

Contrasting effects from snow cover manipulation on two dwarf shrubs along an altitudinal gradient – an investigation on the phenology and performance of *Vaccinium myrtillus* and *Vaccinium vitis-idaea*



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Master Thesis in Climate Change Management

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Sogndal

June, 2019

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Contrasting effect from snow cover manipulation on two dwarf shrubs along an altitudinal gradient – an investigation on the phenology and performance of *Vaccinium myrtillus* and *Vaccinium vitis-idaea*

## Master thesis in Climate Change Management

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Thesis submitted: Spring 2019	Open thesis
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Keywords: Winter ecology, snow cover manipulation, <i>Vaccinium myrtillus</i> , <i>Vaccinium vitis-idaea</i> , climate gradient, phenology, performance, experimental ecology, blåbær, bilberry, tyttebær, lingonberry	Number of pages: 48 + Appendix: 2  Sogndal, 03.06, 2019 Place/Date/year
This thesis is a part of the master's program in Climate Change Management (Planlegging for klimaendringer) at the Department of Environmental Sciences, Faculty of Engineering and Science at the Western Norway University of Applied Sciences. The author(s) is responsible for the methods used, the results that are presented and the conclusions in the thesis.	



## Preface

This thesis is the final part of the Master in Climate Change Management degree, at the Department of Environmental Sciences at the Western Norway University of Applied Sciences (HVL), Sogndal during the spring 2019. The workload of this thesis corresponds to 30 ECTS.

My former background is weighted in physical geography and abiotic processes in the environment. This has motivated me to learn more about the biotic environment and the interactions between abiotic and biotic workings, in which I hope and believe this thesis has provided.

I sincerely wish to thank my supervisors Mark Gillespie and Stein Joar Hegland for their absolute efforts to help me through the different phases of this thesis; all the way from discussing the project design to the several reviews in the end stage. I also want to thank them for being friendly, not only professionally, but also in the social aspect.

I want to thank the class of 2019, due to the good class environment over the two years. The diversity in your backgrounds and knowledge has been invaluable during our discussions.

Lastly, I am grateful for the poor winter conditions which allowed for steady workflow without concerns about testing my new skis.

Sogndal, 03.06.2019

Dag Petter Talleraas Hollekim

## Abstract

*Vaccinium myrtillus* and *Vaccinium vitis-idaea* are key species in boreal ecosystems due to their abundance in biomass, flowering and berry production, yet we know little about how they are affected by ongoing climate change. Current knowledge suggests that snow cover extent and properties have and will change considerably with climate change. The principal objectives of this study were to investigate the effects from spring snow cover manipulation on phenology and performance of the early-flowering *Vaccinium myrtillus* and the later-flowering *Vaccinium vitis-idaea* along a climate gradient.

In order to investigate this, the snow cover was manipulated at three altitudes containing the study species at ca 150, 500 and 900m asl in Sogn, Western Norway in order to advance and delay snow melt timing. Snow was manipulated through shovelling, then followed observation of the phenophases, counting of flowers and berries as well as measurements of growth over the growth season of 2018.

Altitude was the main factor explaining phenophases for both species. Still, varied effects on phenology was found in *V. myrtillus* along the gradient. Phenology in this species was positively affected by snow melt delay at low altitudes, but not at higher altitudes. Combined effects between elevation and snow cover manipulation were not found in reproduction and growth, but snow melt advance negatively affected reproduction. *Vaccinium vitis-idaea* proved resilient to the snow cover manipulation, with only minor delay in flower formation.

The findings in this study suggests that the early-flowering *V. myrtillus* will be negatively affected by reduced snow cover at low altitudes in Western Norway, while *Vaccinium vitis-idaea* is likely to withstand future changes at all altitudes. Responses because of experimentally induced snow change were different between species and along the altitudinal gradient for *V. myrtillus*. With this, the understanding of dwarf shrubs has increased ever so slightly.

## Sammendrag

*Vaccinium myrtillus* (blåbærlyng) og *Vaccinium vitis-idaea* (Tyttebærlyng) er viktige arter i det boreale økosystemet grunnet deres mengde i biomasse, blomstring og bærproduksjon, men vi vet lite om hvordan de påvirkes fra pågående klimaendringene. Nåværende kunnskap tyder på at omfanget og egenskaper ved snø vil forandre seg betydelig med klimaendringene. Hovedformålene med denne studien var å undersøke effekten av manipulering av snø på fenologi og ytelse på *Vaccinium myrtillus* og *Vaccinium vitis-idaea* langs en klimagradient.

For å undersøke dette ble snø manipulert ved tre høyder som inneholdt undersøkelsesartene mellom på ca 150, 500 og 900moh i Sogn på Vestlandet for å fremme og forsinke vårmeltingen. Snø ble manipulert gjennom graving, deretter ble observasjon av fenologi, telling av blomster og bær, samt målinger på vekst utført i vekstsesongen 2018.

Høydegradient er den dominerende forklaringen på tidspunkt for ulike fenofaser hos begge arter. Likevel ble varierende effekter på fenologi funnet i *V. myrtillus* langs gradienten. Fenologi i denne arten ble positivt påvirket av forsinket vårmelting i nedre sjiktet av studieområdet, men ikke på 500 og 900moh. Kombinert effekt mellom høyde og snømanipulasjon ble ikke funnet i reproduksjon og vekst. Likevel, tidlig vårmelting har negativt påvirket reproduksjonskapasiteten. *Vaccinium vitis-idaea* viste seg generelt å være motstandsdyktig til manipulering av tidspunkt for vårmelting.

Funnene i denne studien antyder at *V. myrtillus* vil bli negativt påvirket av redusert snømengde ved lave høydedrag i Vest-Norge, mens *V. vitis-idaea* sannsynligvis vil tåle fremtidige endringer i alle høyder. Med dette forstår vi litt mer om hvordan dverglyngbusker responderer på eksperimentelt manipulert tidspunkt for vårmelting. Studieartene uttrykte ulik respons til manipulasjonen, samtidig viste *V. myrtillus* ulik respons langs høydegradienten.

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## 1. Introduction

Climate change has affected ecosystems across the world in several ways (Hughes, 2000; Parmesan, 2006). Increasing levels of CO<sub>2</sub> and temperatures can increase growth (Hannah, 2014), advance phenology (Parmesan, 2006) but also lead to detrimental stress in plants (Gimenez-Benavides et al., 2007; Hannah, 2014; Inouye, 2008). While much work has been focussed on changing climates during the growth season, less effort is given to understanding winter ecology (Kreyling, 2010). Climate change affects the wind and precipitation patterns at increasing rates towards the extreme latitudes of both hemispheres (Serreze & Barry, 2011), which ultimately is affecting the winter climate (Eckerstorfer & Christiansen, 2011; Marty, 2008). Reduced albedo and glacier shrinkage can further lead to negative feedback loops beyond current understanding of these abiotic processes (Nesje et al., 2008; Serreze & Barry, 2011). The timing and nature of winter and spring processes could be crucial to the performance of many plant species, particularly in growth, reproduction and phenology (Kreyling, 2010), still knowledge about species- and site-specific response are lacking. This study addresses this issue by investigating the effect of manipulating spring snow melt timing on *Vaccinium myrtillus* and *Vaccinium vitis-idaea* along an altitudinal gradient in Western Norway.

Snow is an important environmental driver as it decouples ground temperatures from the atmospheric temperatures (Sturm et al., 1997). Consequently; the freezing depth is shallower in areas with abundant snow. Conversely, thin snow cover allows further cooling of the ground, which can be reduced by several degrees (Kreyling et al., 2012). This has been coined '*Colder soils in a warmer world*' (Kreyling, 2010). With changes in winter snow cover, plants could start dehardening before spring and become more vulnerable to frost (Gerdol et al., 2013; Wipf et al., 2009). This can further lead to changes in ground temperatures during winter and spring which could lead to frost damage (Palacio et al., 2015), as well changes in nutrient cycling in the soil (Bombonato & Gerdol, 2012; Gavazov et al., 2017). Furthermore, snow cover absorbs and collects nutrients and minerals, which during spring melt can be paramount for the early photosynthesis of plants (Rosbakh et al., 2017). Snow can also be an important environmental factor driving phenology (Wipf & Rixen, 2010), growth (Gerdol et al., 2013; Kreyling et al., 2012), reproductive success (Selås, 2000; Wipf et al., 2009) and species composition (Rixen et al., 2010; Rosbakh et al., 2017) of plants in areas with seasonal snow regimes such as the boreal to arctic ecosystems.

Norway is a country in which changes in snow cover extent have, and will change, following climate change (Saloranta & Andersen, 2018). Norway is expected to become warmer and wetter, but also drier in some periods (Hanssen-Bauer I. et al., 2016), due to increased evapotranspiration and prolonged

summer durations (Hannah, 2014; Hanssen-Bauer I. et al., 2016). The total snow cover extent has decreased by 0.8% per decade in the northern hemisphere since 1900 with an increasing rate during the later decades (Vaughan et al., 2013). Models on seasonal snow distribution further predict that there will be a mean reduction of snow thickness of 100cm at 1000-1100m asl mid-winter in Western Norway in 2100. Furthermore, the snow line in Norway is projected to be 300m higher than 1971-2000 levels in 2100 (Saloranta & Andersen, 2018). Similar patterns have been found in other alpine regions. For example, an analysis on the number of snow days in the Swiss alps found a significant reduction after 1988 (Marty, 2008), as in low-pressure systems enter the mountain range more often precipitates as rain, compared to as snow. The same study argues that low-pressure systems are more variable after the late 1980s compared to prior. This is often not caught by snow models as parameters in atmospheric conditions are complicated and often averaged out, creating a great deal of uncertainty in predictions of whether future precipitation will fall as rain or snow (Saloranta & Andersen, 2018; Hanssen-Bauer I. et al., 2016). This notion is further projected in Norway as models on climate project an increase of winter rainfall of 10% by 2100 (Hanssen-Bauer I. et al., 2016). However, data collection over the last 100 years have found great variation in trends on snow distribution in Norway both in area and altitude (Hanssen-Bauer I. et al., 2016).

The uncertainty of future snow regimes in boreal to arctic ecosystems is further complicated by conflicting species responses to different snow conditions (Cooper, 2014; Prevey et al., 2019; Rosbakh et al., 2017; Wipf & Rixen, 2010). The snow cover properties during different parts of the winter has been found to affect multiple aspects of plants in the arctic (Cooper, 2014). Changes in the winter climate, such as thin snow cover or rain on snow events can halt the acclimatisation needed to endure cold temperatures and reduce frost damage (Inouye, 2008; Wipf & Rixen, 2010). At the same time, berry and seed development may see a positive effect from prolonged autumns (Cooper, 2014). With climate change, it has been suggested that earlier snow melt promotes earlier emergence of many plant species, but, there are differences in reaction to warming within early- and late-flowering species (Hegland et al., 2009; Prevey et al., 2019; Wipf & Rixen, 2010). In addition, plants which rely on pollination by insects are found to be more sensitive to increasing temperatures, compared to wind-pollinated plants (Hegland et al., 2009). In interactions between trophic levels, such change in phenology can develop into phenological mismatches. An asynchrony in the coordination of phenological events between interacting species could lead to negative fitness in both actors (Parmesan, 2006). For instance, if the flowering of *Vaccinium myrtillus* occurs earlier than bumblebee queens appear during spring, *V. myrtillus* will have reductions in pollination, and the bumblebee can have reduced availability of fodder (Hegland et al.,

2009; Hughes, 2000). Spring conditions are suggested to be important as snow melt timing, soil water content and nutrient flux may affect the phenology and performance of plants (Gimenez-Benavides et al., 2007; Inouye, 2008; Wipf & Rixen, 2010). Additionally, the susceptibility of frost damage during early spring may be increased with changes in the snow pack properties (Inouye, 2008; Wheeler et al., 2016).

