to the stem of the treated ramet at the ground (ibid.). Thus the bilberry may have been exposed to a higher dose of the hormonal regulator, whereby the more distinct responses, such as significantly reduced insect grazing, compared to the findings of this study could be readily explained. Additionally referring to the cost hypothesis (Agrawal, Tuzun and Bent, 2000, 233), defence mechanisms are only activated if the effort associated with the resource allocation is beneficial for the plant. For instance if the plants are exposed to stresses as for instance herbivory, which may reduce their biomass and threaten their survival. Furthermore the internal constraint hypothesis (Agrawal, Tuzun and Bent, 2000, 233-234, 237) implies that this exterior impact must exceed a certain threshold to activate defence mechanisms. Accordingly to this, the concentration of methyl-jasmonate applied to the plants may have been too little to initiate the cost expensive defence mechanisms against insect grazing.

Opposite to the assumptions based on previous studies, the MeJa application did not prevent the plants from being grazed on by deer, since no distinct difference in grazing pressure could be determined compared to the control plants. Benevenuto et al. (in press) observed a significantly reduced amount of bilberry shoots for MeJa treated plants two years after the application.

⁴⁰ Grace, J., 1977. Plant response to wind. *Experimental botany*, v. 13. London, New York: Academic Press.

Regarding to the delayed response, they hypothesise the activation of an induced long-term defence system against large vertebrate herbivores, which are suggested to be more costly to the plant (ibid.). Hence responses regarding to the shoot grazing may be absent in this study, because the activation of those long-term defences to the plant and has not yet developed its full potential. In that case a regulating effect should be visible in the third year of the study.

5.1.3 Growth

The distinct loss of leaves in MeJa plots may be a further side effect of the hormonal compound. Since opposite to that, the water treated plots provide steady numbers of leaves over the sampling period. Due to the influence on physiological processes (Bennett and Wallsgrave, 1994) the MeJa treatment may cause alterations in the plant morphology as it is known to promote leaf senescence and abscission^{41,42}. Herbivory grazing as a reason for the reduced numbers of leaves can most likely be excluded, based on findings of several previous studies proving a decline in grazing intensities on plants in contact with MeJa. Furthermore the observation of defoliation as a response to methyl-jasmonate induced stress⁴³, can be confirmed by the study of Percival and MacKenzie.

The trend of defoliation in MeJa plots is visible on all sites, though not significant at medium altitude. Since there the growing conditions are assumed to favour the plant development, the plants may be able to devote resources to the activation of defence mechanisms while reducing the abortion of leaves to a minimum.

⁴¹ Curtis, Roy W., 1984. Abscission-Inducing Properties of Methyl Jasmonate, ABA, and ABA-Methyl Ester and their Interactions with Ethephon, AgNO₃, and Malformin: Springer-Verlag. *Journal of Plant Growth Regulation* (3), 157–168. Accessed 15 May 2018.

⁴² Saniewski, Marian, Ueda, Junich and Miyamoto, Kensuke, 2002. Relationships between jasmonates and auxin in regulation of some physiological processes in higher plants. *Acta Physiologiae Plantarum* (Vol. 24.), 211–220. Accessed 16 February 2018.

⁴³ Percival, David and MacKenzie, Joanna L., 2007. Use of plant growth regulators to increase polyphenolic. *Canadian Journal of Plant Science* (87), 333–336. Accessed 16 May 2018.

The inverse phenomenon of reduced plant resistance to insect herbivory has been described by the plant stress hypothesis^{44, 45}. According to this, the food palatability is altered by environmental stresses influencing biochemical source-sink relationships in the plants⁴⁶.

Moreover the peak of leaf abscission at the low site may support the assumption of a local reallocation of plants resources in 2016 induced by the MeJa application and high local grazing pressure (Cheong and Choi, 2003). Coherent with former findings, also the vertical plant growth inside those plots was restricted. This may affirm the thesis of a negative impact on the plant growth due to the costly production of secondary metabolites in terms of defences against herbivory⁴⁷.

Moreover the magnitude of defoliation at the low site may also be associated with local weather conditions, since *V. myrtillus* is known to avoid drought by shedding primarily mature leaves to maintain a sufficient water balance⁴⁸. Especially plants at lower altitude are little flexible to deal with drought stresses⁴⁹ when exposed to direct insolation often followed by a drying-out of the soil. The Norwegian Meteorological Institute registered higher monthly average temperatures for the study period in 2016 compared to the subsequent year (Supplementary Table 3), supporting the hypothesis of increased vulnerability of bilberry due to additionally drought stress.

⁴⁴ White, T. C. R., 1969. An Index to Measure Weather-Induced Stress of Trees Associated With Outbreaks of Psyllids in Australia, vol. 50. *Ecology* (5), 905–909. 10.2307/1933707.

⁴⁵ Joern, Anthony and Mole, Simon, 2005. The plant stress hypothesis and variable responses by blue grama grass (*Bouteloua gracilis*) to water, mineral nitrogen, and insect herbivory, vol. 31. *Journal of chemical ecology* (9), 2069–2090. 10.1007/s10886-005-6078-3.

⁴⁶ Mattson, William J. and Haack, Robert A., 1987. Role of Drought in Outbreaks of Plant-Eating Insects. *Bioscience* (37 (2)), 110–118. Accessed 22 May 2018.

⁴⁷ Simms, E. L., Rausher, M. D., Simms, Ellen L. and Rausher, Mark D., 1992 // 1987. Costs and Benefits of Plant Resistance to Herbivory, vol. 130. *The American Naturalist* (4), 570–581. 10.1086/284731.

⁴⁸ Taulavuori, Erja, Tahkokorpi, Marjaana, Laine, Kari and Taulavuori, Kari, 2010. Drought tolerance of juvenile and mature leaves of a deciduous dwarf shrub *Vaccinium myrtillus* L. in a boreal environment, vol. 241. *Protoplasma* (1-4), 19–27. 10.1007/s00709-009-0096-x.

⁴⁹ Habibi, Ghader and Ajory, Neda, 2015. The effect of drought on photosynthetic plasticity in *Marrubium vulgare* plants growing at low and high altitudes, vol. 128. *Journal of plant research* (6), 987–994. 10.1007/s10265-015-0748-1.