There are several studies that attempt to generalise how plants respond to changes in snow cover. Studies have generalised plants by their functional traits (Rosbakh et al., 2017), early versus late flowering (Prevey et al., 2019) as well as by family (Wipf & Rixen, 2010). Different ways of generalising have achieved different levels of success. An attempt to generalise effects on plants, could lead to increased knowledge about which abiotic processes are beneficial and/or negative to plant phenology and performance, such as in which species or groups are winners and losers regarding decreased snow cover durations. However, it can also average out and hide the effect on single species. Nevertheless, generalisation is necessary as it is not possible to study all species in every way over all time periods. Wipf and Rixen clearly advocate the need for more studies, as few studies address both phenology and performance at the same time, potentially impeding a more holistic understanding (Wipf & Rixen, 2010). Dwarf shrubs are the family which has been the least studied in phenology and performance in regard to snow cover change (Wipf & Rixen, 2010). Hence, there are varied understandings of what environmental cues control phenology and performance of this group, yet they include key species in the boreal forest ecosystems, such as *Vaccinium myrtillus* and *Vaccinium vitis-idaea* (Grime et al., 1989).

### 1.1. Background

One way to gain better understanding on the effects on winter ecology is to physically manipulate the parameters that are thought to affect a plant community. Snow manipulation studies are performed in various ways including snow fences and manual labour (Cooper, 2014; Wipf & Rixen, 2010). Snow fences built perpendicular to the dominating wind direction will accumulate snow behind them, which could delay snow melt by two weeks later than control plots (Cooper et al., 2011). One study using fences put up 30 years earlier, found that there was a community change in front and behind the fence, with *V. myrtillus* having a preference downslope with increased snow thickness (Rixen et al., 2010). Generally, delayed snow melt as in deeper snow increases growth of *V. myrtillus* and snow melt advance as in shallower snow pack was found to decrease the growth of the plant (Rixen et al., 2010; Wipf & Rixen, 2010). However, particularly warm growth seasons exhibit increased growth of this species in higher altitudes in both snow melt delay and -advance plots (Rixen et al., 2010). By comparing *V. myrtillus* growth rings at higher and lower altitudes, Rixen et al (2010) found that growth rings were generally

wider at lower altitude during more normal summers regarding temperature and precipitation. The study found a threshold at their study area where summer mean temperatures above 9°C lead to increased growth at early snowmelt plots at high elevations, but not low (Rixen et al., 2010). They further argue that this discrepancy is due to drought at their lower site.

Studies which manually manipulate snow are often performed over fewer years and are therefore not as good at long term changes, but it can provide more nuanced information on the direct factors which affects phenology and performance. One study doing this found significant reduction in flower abundance in *V. myrtillus* by reducing the snow cover by 40cm in 9 1,5m<sup>2</sup> plots, while supporting the findings of Rixen et al regarding growth (2010; Gerdol et al., 2013). Another study which added and removed snow found no differences in phenology due to the manipulations in *V. vitis-idaea*, but did see an advance in phenology and increased flower abundance in *V. myrtillus* (Saarinen et al., 2016)

There is not a strong confidence in our understanding of dwarf shrub phenology (Wipf & Rixen, 2010), as there seems to be great differences between species in their sensitivity to snow cover manipulation (Saarinen et al., 2016; Wipf & Rixen, 2010). Phenology has been suggested to be affected by snow cover manipulation. Snow melt delay promotes earlier phenophase initiation, and snow melt advance promotes later phenophase initiation in *V. myrtillus* (Saarinen et al., 2016). *Vaccinium myrtillus* is suggested to be more sensitive, compared to *V. vitis-idaea* (Saarinen et al., 2016), contrary to earlier meta-analysis performed by Wipf and Rixen (2010) which advocates that evergreen shrubs are more sensitive to snow manipulation than deciduous dwarf shrubs.

Most studies have not found any effect from snow cover manipulations in *V. vitis-idaea* (Saarinen et al., 2016; Wipf & Rixen, 2010), except by Blume-Werry et al. (2016) and Wipf et al. (2006). Blume-Werry et al. (2016) found a decrease in shoot growth from short term snow removal, but an increase in shoot growth from long term snow removal (11 years) compared to control plots, yet the root system was significantly reduced long term (Blume-Werry et al., 2016). While Wipf et al. (2006) found that early phenophases was affected by snow cover manipulation, that effect diminished in later phenophases (Wipf et al., 2006). This makes comparing the more sensitive *V. myrtillus* with *V. vitis-idaea* potentially interesting as they so far have shown quite different reactions to similar experiments.

Most studies that look at the potential effects of snow cover manipulation do so at small scales. Several studies only look at the timberline (Wipf et al., 2006; Wipf et al., 2009), others are in the flat forests of Northern Sweden (Blume-Werry et al., 2016; Kreyling et al., 2012), and some investigate the upper niche periphery in the alps (Gerdol et al., 2013; Rixen et al., 2010). One exception is Selås (2000), who looked

at berry harvesting of bilberries in Norway. His study found that mild winters with deep snow cover generally leads to increased berry yield in *V. myrtillus*. Though such studies highlight overall reproductive success in *V. myrtillus*, any variation in species range remain elusive. Studies which look at these effects in the full temporal niche of dwarf shrubs have not been found.

Altitudinal gradients are great natural laboratories for ecological studies (Korner, 2007), as they naturally govern certain physical parameters, such as precipitation, temperature and atmospheric pressure. They can also contain the full temporal niche of a species over short distances (Wipf, 2010). Even still, there are few studies which address the full species ranges (Parmesan, 2006), which is understandable as it is laborious. Investigations focussing on species ranges are perhaps done most efficiently through meta-analyses such as Wipf and Rixen (2010) and Prevey et al (2018). For such analyses to prove fruitful, there must be data of high quality, as well as adequate sample pools to perform statistical analyses.

There are conflicting results which could be due to the variation in study areas. Different regions have different snow climates, which could have an impact on how local species tolerate variable snow cover properties. To know this, more studies in a wide range of places are needed. This study on *Vaccinium myrtillus* and *Vaccinium vitis-idaea*, manipulates the spring snow cover by both adding and removing snow across a climate gradient in Western Norway and measures whether there are changes in phenology and performance linked to these treatments. This is the first attempt to conduct a snow cover manipulation study along an altitudinal gradient, aiming to address the range of fitness responses across the niche of two key dwarf shrub species.

## 1.2. Research question

How will experimentally manipulated snow cover affect the performance and phenology of *V. myrtillus* and *V. vitis-idaea* along an elevational gradient?

## 1.3. Hypotheses

I hypothesised that the elevational gradient will have a strong positive effect on phenological variables from low to high elevation as this reflects a climate gradient and spans a wide temperature range. Performance, as in the growth and reproductive capacity, will be highest at mid-montane elevation as I assume that this is close to the climatic optimum of the study species locally as found on *Vaccinium myrtillus* (Berge, 2018; Moen & Lillethun, 1999), while *Vaccinium vitis-idaea* is thought to have a slightly higher optimum in altitude (Wischmann et al., 1986).

Snow cover manipulation is likely to give within-site effects on phenology and performance, with responses impacted by the snow melt gradient as in removal-control and addition of snow. This effect is expected to be greater at the ends of the species range where conditions are thought to be more limiting than at the optimum.

*Vaccinium myrtillus* is an early-flowering species as well as more sensitive to change and is therefore expected to reveal a more prominent effect from snow cover manipulation than *V. vitis-idaea*, which emerges later. This sensitivity is expected to be reflected in particular during the early stages of growth, as in phenological traits.

## 2. Methods

### 2.1 Study area

The study area is situated at Kaupangerhalvøya to the southwest of Kaupanger, Western Norway (61,2°N, 007,2°E, Fig. 1). Three sites were selected which face south to south east and represent three different elevations in which both *V. myrtillus* and *V. vitis-idaea* occur. They are at 100-150 m asl, 450-500m asl as well as 850-900m asl. The two lower sites, namely Low site and Medium Site are found within forestry clearings in a boreal mixed forest. High Site is in the tree line, above the timberline.

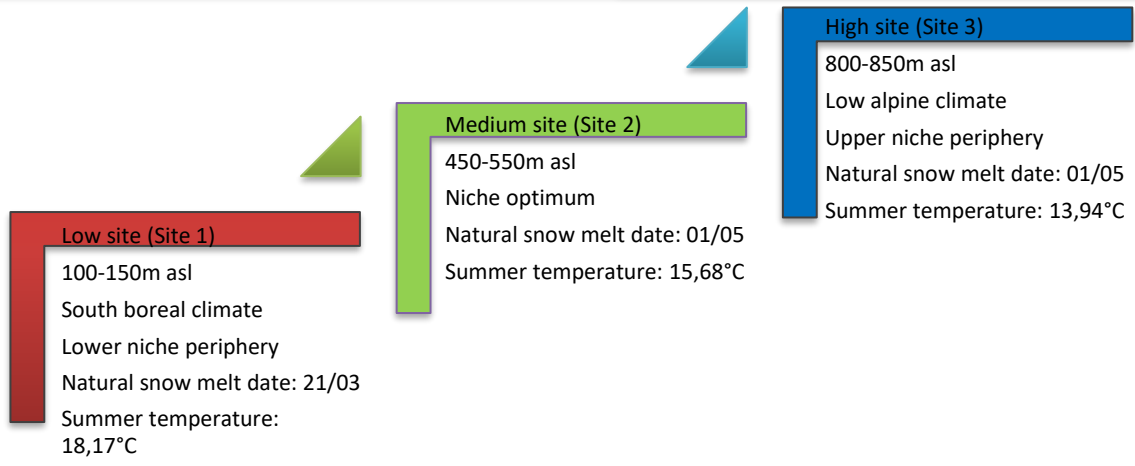
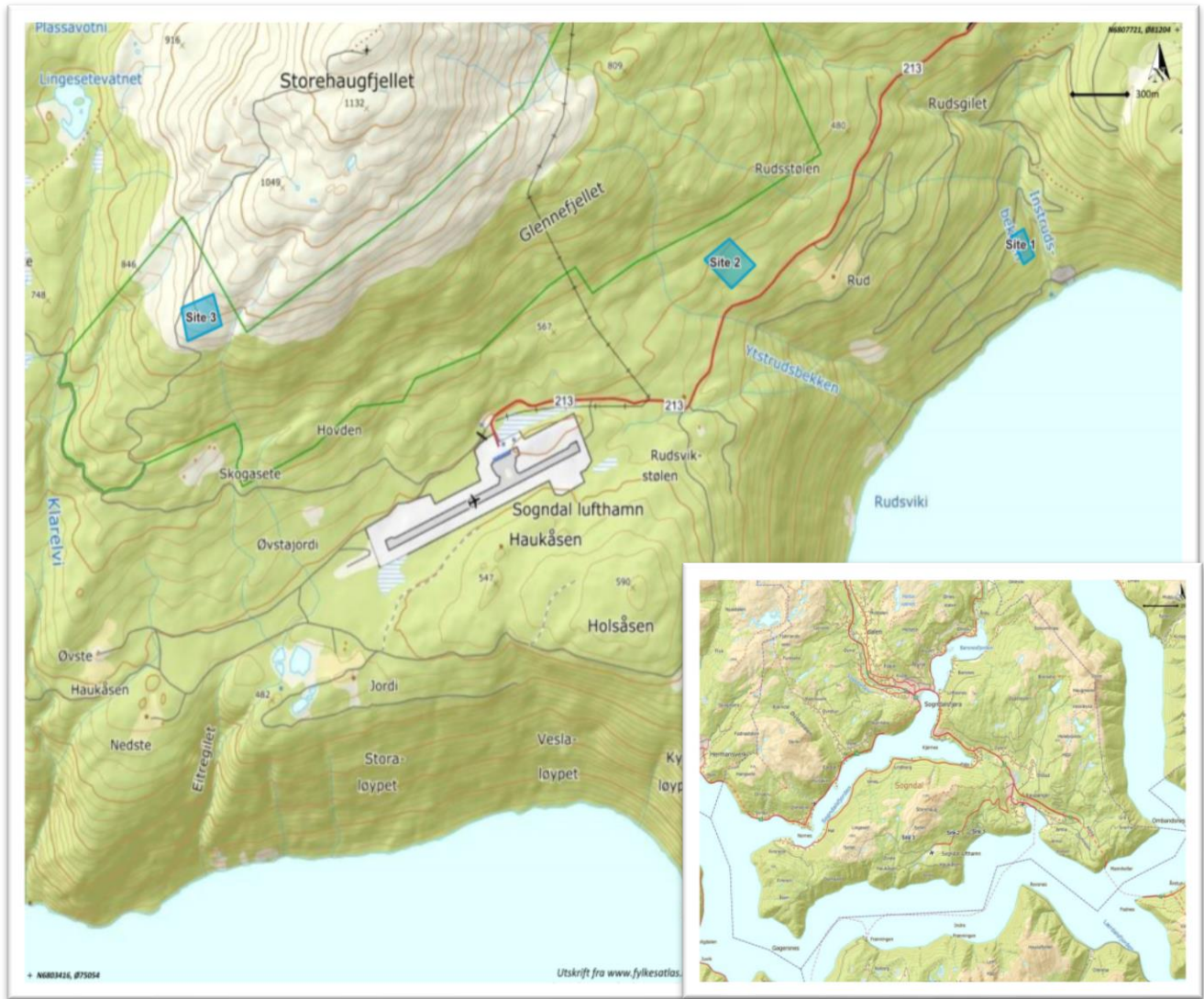
Western Norway features steep mountains and great elevational changes. This can serve as a laboratory with natural changes in temperatures, precipitation rates and atmospheric pressure and further the winter- and spring onset (Korner, 2007). This allows for many vegetational zones over short distances. Kaupangerhalvøya is within the oceanic transitional zone and is dominated by a mixed pine and deciduous forest with peatlands. The position of Haukåsen gives it a climatic gradient with four zones from south boreal to low alpine zone (Moen & Lillethun, 1999).