The lack of a similar behaviour in 2017 does not support this, because an increased impact on the plant was expected in the second year of the study due to the previously mentioned delay in responses. However based on the statement that moisture is a limiting factor for the plant development (Taulavuori, Tahkokorpi, Laine and Taulavuori, 2010), this may be attributed to the high amount of precipitation during the study period in 2017 (Supplementary Table 3). Thereby sufficient water supply may have created favourable growing conditions for bilberry, avoiding the necessity of leaf abscission. Generally warmer temperature can lengthen the growing season for *V. myrtillus* by initiating premature flowering⁵⁰. However bilberry are known to be sensitive to frost damage⁵¹ and hence may be negatively affected by an earlier spring bloom induced by changing climate, as they are endangered to suffer a loss of flowers during a proximate cold period.

⁵⁰ BOKHORST, S., BJERKE, J. W., BOWLES, F. W., MELILLO, J., CALLAGHAN, T. V. and PHOENIX, G. K., 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland, vol. 5. *Global Change Biology*, 445. 10.1111/j.1365-2486.2008.01689.x.

⁵¹ Tolvanen, Anne, 1997. Recovery of the bilberry (*Vaccinium Myrtillus* L.) from artificial spring and summer frost: Springer-Verlag. *Plant Ecology* (130), 35–39. Accessed 23 May 2018.

5.2 Influence of simulated warming

5.2.1 Reproduction

Minor responses to the simulated warming could be determined regarding to the reproductive effort, as the amount of flowers is reduced inside OTCs. Little research is conducted regarding to the effect of temperature and the flower abundance for shrubs species. However studies investigating the influence of climate change on the reproductive traits of other plant species, state alterations in flowering phenology and/ or a reduction in flower production⁵². For instance Karapanos et al. (2008) documented higher abundance of flowers for tomato plants during lower temperatures⁵³ and refers to Dinar and Rudich (1985), who found flower abscission under heat stress due to the restricted supply of assimilates to the flower buds⁵⁴.

The study results though, may be affected by increased grazing pressure inside OTCs at the medium site in 2017, whereby the lower amount of flowers may be a direct impact of grazing in terms of reduced biomass⁵⁵ or induced plant defences⁵⁶. Moreover the intensified insect grazing could affect reproductive traits indirectly, as herbivory is known to reduce the plant fitness and to have a detrimental effect on growth and reproduction⁵⁷.

⁵² Pan, Cheng-Chen, Feng, Qi, Zhao, Ha-Lin, Liu, Lin-De, Li, Yu-Lin, Li, Yu-Qiang, Zhang, Tong-Hui and Yu, Xiao-Ya, 2017. Earlier flowering did not alter pollen limitation in an early flowering shrub under short-term experimental warming, vol. 7. *Scientific reports* (1), 2795. 10.1038/s41598-017-03037-9.

⁵³ Karapanos, Ioannis C., Mahmood, Shreef and Thanopoulos, Charalampos, 2008. Fruit Set in Solanaceous Vegetable Crops as Affected by Floral and Environmental Factors: Global Science Books. *The European Journal of Plant Science and Biotechnology* (2 (Special Issue 1)), 88–105. Accessed 23 May 2018.

⁵⁴ DINAR, M. and RUDICH, J., 1985. Effect of Heat Stress on Assimilate Metabolism in Tomato Flower Buds, vol. 56. *Annals of Botany* (2), 249–257. 10.1093/oxfordjournals.aob.a087009.

⁵⁵ Strengbom, Joachim, Olofsson, Johan, Witzell, Johanna and Dahlgren, Jonas, 2003. Effects of repeated damage and fertilization on palatability of *Vaccinium myrtillus* to grey sided voles, *Clethrionomys rufocanus*, vol. 103. *Oikos* (1), 133–141. 10.1034/j.1600-0706.2003.12680.x.

⁵⁶ Stange, Erik E. and Ayres, Matthew P. Climate Change Impacts: Insects, vol. 262, 75. 10.1002/9780470015902.a0022555.

⁵⁷ Fernandez-Calvo, I. C., 2004. Growth, nutrient content, fruit production and herbivory in bilberry *Vaccinium myrtillus* L. along an altitudinal gradient, vol. 77. *Forestry* (3), 213–223. 10.1093/forestry/77.3.213.

Generally warmer temperature can lengthen the growing season for *V. myrtillus* by initiating premature flowering⁵⁸. However bilberry are known to be sensitive to frost damage⁵⁹ and hence may be negatively affected by an earlier spring bloom induced by changing climate, as they are endangered to suffer a loss of flowers during a proximate cold period.

5.2.2 Grazing

In 2017 the insect grazing was most dominant at mid elevation, whereas primarily plants inside OTCs were attacked. This may be attributed to the favourable growing conditions and the resulting abundant and vigorous biomass there^{60,61}. Consequently, sufficient and nutritious bilberry plants appear to attract invertebrate herbivores. This behaviour conforms to the plant vigour hypothesis⁶², according to which herbivores prefer to feed on vigorous plants.

Furthermore some species preferring the local conditions in the open-top chambers can benefit from the sheltered environment and congregate within OTCs, whereas on the contrary other insects may rather avoid those⁶³. Hence Moise et al. points out the risk of inaccurate interpretation, since possible community interactions may be overlooked when only considering the local response. Therefore to define a direct positive effect of the simulated warming on the grazing intensity, may not be completely correct due to the hypothetically manipulating effect of open-top chambers.

⁵⁸ BOKHORST, S., BJERKE, J. W., BOWLES, F. W., MELILLO, J., CALLAGHAN, T. V. and PHOENIX, G. K., 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland, vol. 5. *Global Change Biology*, 445. 10.1111/j.1365-2486.2008.01689.x.

⁵⁹ Tolvanen, Anne, 1997. Recovery of the bilberry (*Vaccinium Myrtillus* L.) from artificial spring and summer frost: Springer-Verlag. *Plant Ecology* (130), 35–39. Accessed 23 May 2018.

⁶⁰ Pato, Joaquina and Obeso, José Ramón, 2012. Growth and reproductive performance in bilberry (*Vaccinium myrtillus*) along an elevation gradient, vol. 19. *Écoscience* (1), 59–68. 10.2980/19-1-3407.

⁶¹ Rinnan, Riikka, Stark, Sari and Tolvanen, Anne, 2009. Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath, vol. 97. *Journal of Ecology* (4), 788–800. 10.1111/j.1365-2745.2009.01506.x.

⁶² Price, Peter W., 1991. The Plant Vigor Hypothesis and Herbivore Attack. *Oikos* (Vol. 62), 244–251. Accessed 18 May 2018.

⁶³ Moise, Eric R. D. and Henry, Hugh A. L., 2010. Like moths to a street lamp: exaggerated animal densities in plot-level global change field experiments, vol. 119. *Oikos* (5), 791–795. 10.1111/j.1600-0706.2009.18343.x.

5.2.3 Growth

The larger increase in stem diameter and dry mass within plots equipped with OTCs in 2017 allow the assumption of enhanced bilberry growth at warmer temperatures. Similar results were also exhibited in previous studies proving boosted growth and spread of *V. myrtillus* as a response to simulated warming. Rinnan et al. (2009) for instance found that simulated warming triggered an extended cover of bilberry in a subarctic tundra heath in Finland after 10 – 13 years of exposure. In that study other plant groups were not affected positively by the temperature treatment and the shrub was able to outcompete adjacent species (Rinnan, Stark and Tolvanen, 2009). This observation can also be confirmed by the findings of Dawes et al.⁶⁴, who found enhanced shoot growth of *V. myrtillus* influenced by simulated warming⁶⁵. Other investigated dwarf shrubs (*Vaccinium gaultherioides* and *Empetrum hermaphroditum*) were excluded from the adolescence stimulating effect. Hence warmer climatic conditions⁶⁶ may have a beneficial impact on the growth of *V. myrtillus*, especially due to its advantage over coexisting plant species (Dawes, Hagedorn, Zumbunn, Handa, Hättenschwiler, Wipf and Rixen, 2011).

Considering the interaction between site and temperature, the thesis of enhanced growth at elevated temperature can be underlined to a limited extent. The significant responses there are restricted to the medium site and again only visible in 2017. The lacking impacts on growth in 2016 may be attributed to less optimal weather conditions due to the former stated high temperatures and the corresponding drought potential. Moreover the assumption of optimal conditions for plant development at mid site (Pato and Obeso, 2012) and sufficient water supply because of extensive precipitation in 2017 may have caused the significant increase in dry mass in OTCs there, while no trend is visible at low or high elevation.

⁶⁴ Dawes, Melissa A., Hagedorn, Frank, Zumbunn, Thomas, Handa, Ira Tanya, Hättenschwiler, Stephan, Wipf, Sonja and Rixen, Christian, 2011. Growth and community responses of alpine dwarf shrubs to in situ CO₂ enrichment and soil warming, vol. 191. *The New phytologist* (3), 806–818. 10.1111/j.1469-8137.2011.03722.x.

⁶⁵ Simulated warming there was effectuated with heating cables on the ground surface causing a soil warming instead of OTC usage.

⁶⁶ The study also tested the influence of enriched CO₂ of bilberry, as its atmospheric concentration is predicted to continue rising in future climate scenarios. The combination of elevated CO₂ levels and increased temperature reinforced the positive effect on bilberry.

This also confirms the previous stated hypothesis of sufficient and high quality food supply within the OTC plots attracting invertebrate herbivores. Even though not significant in the general dry mass data, the increase in plant height was positively affected by OTCs in 2016 at high elevation, where the simulated warming appears to have the strongest advantageous impact on the vertical plant growth. The OTC plots at the high site depict an enhanced growth not only compared to the ambient temperate plots at the same elevation, but also compared to the average growth in OTC plots of both other sites (Low, Medium). The particular sensitivity may be attributed to the fact, that temperature is one of the growth restricting parameters at the high site (Grace, 1977). Therefore, a slight increase in temperature and protection from wind (Marion et al., 1997) seems to have enabled a boost in growth, compared to medium or low site plots. There the prevailing ambient temperature is already close to optimal growing conditions and hence a larger temperature increase may be necessary to enhance the plant growth at medium site.

Even though the observed responses to the temperature treatment appear to be coherent with former findings, the single results of the growth variables lack a consistent trend. Despite its statistical significance, the trustworthiness of the single responses may be limited due to possible measurement inaccuracies especially for the height or stem variables.

6 Conclusion

This study discovered a significantly reduced amount of flowers after the application of the hormonal regulator methyl-jasmonate. This trend could be observed at all investigated sites (circa 100, 450 and 900 masl) indicating a reallocation of the plants resources from reproduction to defence mechanisms (Cheong and Choi, 2003), whereas already resource restricted plants were affected the most. However no significant impact on the plant growth was observed in the same year (2017), suggesting that reproduction is the first to lose out in case of limited resources during herbivore attacks.

Moreover a significant defoliation process (Curtis, 1984) could be registered for MeJa treated bilberry in 2016, whereas the most significant difference compared to the control plots could be found at the lowest elevation. At the same site the vertical growth was negatively affected by the MeJa treatment, whereas the resistance against invertebrate herbivores significantly increased. Leading to the assumption that plant defence genes were successfully mobilized, whereby less resources were devoted to the plant growth. However this consistent behaviour was only observed at the low site, where the increase in invertebrate grazed leaves was the highest in 2016. Hence one can assume that the natural grazing pressure contributed to the local activation of defence mechanisms against herbivores. To sum up, those uniform trends may confirm the hypothesis that the upregulation of defence genes induced by MeJa and/ or natural grazing increase the protection of *V. myrtillus* against herbivory at the expense of growth and reproduction.

On the other hand the MeJa treatment did not prevent bilberry to be grazed on by ungulates, since no significant differences to the control plots could be discovered in both years. The lack of responses may be attributed to an underdose of the VOC concentration or the delay in responses as observed by Benevenuto et al. (in press). Additionally the gains in dry mass were increased inside OTCs in the second study year, supporting the assumption of favourable growing conditions at elevated temperature. Whereas this single response to the simulated warming is little meaningful, since this effect was not underlined by other growth variables.

Moreover the combined effect of MeJa and simulated warming can not be evaluated, since the data analysis did not provide significant responses regarding to this interaction. Former findings claim that bilberry may benefit from climate change and outcompete other species (Rinnan, Stark and Tolvanen, 2009), which may cause a negative feedback on the plant as the increased food supply may favour the populations of several herbivore species grazing on bilberry. Referring to the findings of this study, especially plants under poor conditions may suffer a loss of reproductive traits, when activating defences against herbivores. Further research is necessary to gain more information about how the changing climate may affect key species, such as the shrub *V. myrtillus*, as it fulfils an essential role as primary producer within ecosystems.