This study was conducted in the growth season of 2018, which was an abnormal year in Norway in terms of temperatures and precipitation. The spring was cold, with three cold spells in March (met.no, see fig. 2). After these cold spells, a warm spring followed. The warmest day ever recorded in both May and July was updated in 2018, and May was 4,5°C (12,5°C) warmer than the climatic norm (8°C) (met.no). June was less warm, and closer to the climatic norm. July however was again 4°C(16°C) warmer than the norm (12°C). These abrupt transitions between the seasons could lead to odd responses. The closest weather station with a precipitation gauge to the study site is at Selseng in the innermost parts of Sogndalsdalen and the magnitudes of precipitation does not represent Haukåsen well, because this station is 30km away from the study site. Interpolated data from climate models estimates average annual precipitation to be 1157mm (met.no).

Western Norway has a maritime/transitional snow climate (Schaerer & McClung, 2006). A maritime snow climate is characterised by mild winters with heavy snow falls. This leads to deep snow packs, while both rain on snow-events and arctic cold spells are common (Schaerer & McClung, 2006). The Low site is

*Table 1: Snow depth 1/3/18 to illustrate the differences. Data is collected from senorge.no which is based on observations together with interpolations (senorge.no).*

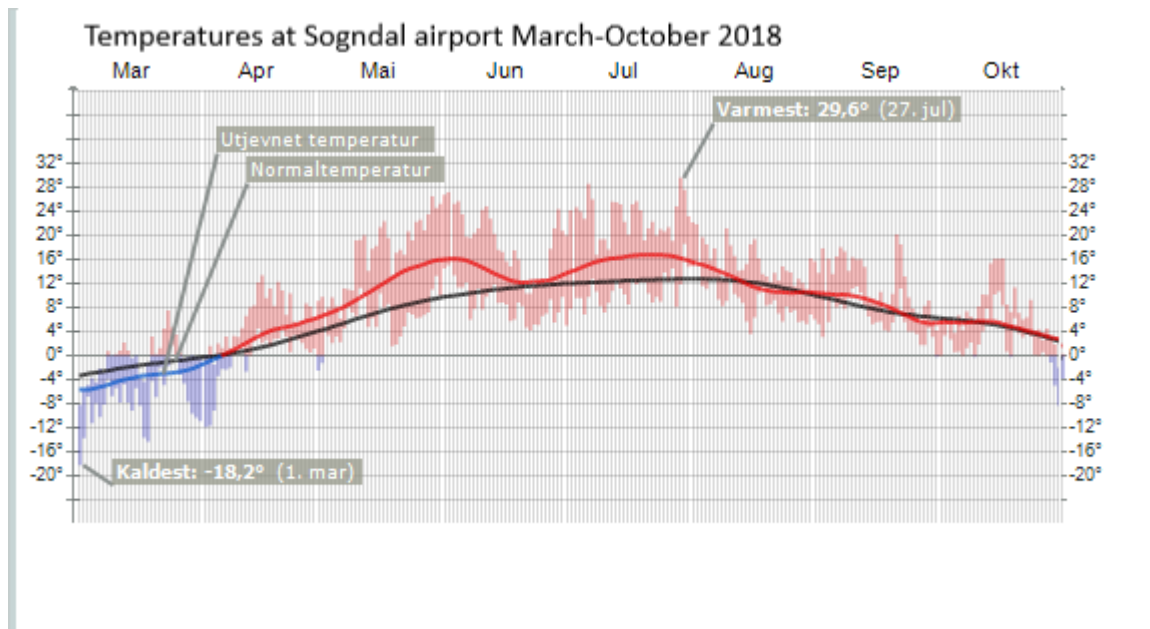
<b>Snow depths 01/03/18</b>	
<b>Low site</b>	<25 cm
<b>Medium Site</b>	50-100 cm
<b>High Site</b>	100-150 cm



**Figure 1:** Storhaugen in Kaupanger – The study area in this project. The blue squares are the study sites. Below the map is an overview of the study area with key environmental information. The natural snow melt date is the date which the control plots melted out in 2018. The summer temperature is the average ground temperature between May and August in 2018, temperature was logged every two hours.



situated in a snow poor environment as it is close to the fjord and have particularly mild temperatures throughout the winter. Higher altitudes are generally colder, with a gradient of snow accumulation upslope (See table 1).



**Figure 2:** Temperatures at Haukåsen airport over the growth season 2018 (met.no). Blue is below 0°C and red is above 0°C. The black line is the climatic norm, and the blue/red line is the running mean temperature. This weather station is to the west of Medium site, at approximately same elevation.

## 2.2 Study species

*Vaccinium myrtillus* and *V. vitis-idaea* are long-lived, slow growing and woody species, and prefer areas with deep snow packs for protection from frost (Grime et al., 1989). They can reproduce through both clonal and sexual reproduction (J. C. Ritchie, 1956). The stems are therefore called ramets, as a stem infer that it is a single specimen, which is not necessarily the case for *V vitis-idaea* and *V. myrtillus*, as they can be connected by root systems for several metres. *Vaccinium myrtillus* is a taller species (10-60cm), while *V. vitis-idaea* generally grows to 10-30cm height (J. C. Ritchie, 1955; J. C. Ritchie, 1956). *Vaccinium vitis-idaea* is often found to develop an understory below *V. myrtillus* (Grime et al., 1989).

Both *Vaccinium myrtillus* and *Vaccinium vitis-idaea* are dwarf shrubs with boreal to alpine distribution. They are both abundant in the cold regions of the northern hemisphere, including the sub-arctic and boreal zone (Gerdol et al., 2013). In Norway specifically, *V. myrtillus* and *V. vitis-idaea* are found to thrive up to the low-alpine zone with some populations extending to the mid-alpine zone (Moen & Lillethun, 1999). They are both found to be generally stress-tolerant species, however *V. myrtillus* is more frost sensitive and its distribution has been found to be dependent on protection from snow cover (Grime et

al., 1989; Palacio et al., 2015). *Vaccinium vitis-idaea* can withstand temperatures down to  $-25,1^{\circ}\text{C}$  and *V. myrtillus* can withstand temperatures down to  $-14^{\circ}\text{C}$  (Palacio et al., 2015). These data are suggested to be maximum tolerance and would be lower after dehardening, which normally occurs during early spring for most species.

*Vaccinium myrtillus* is one of the most common plants in Norway, and can be found within altitudes from 0 and up to 1700m asl in Jotunheimen (Wischmann et al., 1986). It is a deciduous plant with evergreen stems and is considered an early-flowering plant (Wischmann et al., 1986). New shoot growth commences in spring, and flowers normally develop in May, which further becomes berries in July-August. *Vaccinium vitis-idaea* is relatively common and can be found up to 1800m asl in Norway (Wischmann et al., 1986). It develops flowers from late May. *Vaccinium vitis-idaea's* morphology is tougher and thus more resistant to browsing compared to *V. myrtillus* (Wischmann et al., 1986).

*Vaccinium myrtillus* has been found to have its niche optimum at 450-550 m asl in a study area close to Haukåsen (Berge, 2018; Moen & Lillethun, 1999). Low, Medium and High sites are the boundaries and the optimum for growth in *V. myrtillus* locally (Berge, 2018). It is suggested that the altitudinal range of *V. vitis-idaea* is similar, with its optimum at slightly higher altitudes (Wischmann et al., 1986).

### 2.3 Experimental design

At each site, the design was planned to contain 6 blocks of three plots each; snow addition, snow control and snow removal plots (see fig. 3). This structure was intended to be the same at all three sites, resulting in a total of 18 blocks. I ended up establishing 5 blocks at Low site, 6 blocks at Medium site and 4 blocks at High site.

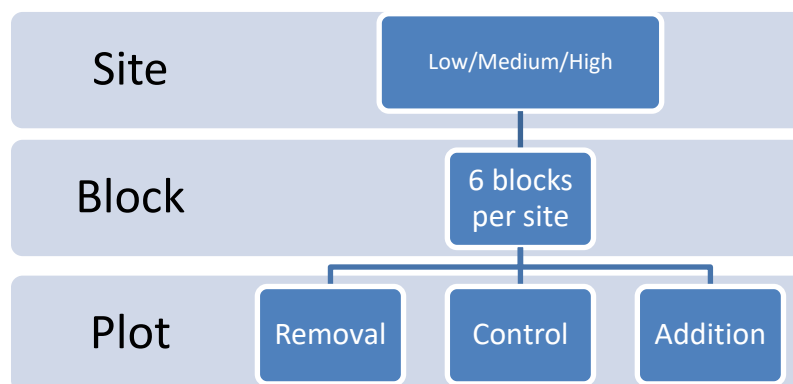


Figure 3: Schematic of the Site, Block and Plot structure of the study design

Plots within blocks were allotted and marked during the late autumn at Low site and Medium site. Selection criteria were that the microtopography and aspect should be similar to each other, and that there was an abundance of both species at the plots. Removal plots were always located above or besides the addition plot to make sure that the additional snow did not affect the removal plot during spring melt by increasing humidity for instance. The centre of plots was > 4 m away from of each other, to ensure that ramets were not likely to be related. Root systems are assumed to be no longer than 200cm long (Flower-Ellis, 1971). The treatment plots were positioned to the east of the control plot as far as possible while still ensuring other restrictions being fulfilled. The addition- and removal plots were allocated during autumn 2017 at Low site and Medium site. During this day it snowed heavily and an attempt to establish plots at High site was aborted. I used control plots which are already established within another project (Gillespie and Hegland, unpublished data).