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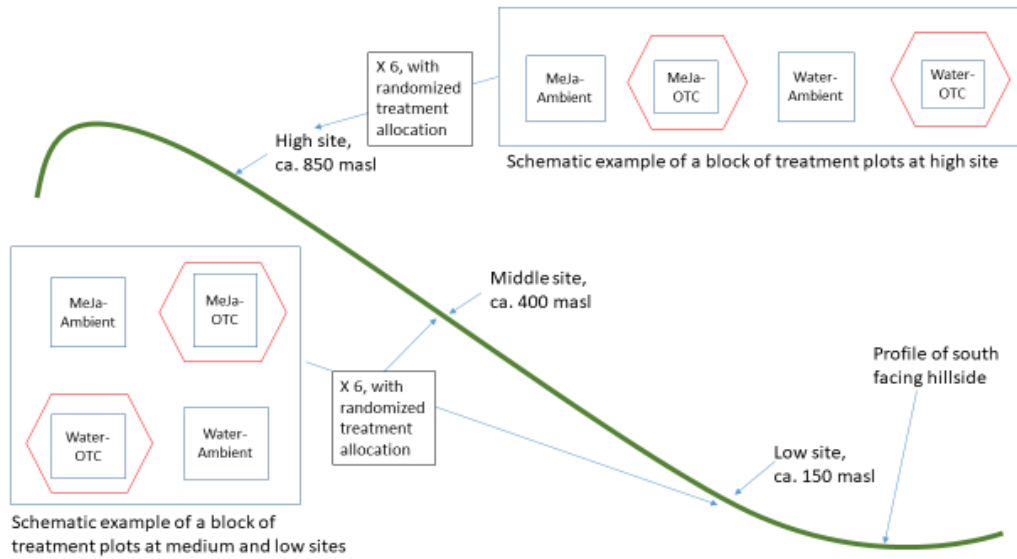
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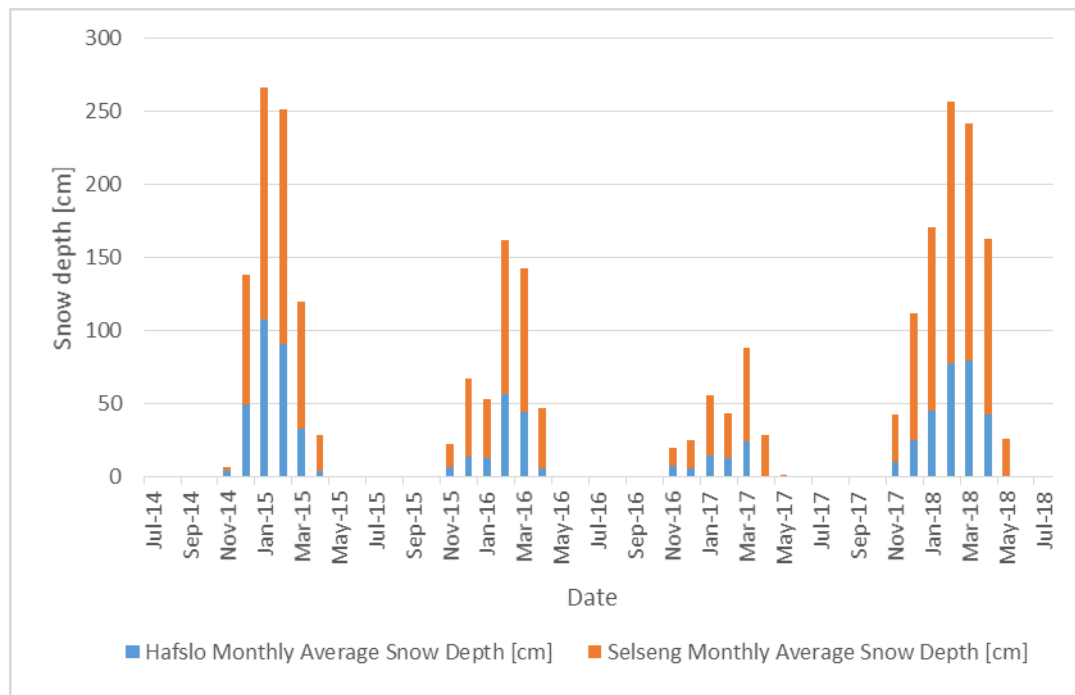
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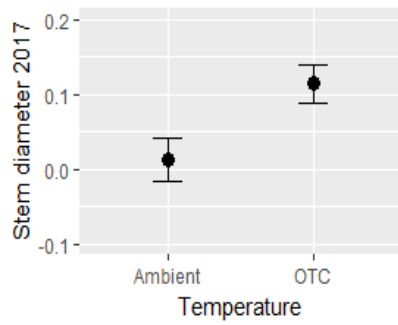
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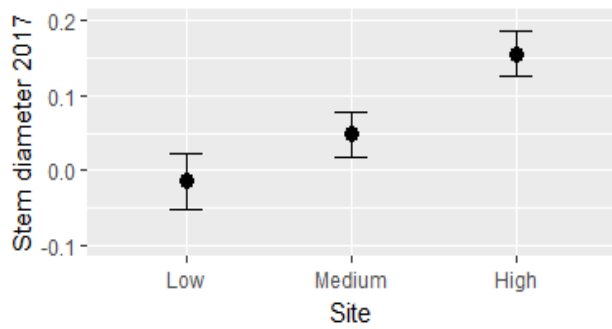
Supplementary Figure 1: Sketch of the study design including three different elevated sites and the schematical set-up of the treatment plots



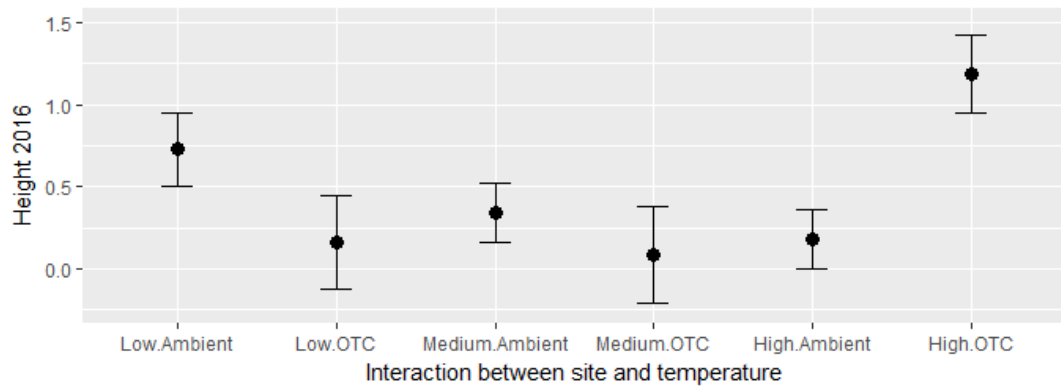
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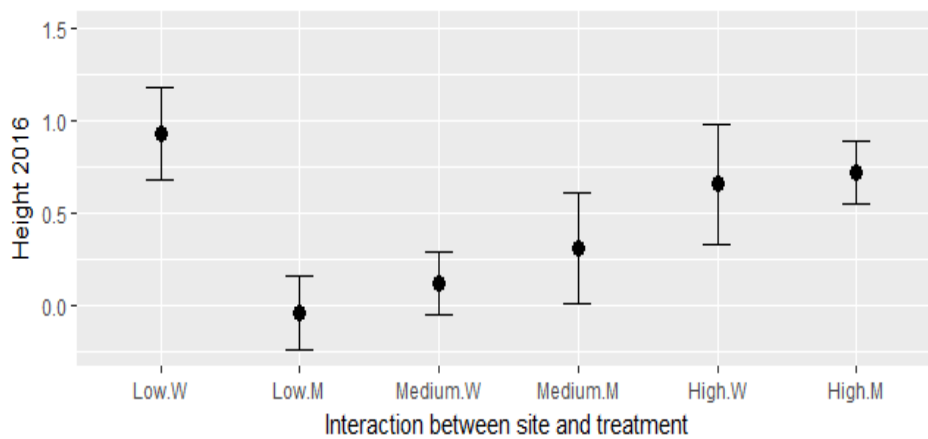
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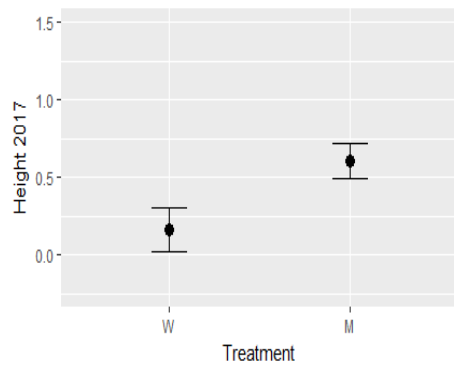
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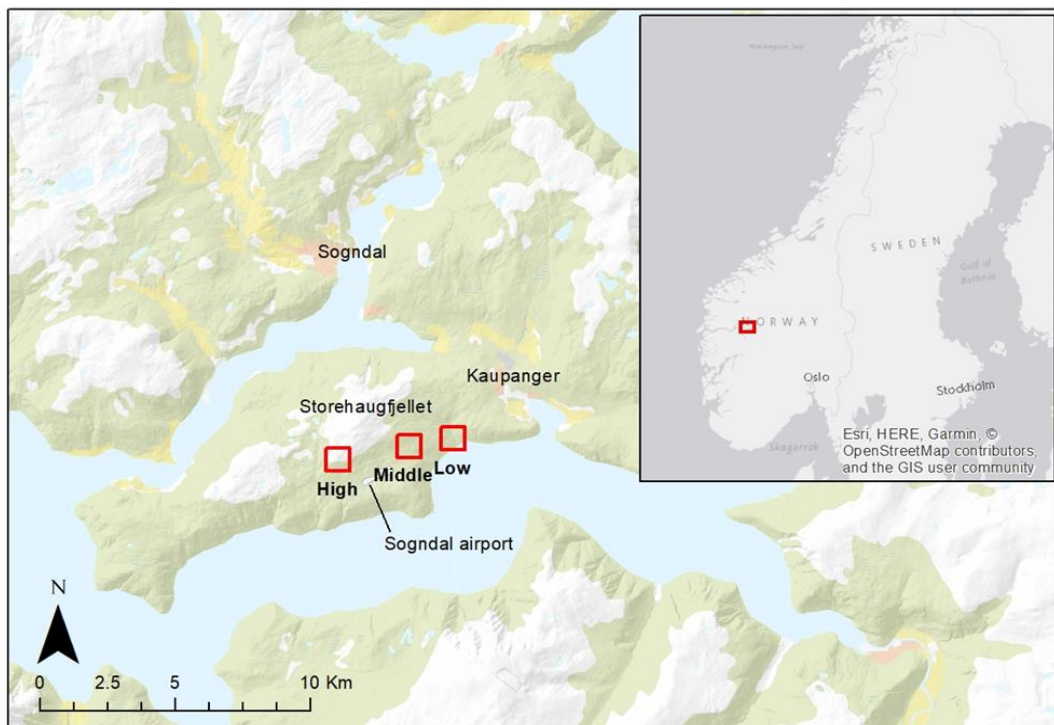


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Supplementary Maps



Supplementary Map 1: Map of study location situated in Western Norway and a close-up view displaying the positions of the three study sites

Supplementary Tables

Supplementary Table 1: Overview of statistical responses after running the maximal linear mixed effect models fitted for the supplementary response variables (stem diameter, height, amount of annual shoots) including the three explanatory variables (site, temperature, treatment) and all two-way interactions.

Response	Treatment	DF	2016		2017	
			F	P	F	P
Stem diameter	Treatment	1	2.208	0.144	0.010	0.922
	Temperature	1	0.029	0.865	7.864	0.007
	Site	2	2.429	0.099	7.571	0.001
	Site:Treatment	2	0.690	0.507	1.880	0.162
	Site:Temperature	2	0.390	0.680	1.394	0.257
	Temperature:Treatment	1	1.642	0.206	0.145	0.705
Height	Treatment	1	1.753	0.191	5.375	0.024
	Temperature	1	0.115	0.736	0.433	0.513
	Site	2	2.236	0.116	0.175	0.840
	Site:Treatment	2	4.069	0.022	0.453	0.638
	Site:Temperature	2	7.013	0.002	0.884	0.419
	Temperature:Treatment	1	2.765	0.102	0.376	0.542
Shoots	Treatment	1	0.022	0.884	0.369	0.546
	Temperature	1	0.257	0.614	0.126	0.724
	Site	2	1.464	0.240	0.087	0.917
	Site:Treatment	2	3.943	0.025	0.935	0.399
	Site:Temperature	2	0.695	0.503	0.903	0.411
	Temperature:Treatment	1	0.080	0.779	0.011	0.916