All blocks at Low and Medium site had 3 plots each with *V. myrtillus* and *V. vitis-idaea*. High site had a total of 4 addition plots, 3 removal plots and 4 control plots with *V. myrtillus* and 2 addition plots, 1 removal plot and 4 control plots containing *V. vitis-idaea*. The plots at High site was allotted at the same time as snow manipulation was performed. Due to the early snowfall in autumn 2017, it was not possible to assign these before winter. Using an avalanche probe to feel for hard vs soft ground during spring was not found to be an advisable method to select plots containing dwarf shrubs. During spring, snow was shovelled off and onto designated spots selected in November (See fig. 4 for visualisation of addition plots). In accordance with suggested best practice, the snow manipulation was performed with a blunt shovel to reduce potential damage on vegetation (Wipf & Rixen, 2010). Average snow cover thickness in centimetres on a site level before and after snow cover manipulation is shown in table 2. Each plot was approximately 1,5m<sup>2</sup>.

Low site was manipulated on the 20<sup>th</sup> of February. Due to the lack of snow currently, the two lower blocks did not contain enough snow to perform manipulations. One more block was added, and the low site contained 5 blocks. Due to varied snow depths within the sites combined with time constraints, manipulations were performed over two days at Medium site and High site. One block at High site was not found during the second day of digging and was left out. A new block was not established in fear of damaging already established plots.

A frame of 0,5m<sup>2</sup> was positioned at the centre of the plots shortly after snow melt. This frame confined the future area of data collection. A plastic stick was inserted into the soil at the corner of an inner square compiled of the four inner cubes at all plots (See figure 5). The closest ramet to each stick of both *V. myrtillus* and *V. vitis-idaea* which was between 5-25cm tall was chosen. These four ramets of each species were the targets for observations on phenological development and growth measurements. The

**Table 2:** Date and snow depth of snow cover manipulations. Due to difference in snow, some blocks were manipulated on a second day. The date of snow melt of addition plots at high site was not recorded. The dates of snow melt are presented in Julian dates, meaning day 1 is 01/01/xxxx.

Site/date	Plot	Average depth (cm)	Average snow melt date
<b>Low site</b>	Control plots	14,6	81
	<b>20/02/18</b> Removal plots	4,9	78,4
	Addition plots	42,5	87
<b>Medium site</b>	Control plots	41,6	121,5
	<b>17/04/18</b> Removal plots	9,5	118
	<b>23/04/18</b> Addition plots	103,8	126,67
<b>High site</b>	Control plots	30,5	121,4
	<b>19/04/18</b> Removal plots	11,5	117
	<b>27/04/18</b> Addition plots	110,6	



**Figure 4:** Shows a snow addition plot at Medium site. The stick was used as reference point after snow melt.

selected ramets were marked with a bead of specific colour. For reproductive variables, the whole area within the frame was used.

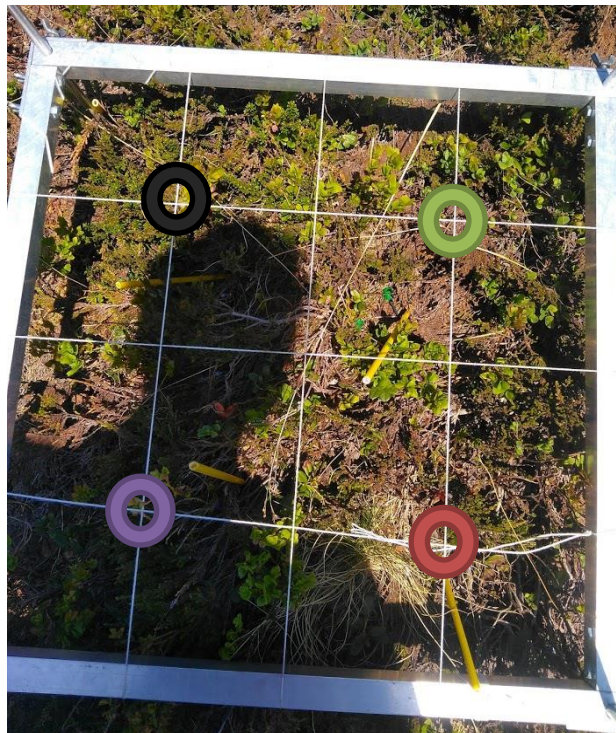
## 2.4 Data collection

All beaded ramets of both *V. myrtillus* and *V. vitis-idaea* were monitored twice per week. On these ramets, the progression of phenophases were recorded. Selected stages were budburst and shoot elongation for vegetative phenology, and date of first flower and first berry within the frame.

Budburst was defined as the day that the first bud started opening. The day that the first shoot began extending from the bud became the day of shoot elongation. The day that the first flower in the plot opened up, meaning that nectar could be extracted by pollinators is the day of first flower. The day of which the first berry in the plot was ripe, became the variable First berry. The berry was deemed ripe when it had acquired a strong blue colour and fully bulged for *V. myrtillus* and had a bright red colour of the whole berry in *V. vitis-idaea*. Data on phenology was collected on plot level, except budburst and shoot elongation.

Reproductive capacity was measured at the plot level as abundance of flowers and berries divided per unit cover. Dividing the abundance by cover serves to standardise the results. Cover was used as a proxy

**Figure 5:** The frame used to confine the study plot and select ramets. It was also used as a boundary when counting flowers and berries.



for abundance of ramets and was measured by observing the amount of cover occupied by either *V. myrtillus* or *V. vitis-idaea* within the plot. The frame which has 16 squares was used to estimate the amount of cover as a percentage. They were measured on plot level instead of ramet level because of the uncertainty of getting flowers and berries on the targeted ramets.

*Vaccinium vitis-idaea* produces inflorescences, thus each single flower was not counted. Rather, the number of inflorescences per plot was counted and then the number of flowers on three random clusters were counted. The average number of flowers per inflorescence was calculated from these three inflorescences and then multiplied by the number of inflorescences to estimate a plot total number of flowers. The day of first flower – the day of last flower was used as the response variable flowering period and berry to flower ratio was found by dividing the maximum number of berries over flowers. When the target species started producing ripe berries, I counted all the ripe berries within the plot. The day of highest abundance of berries became the data point of peak berries.

Caution advised regarding budburst and first berry for *V. myrtillus*. Budburst was observed before the snow had fully melted and can in some cases be off by several days between actual budburst and recorded budburst. The model on first berry has its assumptions broken. The results are however supported by other models using ranked data.

Growth was modelled by using a non-destructive biomass index (Hegland et al., 2010). Measurements were done twice, and the biomass calculated for both times. Data first was collected after all phenophases had initiated, and the second measurement was done during the end of the growth season (See table 3). The relative change from measurement 2-measurement 1 is the change of biomass, which has been used for analysis.

900 ramets of *V. myrtillus* were collected at Svanøy and several parameters were measured for each ramet, including height, stem diameter and number of shoots (Hegland et al., 2010). These ramets were then dried and weighed. The importance of these explanatory variables were tested against dry weight using linear models to derive a non-destructive model of dry mass for future measurements (Hegland et al., 2010). During measurements of my ramets, the measurement of stem diameter proved

untrustworthy. There were difficulties measuring the stem at the same point during the second measurement, as more vegetation had developed, such as grasses and mosses. Additionally, the digital calliper malfunctioned during the second measurement round. The Hegland et al. (2010) models were therefore re-run without stem diameter to derive a dry mass model consisting of only height and number of shoots (Formula 1, M Gillespie, unpublished).

**Table 3:** Dates of growth measurements used in the non-destructive biomass index

Growth measurements	Measurement 1	Measurement 2
Low Site	24.05.18	09.08.18
Medium Site	28.05.18	09.08.18
High Site	07.06.18	14.08.18 and 18.08.18

It did not reduce the R coefficient of the model considerably (0.94 vs 0.88), and the variable was left out of the model. Therefore, during the field season of 2018, total height from the ground was measured for each marked ramet, and the number of shoots were counted, and this data was used to estimate dry mass using the Formula 1.

For *V. vitis-idaea*, 165 ramets were collected at the three study sites in 2016, measured and weighed in a similar manner to the *V. myrtillus* (Rydgren, K., unpublished). Crown diameter 1 was the widest part of the canopy of a ramet, and crown diameter 2 was the diameter measured perpendicular to crown diameter 1. Number of shoots is how many branches each ramet had, and height is the total height from ground level. This model was parameterised by M. Gillespie and explained 83% of the variation in the biomass (Formel 2). In both cases, the change in biomass was calculated as the biomass from measurement 2 divided by the biomass from measurement 1. Therefore, a change measurement of 1 indicates no growth, below 1 indicates reduced biomass and above 1 indicates growth.

$$\text{Log}_2(DM) = 0,58 \times \text{Log}_2(\text{Number of shoots}) + 1,57 \times \text{Log}_2(\text{Height}) - 8,62$$

**Formula 1:** Equation for non-destructive biomass index for *V. myrtillus*

$$\text{Log}_2(DM) = 3.19 \times \text{log}_2(\text{Crown diameter 1}) + 0.42 \times \text{log}_2(\text{crown diameter 2}) + 2.55 \times \text{log}_2(\text{Height}) + 0.67 \times \text{log}_2(\text{number of shoots}) - 0.37 \times \text{log}_2(\text{crown diameter 1}) \times \text{log}_2(\text{Height}) - 24.98$$

**Formula 2:** Equation for non-destructive biomass index for *V. vitis-idaea*

## 2.5 Data analysis

Ramet level data was averaged to one data point per plot as we are interested in the overall effect per plot. There are interdependency issues in analysing single ramets, as they may be part of the same specimen and can possibly influence each other, resulting in pseudo-replication. The data collection gave data on ramet level and plot level and elevational level, tested as "Site". The pseudo-replication could have been dealt with through nested random effects but was accounted for through averaging out the ramet level information up to plot level for ease of interpretation.

Analysis was done using linear mixed models with R (R Core Team, 2017) with the Lme4 (D. Bates et al., 2015) and Nlme packages (Pinheiro et al., 2019). Linear mixed models can further account for the independence issues. A linear mixed model consists of a response variable, together with fixed and random effects. Site and Treatment were the fixed effects. Site:Block were random effects included to account for pseudo-replication. A typical model Model1 =  $Y \sim (X_1 * X_2) + (1 | \text{Site:Block})$ . where Y is the response which is tested, and  $X_n$  is the fixed explanatory variables. Multiplying the explanatory variables allow for an interaction between the explanatory variables' effect on the response variable, as well as their individual effects. If an explanatory variable was insignificant and did little explanation in the model, it was dropped as a form of model simplification. The most complicated variable, interaction was dropped first.