Supplementary Table 2: Overview of statistical responses after model simplification for all response variables

Response	Treatment	DF	2016		2017	
			F	P	F	P
Stem diameter	Temperature	1	-	-	7.864	0.007
	Site	2	-	-	7.571	0.001
Shoots	Treatment	1	0.023	0.881	-	-
	Site	2	1.518	0.227	-	-
	Site:Treatment	2	4.089	0.021	-	-
Height	Treatment	1	1.706	0.196	5.840	0.018
	Temperature	1	0.112	0.739	-	-
	Site	2	2.175	0.122	-	-
	Site:Treatment	2	3.958	0.024	-	-
Dry mass	Site:Temperature	2	6.822	0.002	-	-
	Temperature	1	-	-	4.326	0.042
	Site	2	-	-	2.8555	0.06512
Leaves	Site:Temperature	2	-	-	6.334	0.003
	Treatment	1	42.745	1.13E-08	-	-
	Site	2	2.5805	0.08348	-	-
Grazed leaves	Site:Treatment	2	2.999	0.025	-	-
	Treatment	1	1.5266	0.221	-	-
	Temperature	1	-	-	2.229	0.140
	Site	2	10.868	8.32E-05	3.423	0.039
Grazed leaves	Site:Treatment	2	4.921	0.010	-	-
	Site:Temperature	2	-	-	3.954	0.024

Response	Treatment	DF	2016		2017	
			Dev	P	Dev	P
Total amount of flowers	Cover	1	-	-	-	2.04E-07
	Treatment	1	-	-	-	< 2.2E-16
	Temperature	1	-	-	-	0.035
	Site	2	-	-	-	0.436
	Treatment:Site	2	-	-	-	0.010

Supplementary Table 3: Monthly average temperature and precipitation values during both study periods from MET Norway⁶⁷

Date	Average temperature [°C]		Normal Temperaturen [°C]	Total precipitation [mm]		Normal precipitation [mm]
	2016	2017		2016	2017	
January	-5.6	-1.4	-5.2	169	133	154
February	-2.9	-1.5	-4.7	105	96	104
March	0.3	-0.4	-1.7	49	171	118
April	2.1	1.9	1.7	53	110	57
May	8.6	8.5	7.5	70	85	63
June	13.0	10.4	11.2	77	96	78
July	12.5	12.3	12.5	131	99	85
August	11.7	11.2	11.7	177	105	115
September	11.4	9.9	7.6	204	125	208
October	4.2	4.5	4.4	93	258	205
November	-1.4	-0.7	-0.7	140	284	178
December	1.0	-2.3	-3.1	313	253	178
Mean	4.6	4.4	3.4	-	-	-
Total	-	-	-	1582	1814	1543

⁶⁷ Temperature data collected from weather station “Sogndal Lufthamn” (located 479 masl on the mountain investigated in this study). Precipitation data is not available for the same location, and hence is listed for the weather station “Selseng” (app. 406 masl, 30km distanced from the study area). Normal temperature and precipitation are averaged over the period from 1961 – 1990.

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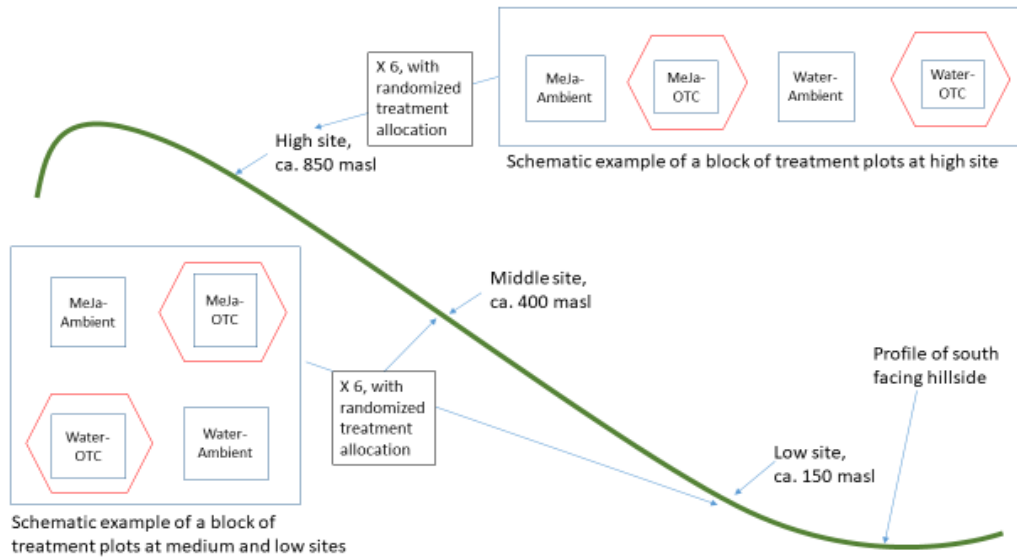
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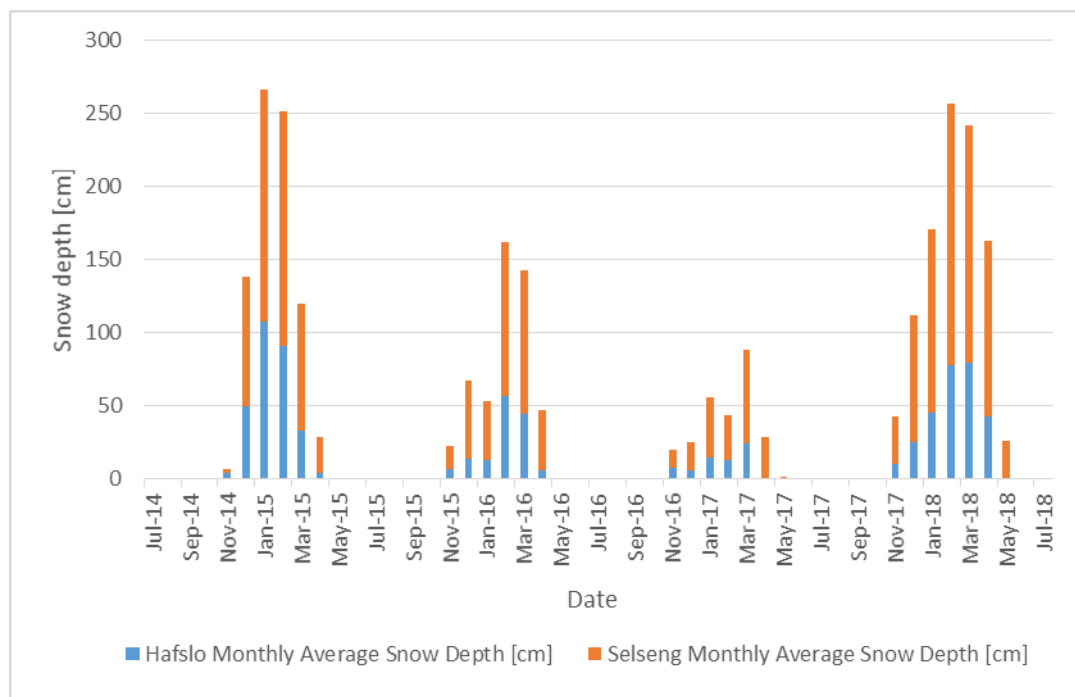
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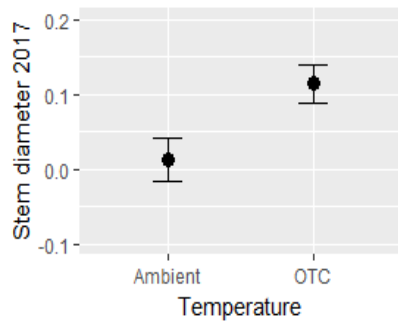
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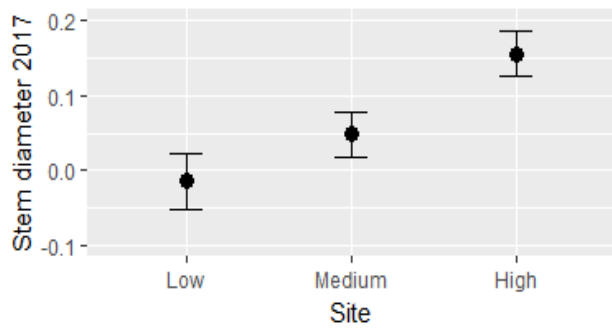
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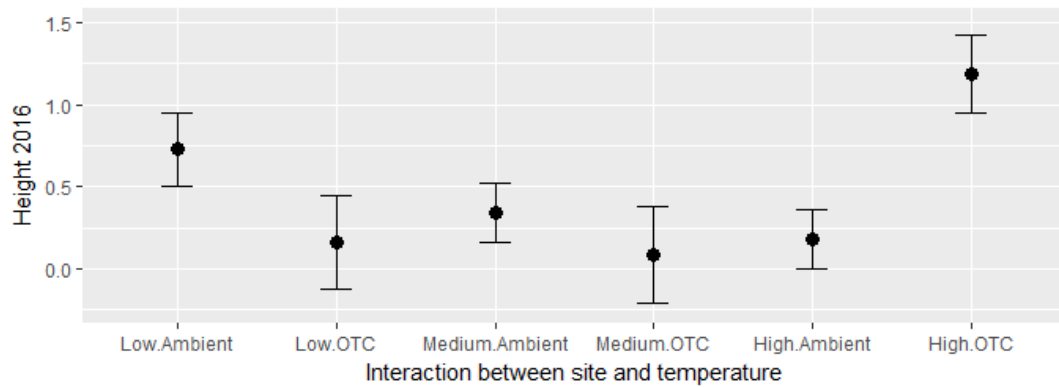
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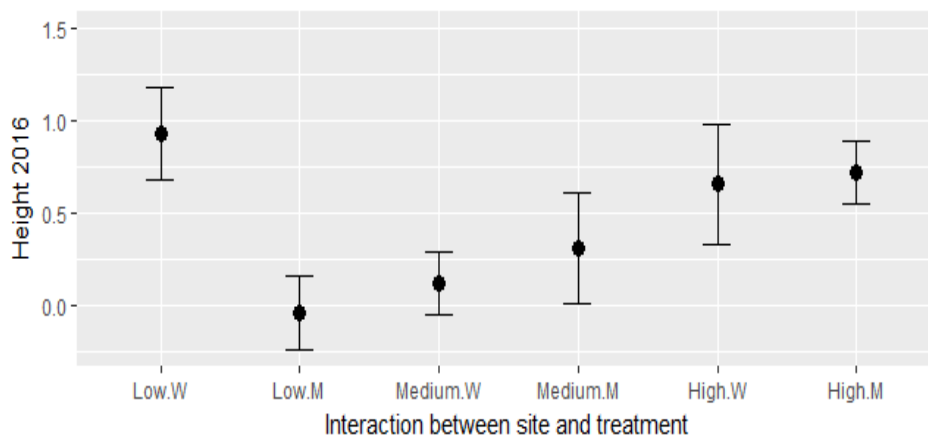
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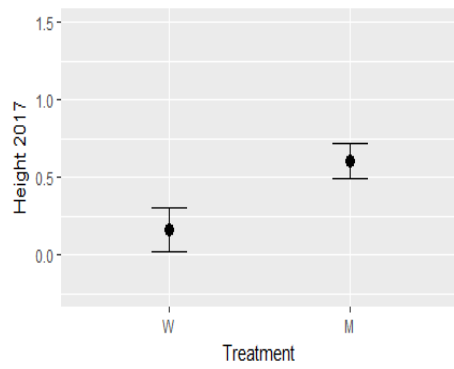
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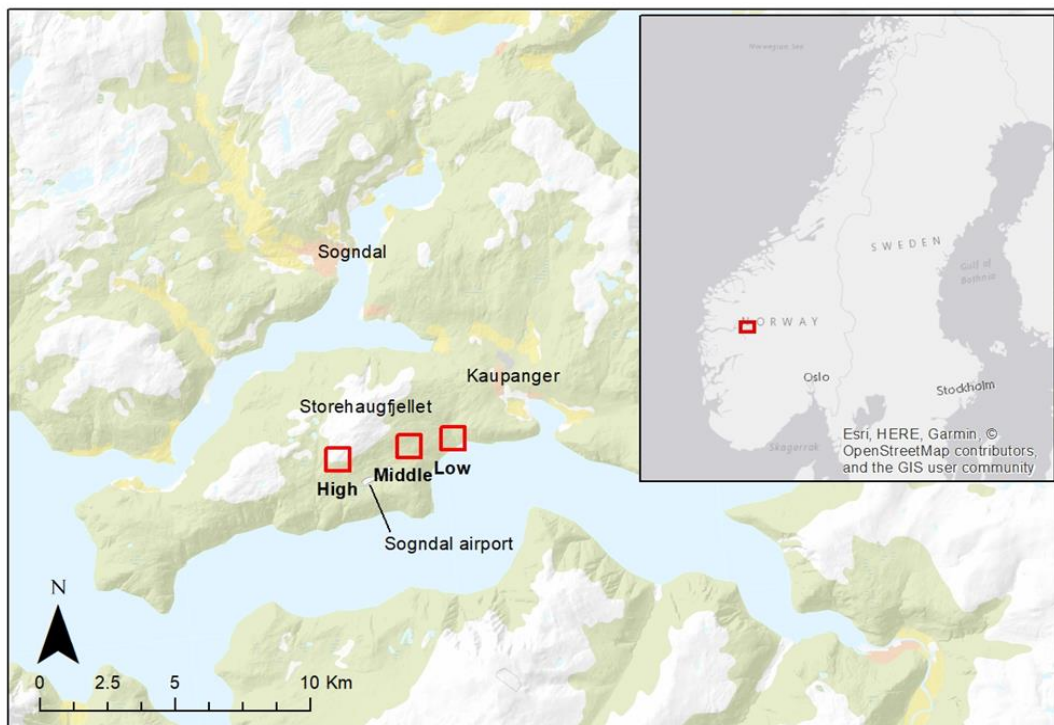