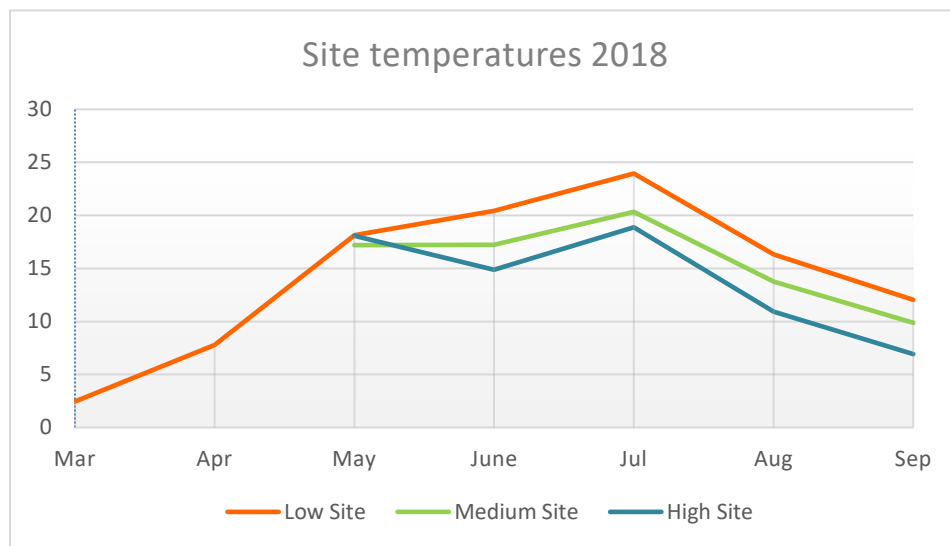
There are two main assumptions within linear mixed models. Residuals needs to be normally distributed, and they need to have equal variation. This was checked visually, and when in doubt the Fligner-Killeen test was used to check for homogeneity of variances and Shapiro-Wilk test was used to check for normality in residuals. If these assumptions are not met, the model can give false results and the model is prone to type I error, as in the alternative hypothesis is accepted as significant when in reality it is not. In cases where models were invalid, problem sources such as outliers were identified and removed, or a variation such as the varIdent function in NLME models (Pinheiro et al., 2019) was attempted until a valid model was acquired. If it was not possible to derive a valid mixed model, the non-parametric equivalent ARTool (Wobbrock et al., 2011) was used to ensure the results were comparable. If this gave similar results, then the original model was deemed robust regarding the assumption criteria not being met. ARTool is a nonparametric analysis on factors, similar to the better known Kruskal-Wallis test. However it can test multiple explanatory variables together including interactive and random effects (Wobbrock et al., 2011). As ARTool is a ranked-based test, it does not provide a degree of change, only whether there is change or not.



## 3. Results

### 3.1 Abiotic data

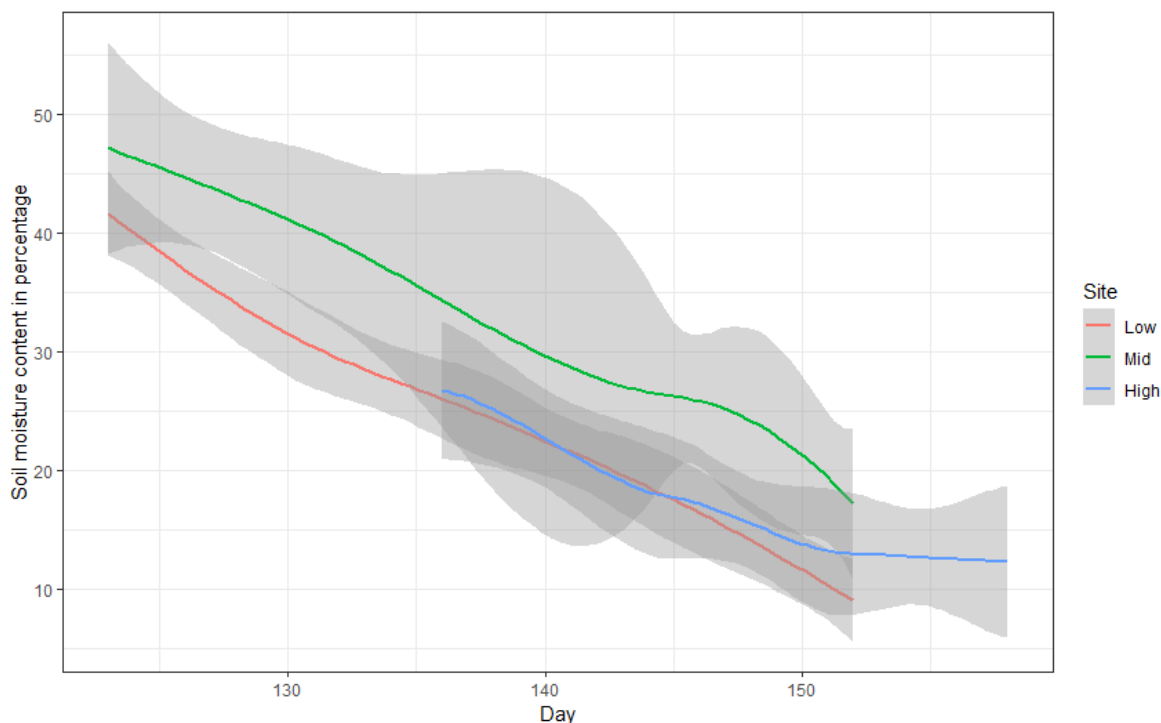
Soil moisture and temperature was measured during the growth season. Temperature loggers were put out when the snow melted. Figure 6 shows the ground temperature gradient between the sites. It is important to note that weather stations have their temperature gauges at 200cm altitude above the ground. This means that the temperatures presented does not reflect the atmospheric temperatures and should not be compared with the temperatures reported above. There was a temperature difference of 1,74°C between Low and Medium site, and 2,49°C between Medium and High site over the growth season (Fig 6). The ground temperatures are thought to be extremely high during this growth season, as for instance the average temperature in July was 24,7°C (fig 6).



**Figure 6:** Site temperatures averaged per month. The data is ground temperature, and not atmospheric temperature. Temperature data is from the 23rd of March at low site, 8th of May at Medium and 15th of May at High site. Loggers were put out after snow melt.

Soil moisture content was highest at Medium site, while Low and High site had similar trends. High site however, started at 26% soil moisture. Medium site had between 5 to 10% higher soil moisture content compared to Low site throughout measurements. There was little to no variation between treatments (not shown) at the respective sites. The soil moisture content did not increase expressively after the initial snow melt. Soil moisture was collected during May until the 1<sup>st</sup> of June (Fig. 7). There was a significant drought in Kaupanger during the summer of 2018 (Grinde et al., 2019). Most of the precipitation which fell during summer, fell as short high intensity precipitation events. 100% of the

monthly precipitation of June fell during four days and provided little moisture to the environment. The autumn had 200% precipitation compared to the norm (Grinde et al., 2019).



**Figure 7:** Soil moisture in the study plots in %. Green is Medium site, Red is Low site and blue is High site. The grey spread is the variation of data. The x-axis is days in Julian date.

### 3.2 *Vaccinium myrtillus* – phenology

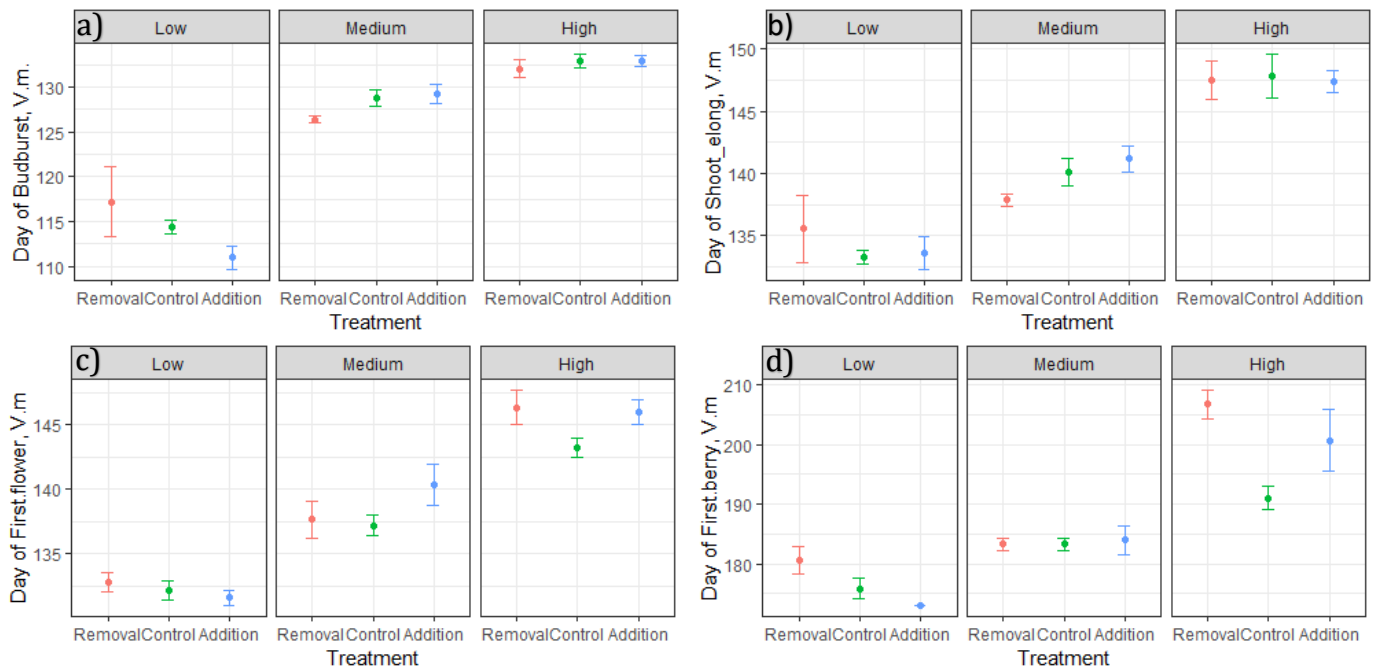
There was a dominant altitudinal effect of site for phenological timing (e.g. budburst,  $F = 219,93$ ). The different phases occur first at Low site, and last at High site. There are effects of treatment and interactive effects between site and treatment. There were no consistent interaction patterns across the response variables. All the responses with effect, t-value and p-value can be found in table 4.

For budburst (Fig 8a) there was an interactive effect for snow addition at low site (see appendix for post-hoc interaction plots), compared to other addition plots. Addition plots at Low site had budburst occur  $3,94 \pm 1,47$  days earlier ( $t = -2,68$ ,  $p < 0,01$ ), and at Medium and High site, there was no difference between control and addition plots ( $t = 0,55$ ,  $p = 0,59$ ). Budburst snow removal led to an advance in timing of  $2,33 \pm 0,99$  days compared to the intercept ( $t = -2,35$ ,  $p < 0,01$ ). The delay in budburst of snow removal at Low site ( $1,78 \pm 1,53$  days) was not significant. Site was by far the dominant factor, as Low site occurred  $14,36 \pm 1,24$  days earlier than the medium site ( $t = -11,57$ ,  $p < 0,01$ ) and High site  $4,14 \pm 1,24$  days later than the medium site ( $t = 3,36$ ,  $p < 0,01$ ).

For shoot elongation, there was no interactive nor effect from treatment. There are tendencies of medium site tracking the snow, meaning that snow removal plots had shoot elongation first, and snow addition last. This was not significant in the model. Shoot elongation is clearly affected by elevation with High site being  $7,87 \pm 1,06$  days later than Medium site ( $t=7,447$ ,  $p<0,01$ ), and Low site being  $6,41 \pm 1,05$  days earlier ( $t=-6,15$ ,  $p<0,01$ ).