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Supplementary Map 1: Map of study location situated in Western Norway and a close-up view displaying the positions of the three study sites

Supplementary Tables

Supplementary Table 1: Overview of statistical responses after running the maximal linear mixed effect models fitted for the supplementary response variables (stem diameter, height, amount of annual shoots) including the three explanatory variables (site, temperature, treatment) and all two-way interactions.

Response	Treatment	DF	2016		2017	
			F	P	F	P
Stem diameter	Treatment	1	2.208	0.144	0.010	0.922
	Temperature	1	0.029	0.865	7.864	0.007
	Site	2	2.429	0.099	7.571	0.001
	Site:Treatment	2	0.690	0.507	1.880	0.162
	Site:Temperature	2	0.390	0.680	1.394	0.257
	Temperature:Treatment	1	1.642	0.206	0.145	0.705
Height	Treatment	1	1.753	0.191	5.375	0.024
	Temperature	1	0.115	0.736	0.433	0.513
	Site	2	2.236	0.116	0.175	0.840
	Site:Treatment	2	4.069	0.022	0.453	0.638
	Site:Temperature	2	7.013	0.002	0.884	0.419
	Temperature:Treatment	1	2.765	0.102	0.376	0.542
Shoots	Treatment	1	0.022	0.884	0.369	0.546
	Temperature	1	0.257	0.614	0.126	0.724
	Site	2	1.464	0.240	0.087	0.917
	Site:Treatment	2	3.943	0.025	0.935	0.399
	Site:Temperature	2	0.695	0.503	0.903	0.411
	Temperature:Treatment	1	0.080	0.779	0.011	0.916

Supplementary Table 2: Overview of statistical responses after model simplification for all response variables

Response	Treatment	DF	2016		2017	
			F	P	F	P
Stem diameter	Temperature	1	-	-	7.864	0.007
	Site	2	-	-	7.571	0.001
Shoots	Treatment	1	0.023	0.881	-	-
	Site	2	1.518	0.227	-	-
	Site:Treatment	2	4.089	0.021	-	-
Height	Treatment	1	1.706	0.196	5.840	0.018
	Temperature	1	0.112	0.739	-	-
	Site	2	2.175	0.122	-	-
	Site:Treatment	2	3.958	0.024	-	-
Dry mass	Site:Temperature	2	6.822	0.002	-	-
	Temperature	1	-	-	4.326	0.042
	Site	2	-	-	2.8555	0.06512
Leaves	Site:Temperature	2	-	-	6.334	0.003
	Treatment	1	42.745	1.13E-08	-	-
	Site	2	2.5805	0.08348	-	-
Grazed leaves	Site:Treatment	2	2.999	0.025	-	-
	Treatment	1	1.5266	0.221	-	-
	Temperature	1	-	-	2.229	0.140
	Site	2	10.868	8.32E-05	3.423	0.039
Grazed leaves	Site:Treatment	2	4.921	0.010	-	-
	Site:Temperature	2	-	-	3.954	0.024

Response	Treatment	DF	2016		2017	
			Dev	P	Dev	P
Total amount of flowers	Cover	1	-	-	-	2.04E-07
	Treatment	1	-	-	-	< 2.2E-16
	Temperature	1	-	-	-	0.035
	Site	2	-	-	-	0.436
	Treatment:Site	2	-	-	-	0.010

Supplementary Table 3: Monthly average temperature and precipitation values during both study periods from MET Norway⁶⁷

Date	Average temperature [°C]		Normal Temperaturen [°C]	Total precipitation [mm]		Normal precipitation [mm]
	2016	2017		2016	2017	
January	-5.6	-1.4	-5.2	169	133	154
February	-2.9	-1.5	-4.7	105	96	104
March	0.3	-0.4	-1.7	49	171	118
April	2.1	1.9	1.7	53	110	57
May	8.6	8.5	7.5	70	85	63
June	13.0	10.4	11.2	77	96	78
July	12.5	12.3	12.5	131	99	85
August	11.7	11.2	11.7	177	105	115
September	11.4	9.9	7.6	204	125	208
October	4.2	4.5	4.4	93	258	205
November	-1.4	-0.7	-0.7	140	284	178
December	1.0	-2.3	-3.1	313	253	178
Mean	4.6	4.4	3.4	-	-	-
Total	-	-	-	1582	1814	1543

⁶⁷ Temperature data collected from weather station “Sogndal Lufthamn” (located 479 masl on the mountain investigated in this study). Precipitation data is not available for the same location, and hence is listed for the weather station “Selseng” (app. 406 masl, 30km distanced from the study area). Normal temperature and precipitation are averaged over the period from 1961 – 1990.

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