First flower had significant differences due to an interaction of addition plots at low site as well as addition treatment ( $2,74 \pm 1,12$  days.  $t=2,45$ ,  $p=0,02$ ) and site. Site explains most of the variation in the model. The interaction effect comes in from addition plots at Low site compared to Medium and site ( $-3,34 \pm 1,56$  days,  $t=-2,15$ ,  $p=0,043$ ). High site removal plots were removed from the model as it compromised the validity. There was no effect from snow removal ( $p=0,93$ ).

First berry shows varied effects across the gradient (Fig 8d, table 3). Both treatments led to delay in emergence at High site compared to the high site control plots; berries with removal treatment ripened  $14,92 \pm 3,76$  days later ( $p<0,01$ ) and berries with addition treatment ripened  $9,1 \pm 3,76$  days later ( $p<0,01$ ). There was no interaction effect at Low site, however Low site addition and removal plots were statistically different from one another (7,6 days,  $\text{Chi}^2=9,048$ ,  $p=0,018$ ), see appendix for visualisation. On average, the first berry was ripe  $7,53 \pm 2,65$  days earlier ( $p<0,01$ ) at Low site and  $7,67 \pm 2,65$  days later at High site ( $p<0,01$ ) compared to the Medium site control. There was no treatment effect on its own.



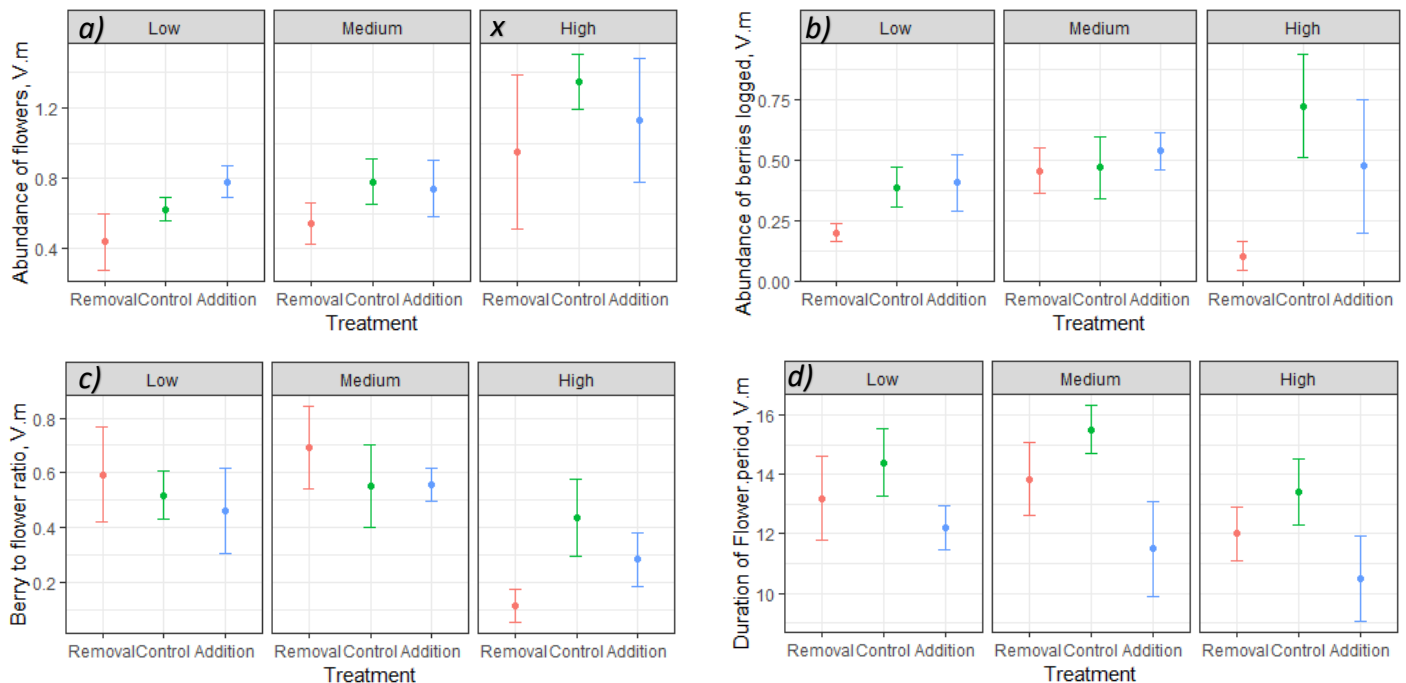
**Figure 8:** Results on phenology in *V. myrtillus*. The red bar is snow removal plots, green is control and blue are snow addition plots. Low is the lowermost site, Medium is the middle site and High is the high site. All figures have the y-axis is the date of emergence in Julian day, where day 1 is the 1<sup>st</sup> of January. A) shows budburst for *V. myrtillus*. B) shows day of initiation of shoot elongation. C) shows emergence of first flower and D) shows the day of the first ripe berry.

**Table 4:** Data output of the statistical modelling on phenology in *V. myrtillus*. The intercept is the "control" in the model, in which other responses are tested against. The effect is the Julian day of the year. The effect is days later or earlier than the intercept. P-values in red are not statistically significant.

Response	Explanatory		Effect ± S.E.	t-value	P-value
<b>Budburst</b> a)	Intercept	Medium site+ control plot	128,71±0,84	153,78	<0,01
	Site	High	4,14±1,24	3,36	<0,01
		Low	-14,36±1,24	-11,57	<0,01
	Treatment	Add	0,54±0,99	0,55	0,59
		Rem	-2,33±0,99	-2,35	<0,01
Interaction	Treatment add: Site Low	-3,94±1,47	-2,68	0,01	
<b>Shoot elongation</b> b)	Intercept	Medium	139,74±0,69	201,54	<0,01
	Site	High	7,87±1,06	7,447	<0,01
		Low	-6,41±1,05	-6,15	<0,01
	Treatment		No effect		
<b>First flower</b> c)	Intercept	Medium+Control	137,58±1,02	135,28	<0,01
	Site	High	5,62±1,46	3,86	<0,01
		Low	-5,38±1,46	-3,69	<0,01
	Treatment	Add	2,74±1,12	2,45	0,02
		Rem	0,09±1,05	0,08	0,93
Interaction	Treatment add: Site Low	-3,34±1,56	-2,15	0,043	
<b>First berry</b> c)	Intercept	Medium site+ control plot	183,3±1,78	102,63	<0,01
	Site	High	7,67±2,65	2,89	<0,01
		Low	-7,53±2,65	-2,84	<0,01
	Treatment		No effect		
	Interaction	Treatment rem: Site High	14,92±3,76	3,97	<0,01
Treatment add: Site High		9,1±3,76	2,42	<0,01	

### 3.3 *Vaccinium myrtillus* – reproduction

Neither flower- or berry abundance showed an interactive effect nor an effect of Site (see Figure 9a and b). High site was removed from the model on flower abundance because it compromised the validity of the model due to high variance in the residuals (shown as x in fig. 9a). For both elevations, there was a reduction in abundance from snow removal ( $-0,38 \pm 18$ ,  $t = -2,07$ ,  $p = 0,0522$ ). Berry to flower ratio was only affected by Site, and there was little within site variation (table 4). Low site was not different from Medium site ( $t = -0,69$ ,  $p = 0,50$ ). High site had a lower berry to flower ratio ( $-0,33$ ,  $t = -2,76$ ,  $p = 0,017$ ). Flower period was on the other hand only affected by treatment, with addition plots having a shorter flower period than control plots ( $-3,03 \pm 0,95$  days,  $p < 0,01$ ,  $t = -3,18$ ). Removal plots had a shorter flower period as well, however not significant ( $t = -1,43$ ,  $p = 0,16$ ).



**Figure 9:** The effect of altitudinal gradient and snow treatment on reproduction of *Vaccinium myrtillus*. Number of flowers and berries were both log-transformed and divided by cover. The results for a) flower- and b) berry abundance are  $\log(n/\text{cover})$ . C) Berry to flower ratio is berries / flowers, and d) flower period is the day of first flower – day of last flower. The x in 9a is to signify that high site was excluded from the statistical model.

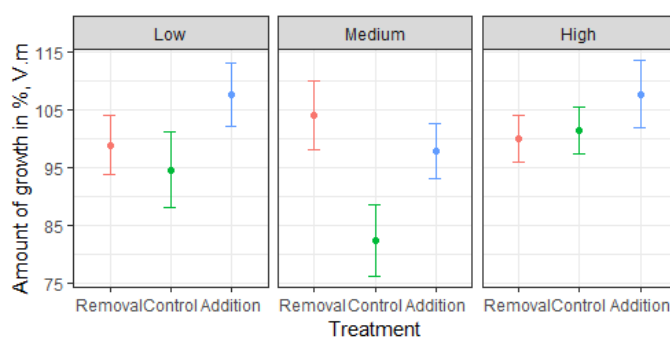
**Table 5:** Data output of the statistical modelling on reproduction in *V. myrtillus*. The intercept is the "control" in the model, in which other responses are tested against. The effect is the Julian day of the year. The effect is days later or earlier than the intercept. P-values in red are not statistically significant.

Response	Explanatory		Effect±S.E.	T-value	P-value
<b>Flower abundance</b> log(n/cover)	Intercept	Con	2,09±0,16	12,57	<0,01
	Site		No effect		
	Treatment	Add	0,13±0,18	0,7	0,49
<b>a)</b>		Rem	-0,38±0,18	-2,07	0,0522
	<hr/>				
<b>Berry abundance</b> log(n/cover)	Intercept	Con	0,42±0,62	7,36	<0,01
	Site		No effect		
	Treatment	Add	0,02±0,08	0,246	0,81
<b>b)</b>		Rem	-0,18±0,08	-2,31	0,034
	<hr/>				
<b>Berry to flower ratio</b>	Intercept	Medium	0,60±0,08	7,39	<0,01
	Site	High	-0,33±0,12	-2,76	0,017
		Low	-0,08±0,01	-0,69	0,50
<b>c)</b>	Treatment		No effect		
	<hr/>				
<b>Flower period</b>	Intercept	Con	14,50±0,67	21,83	<0,01
	Site		No effect		
	Treatment	Add	-3,03±0,95	-3,18	<0,01
<b>d)</b>		Rem	-1,37±0,95	-1,43	0,16

### 3.4 *Vaccinium myrtillus* – growth

No interaction between site and treatment or site effect was found during analysis regarding growth in *V. myrtillus*. Addition plots have 11,61% increased growth compared to control plots (p=0,019, fig 10). Control had negative growth 92,14±3,24%, which nets 7,86% reduction in biomass. Removal had +9,12% growth compared to control with a p-value of 0.06, making the result borderline on whether to accept it as a difference from control as of classical tradition in statistics. Though the interaction was not significant, Medium site removal plots show greater growth than both control and addition plots.

Only addition plots had actual growth in biomass between measurement 1 and 2. Control plots experienced a decrease in biomass while removal plots were close to no net change (101,26±4,66%).



Response	Explanatory	Percentage ±S.E.	T-value	P-value	
<b>Growth</b>	Intercept	Con	92,14±3,24	28,43	<0,01
	Site	No effect			
	Treatment	Add	11,61±4,66	2,49	0,019
		Rem	9,12±4,66	1,96	0,060

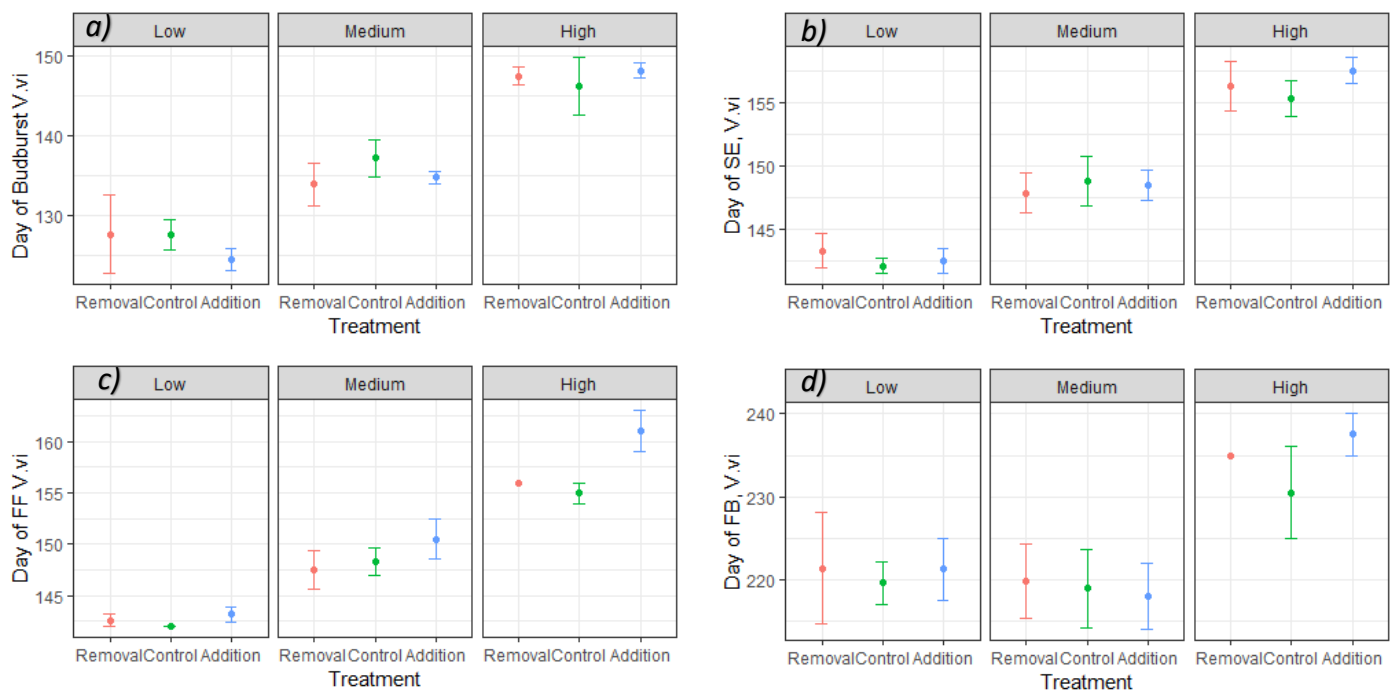
**Figure 10:** Figure shows change in growth between measurement 1 and 2. A result of 100% means that there was no change, lower numbers shows decrease in mass and higher numbers show increase in biomass. The table shows the output from the statistical model. Percentage means the relative change between measurement 1 and 2.



### 3.5 *Vaccinium vitis-idaea* – phenology

There was no interactive effect found on *V. vitis-idaea* regarding phenology from snow cover manipulation. There was a significant difference in all phenology variables from site, i.e. budburst ( $\text{Chi}^2=72,91$ ,  $\text{df}=2$ ,  $p<0,01$ ). All responses followed the altitudinal gradient, with Low site occurring first, and high site latest. Budburst occurred  $8,73\pm2,22$  days earlier at Low site ( $t=-3,93$ ,  $p<0,01$ ) and  $11,86\pm2,32$  days later at High site ( $t=5,11$ ,  $p<0,01$ ). See table 5 for all results.

Day of first flower was the only response variable which showed an effect from snow cover manipulation. Day of first flower in addition plots was  $1,69\pm0,71$  days later than the control plots ( $t=2,39$ ,  $p=0,026$ ). There was no effect from snow removal. This change was not carried through to first berry. For first berry, Low site was not different from Medium site (see fig 11d).



**Figure 11:** The effect of climate gradient and snow treatment on phenology of *Vaccinium vitis-idaea*. The table shows the model outputs. The effect is measured in Julian day, as difference from the intercept which is the Medium site, with or without control plots dependant on whether treatment explained variation in the model.

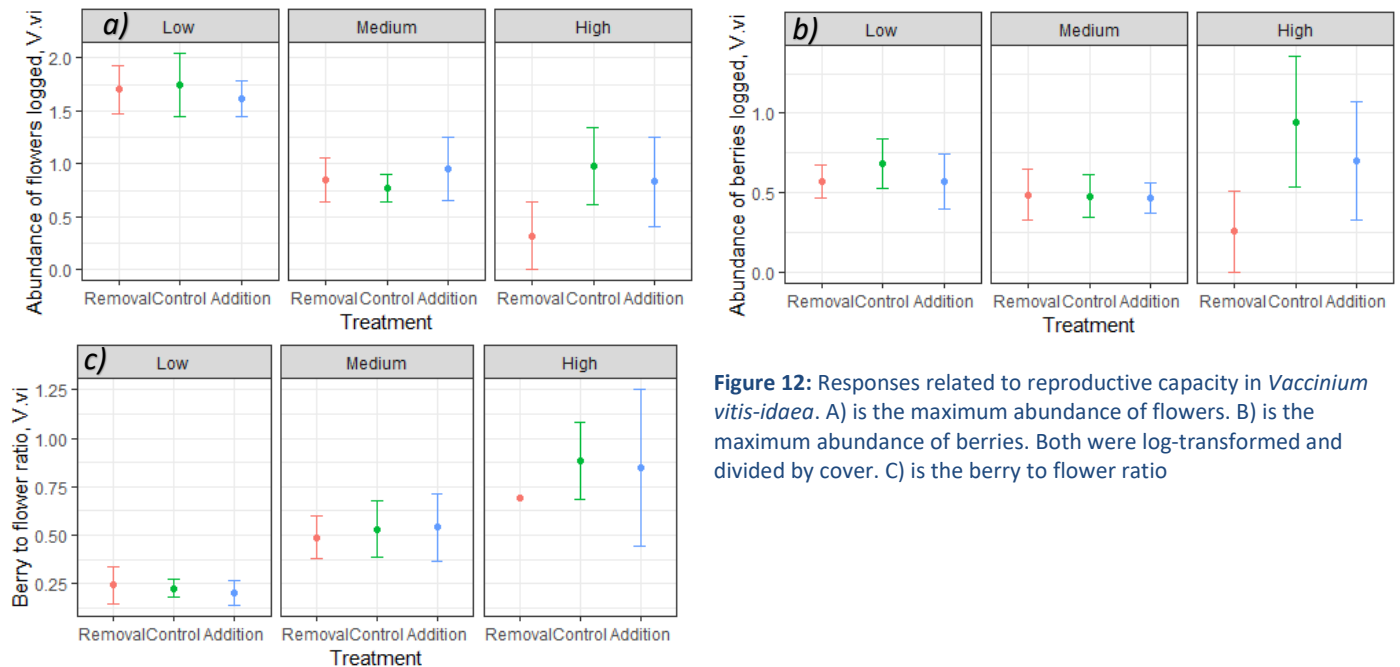
**Table 6:** Data output of the statistical modelling on phenology in *V. vitis-idaea*. The intercept is the "control" in the model, in which other responses are tested against. The effect is the Julian day of the year. The effect is days later or earlier than the intercept. P-values in red are not statistically significant.

Response	Explanatory		Effect ± S.E.	T-value	P-value
<b>Budburst</b> a)	Intercept	Medium	135,31±1,50	90,41	<0,01
	Site	High	11,86±2,32	5,11	<0,01
		Low	-8,73±2,22	-3,93	<0,01
	Treatment	No effect			
<b>Shoot elongation</b> b)	Intercept	Medium	147.71±0,8	180,22	<0,01
	Site	High	+8,34±1,2	6,76	<0,01
		Low	-5.11±1,2	-4,24	<0,01
	Treatment	No effect			
<b>First flower</b> c)	Intercept	Medium + control	148,01±1,04	141,94	<0,01
	Site	High	8,28±1,43	5,77	<0,01
		Low	-6,18±1,01	-6,11	<0,01
	Treatment	Add	1,69±0,71	2,39	0,026
		Rem	0,61±0,71	0,84	0,41
<b>First berry</b> d)	Intercept	Medium	218,94±2,59	84,61	<0,01
	Site	High	14,00±4,93	2,84	0,01
		Low	1,64±3,89	9,73	0,68
	Treatment	No effect			

### 3.6 *Vaccinium vitis-idaea* – reproduction

No effect was found from snow cover manipulation on reproductive capacity on its own or as an interaction with site (see fig. 12, table 7). Flower period was not included for *V. vitis-idaea* as the data was considered irredeemable due to large differences in variation. I was therefore not able to make a valid model. Caution is advised considering berry to flower ratio, as the variation between sites was bigger than ideal. This model was however cross validated with rank-based tests, with similar results.

The high reproductive success at High site is thought to be skewed by the lack of data. Low site had more flowers (back-transformed,  $n=+6,76\pm 1,74$ ,  $p<0,01$ ) compared to Medium and High, but a similar abundance of berries (table 7). This led to a lower reproductive success as seen in the berry to flower ratio (Low site  $-0,30\pm 0,11$ ,  $t= 2,82$ ,  $p=0,022$ ).



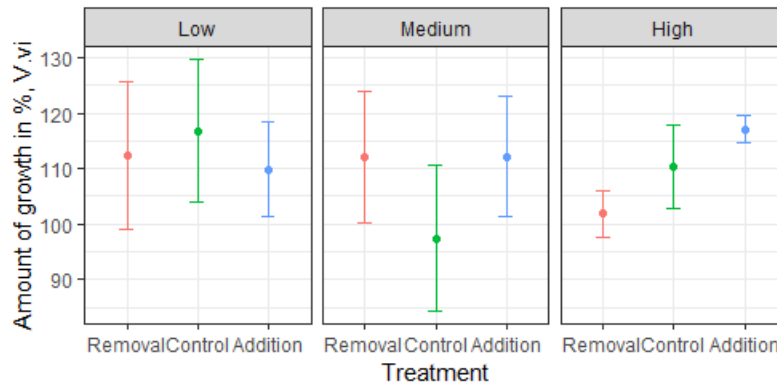
**Figure 12:** Responses related to reproductive capacity in *Vaccinium vitis-idaea*. A) is the maximum abundance of flowers. B) is the maximum abundance of berries. Both were log-transformed and divided by cover. C) is the berry to flower ratio

**Table 7:** Data output of the statistical modelling on reproductive capacity in *V. vitis-idaea*. The intercept is the "control" in the model, in which other responses are tested against. Abundance of flowers and berries are log-transformed and divided by unit cover. The berry to flower ratio is the total amount of berries in a plot divided by the total amount of flowers of the same plot. P-values in red are not statistically significant.

Response	Explanatory		Amount $\pm$ S.E.	T-value	P-value
<b>Abundance of flowers</b> log(n/cover)	Intercept	Medium	0,86 $\pm$ 0,16	5,34	<0,01
	Site	High	-0,13 $\pm$ 0,32	-0,40	0,69
		Low	0,83 $\pm$ 0,24	3,43	<0,01
	Treatment	No effect			
<b>Abundance of berries</b> log(n/cover)	Site	No effect			
	Treatment	No effect			
<b>Berry to flower ratio</b>	Intercept	Medium	0,52 $\pm$ 0,07	7,34	<0,01
	Site	High	0,32 $\pm$ 0,13	2,47	0,024
		Low	-0,30 $\pm$ 0,11	-2,82	0,022
	Treatment	No effect			

### 3.7 *Vaccinium vitis-idaea* – growth

There is no difference in growth between the sites or treatments (See fig 14). There is a trend at high site, but this trend is likely to be due to the lack of data and was not significant during analysis. The average on all plots were +17% growth in biomass. *V. vitis-idaea* shows no effect from treatments in this study, and has more growth, compared to *V. myrtillus*.



Response	Percentage	
<b>Growth</b>	Site	No effect
	Treatment	No effect
	Average growth	117,74%

**Figure 13:** Growth of *Vaccinium vitis-idaea* along the altitudinal gradient. Figure shows change in growth between measurement 1 and 2. A result of 100% means that there was no change, lower numbers show decrease in mass and higher numbers show increase in biomass. The table shows the output from the statistical model. Percentage means the relative change between measurement 1 and 2.

## 4. Discussion

The main interest in this study was to see if there are changing trends in plant performance and phenology in response to the snow treatments along the altitudinal gradient. *Vaccinium myrtillus* did indeed have differences along the gradient, but less than expected as they were mainly seen in Low site. At Low site there was a trend of positive effects from snow addition, and a negative response from snow melt advance. This effect was not present to the same degree at the other sites. *Vaccinium vitis-idaea* demonstrated with exceptions to be robust to the stress induced from the snow cover manipulations.

### 4.1 *Vaccinium myrtillus*

Most of the variation in phenology was due to the elevation. This is not surprising as I expected the temperature gradient to have the strongest effect on phenology (Hughes, 2000; Parmesan, 2006). Temperature is thought to be the key control of phenology and performance (Hughes, 2000; Inouye et al., 2000; Parmesan, 2006). To which, my results concur.

The phenophases budburst, first flower and first berry showed interactive effects between treatment and elevation. Even though Low site removal plots had snowmelt occurring 9,6 days before the addition plots, the latter still had its budburst ( $3,94 \pm 1,47$  days before the Low site control Fig 8a), first flower ( $3,45 \pm 1,56$  days before the control Fig 8c) and first berry (7,6 days earlier than removal plots Fig 8d) emerge earliest. This is in line with other studies on *V. myrtillus*, such as Bokhorst et al (2011), finding delay in phenology as well as reduced reproduction and growth from warm spells during winter and Saarinen et al, (2016) finding a slight advance in phenology and increase in flower abundance from snow melt delay. This in dispute with Wipf and Rixen (2010), suggesting that deciduous dwarf shrubs are little affected by snow melt delay and advance. These responses may reflect the prevailing weather conditions during 2018. The spring of the study year was colder than normal with temperatures down to  $-18^{\circ}\text{C}$  during mid-March (met.no). Frost events have been found to impact growth and flower production in *V. myrtillus* (Gerdol et al., 2013; Inouye, 2008; Palacio et al., 2015). It is therefore likely that it affects phenology as well (Bokhorst et al., 2011). Soil temperature was not measured, but the reduction of snow at removal plots is likely to lead to deeper ground frost compared to addition plots. Therefore the removal plots at Low site may not have thawed before snow at addition plots melted (Kreyling et al., 2012). It was perhaps not possible for plants at removal plots to leave dormancy before plants at addition plots. There were higher temperatures during the snow cover manipulations at both Medium and High site, and it is unlikely that they experienced cold spells after snow cover manipulations (see fig

2). This suggests that the interaction between advance and delay in phenology with treatment at Low site in *V. myrtillus* is related to the cold spells in March.

There was an interactive effect of High site and both treatments on the emergence of first berry. Both treatments lead to significant delays in timing of emergence compared to control plots. Potential reasons for high site treatment plots emerging later than control plots are that later phenophases may be controlled by growing degree days (Wipf, 2010), frost damage (Gerdol et al., 2013), drought (Gimenez-Benavides et al., 2007) or experimental design. The delay in emergence of first berry in both treatments could be due to a combination of these factors, such as drought and growing degree days. Snow removal plots were possibly delayed due to drought, while addition plots may have been delayed by less growing degree days. Alternatively, my treatment plots were generally allotted in poorly vegetated areas, and the difference in phenology may have been resultant of the experimental design.

Reproductive capacity was expected to be higher at the Medium site as it is closer to the niche optimum (Berge, 2018; Moen & Lillethun, 1999). Interactive effects were expected at both peripheries, but for different reasons. *Vaccinium myrtillus* at Low site was thought to benefit more from snow addition, mainly because of the insulating properties of snow (Sturm et al., 1997). The reproductive organs of *V. myrtillus* are sensitive to frost spells (Gerdol et al., 2013; Inouye, 2008; Inouye et al., 2000; Tolvanen & Laine, 1997), which has increased probability of impacting plants at snow removal plots. High site was thought to have plants at snow addition plots come out too late, as the growth season is significantly shorter at higher altitudes (Wipf et al., 2009). In addition, the increased nutrient flux of snow addition has been suggested to be important for plants living at higher altitudes (Bombonato & Gerdol, 2012; Kreyling et al., 2010). Reproductive capacity was highest at Medium site, but there was no significant interaction between elevation (site) and treatment effect.

At Low site, abundance of flowers had a similar pattern to budburst and first flower phenophases, but the increase in flowers in snow addition plots is not significant in the model and there was no interaction which was significant either. Interestingly, snow removal led to negative effects in both Low and Medium site. This is as expected at Low site since removal plots were likely to experience frost (Gerdol et al., 2013; Inouye et al., 2000) and had relatively delayed emergence, but not at Medium site in which removal plots had earlier phenology. Possibly suggesting that early phenophases were not negatively affected by early melt out. Cold spells are not thought to have influenced Medium site after the treatments were performed. This suggests that the capacity of *Vaccinium myrtillus* to produce flowers

are linked to snow melt timing due to other reasons than through the insulating capacity of snow (Sturm et al., 1997).

The lower abundance in flowers in *V. myrtillus* snow removal plots at Medium site did not translate into lower abundance of berries. This indicates that either *V. myrtillus* can adapt to the conditions (Wipf, 2010), or that the soil water content was not negatively affecting berry production resulting in a high capacity to produce berries relative to the antecedent circumstances (Gimenez-Benavides et al., 2007).

Duration of flower period is longer for control plots at all sites compared to both removal and addition plots. *Vaccinium myrtillus* had  $3,03 \pm 0,95$  fewer flowering days when manipulated with snow addition. A possible reason is that added snow increased protection or resource availability (Gimenez-Benavides et al., 2007), which allow berries to develop faster, and give more time for seed maturation (Selås, 2000). At the same time, it could give pollinators a smaller window for interaction (Prevey et al., 2019). Later phenophases may be cued by photoperiod or growing degrees days contrary to earlier phases (Wipf, 2010). This has been found to be mostly prominent in later-emerging plants (Wipf, 2010). Alternatively, flower emergence can have a plastic initiation while wilting occurs at the same time at all treatments (see appendix: fig 15)(Wipf & Rixen, 2010). This suggests that phenophases have different cues regarding the onset and finishing stage, hence there are several environmental cues together which controls the first reproductive phenophases (Parmesan, 2006). One berry per plot was collected, a quick analysis on the berry weight unfortunately did not prove fruitful. However, seed maturation was not investigated, which could give further clues as in whether flowering period had an effect. Shoot elongation was not affected by snow cover manipulation. This suggests that *V. myrtillus* is able to recover to some extent (Tolvanen & Laine, 1997), or that later phenophases are more controlled by growing degree days compared to snow melt date (Gerdol et al., 2013). The shortening of flower period could lead more flowers having their peak flowering date at the same time (Prevey et al., 2019), which could be important for the pollination event (Parmesan, 2006).

There was increased growth for both treatments compared to the control, however this was only statistically significant for snow melt delay. Control plots lost mass between the measurements and removal plots had no net change. This is to some degree in line with both Gerdol et al (2013) and Rixen et al (2010) which had increased growth in both snow melt- delay and advance plots in 2006, which also was a warm growth season. Rixen et al (2010) found a correlation between summer temperatures above 9°C as a threshold at high elevations for increased growth at early snow melt. My High site had average temperature between May and August of 13,94°C. My Low and High site removal plots did not have



increased growth compared to control. This is opposite to Rixen et al (2010) and Gerdol et al (2013), as they found more growth in higher elevations. A potential reason for this is that the soil moisture was higher at Medium site, reducing the stress from heat. This logic is incoherent, given that Medium site control were the plots which saw the biggest reduction in biomass (-17%). I have not been able to find a link between the negative growth at Medium site control and treatment plots. A bachelor thesis using the same control plots did however have a net reduction of 20% at Medium site prior to 2018 (Steuer, 2018). She argues that this reduction in growth could be related to the distribution of resources. In harsher conditions, it has been found that alpine plants prioritise allocation of resources to reproductive efforts, rather than maximisation of growth (Fabbro & Korner, 2004). If this was the case in 2018, then the negative biomass should have been prominent in High site control plots as well, which it was not.

An initial explanation for the strange differences in biomass was that there was a high amount of grazing on the plots between measurements, which do impact growth (Hegland & Rydgren, 2016). Further investigation did however not find grazing as significantly different between measurement 1 and 2 (not shown). It is possible that the heat stress reduced the biomass through actual wilting (Inouye, 2008), as the summer of 2018 was very warm and very dry. It could also be due to measurement error. All plants were measured at the same time, regardless of plot phenological advancement. However, that can still not explain physical reduction. Furthermore, experimental warming of 4°C has been found to increase total above-ground biomass in *V. myrtillus* by 36% (Anadon-Rosell et al., 2014). This experimentally induced increase in temperature is similar to the experienced temperatures over the growth season of 2018. It is possible that the extreme temperatures were beyond the threshold of temperatures acceptable to *V. myrtillus*.

## 4.2 *Vaccinium vitis-idaea*

It was hypothesised that *V. vitis-idaea* would not show a strong effect from snow cover manipulation at any elevation. There are varied results published regarding the effect from snow cover manipulation on phenophase initiation (Saarinen et al., 2016; Wipf & Rixen, 2010). The response may be there but hidden within the standard errors of the statistical model, and that several studies may not have statistically representative data material which detect smaller signatures of effect. A study which was performed in the timberline in Fairbanks, Alaska found a negative relationship between timing of snowmelt and onset of greening for *V. vitis-idaea*, but that the effect from snow cover manipulation diminished during the later phenophases (Wipf, 2010). This is dissimilar to my results as the early phenophases have very little within-site variation in timing. Wipf states that the onset of greening in her data collection is ‘*when the*

*first leaf is entirely green*' (Wipf, 2010). It is unclear whether she means the first new leaf of the year or increase in chlorophyll in the lowermost leaf on the ramet.

The only phenophase which was affected by snow cover manipulation was the emergence of first flower (fig 11c), with an overall delay of  $1,69 \pm 0,71$  days in the addition plots. This delay could be explained by the number of growing degree days (Wipf, 2010). As addition plots were snow free slightly later, it would take longer to acquire the same sum of growing degree days (Inouye, 2008; Prevey et al., 2019; Wipf & Rixen, 2010).

There was no direct link between reproductive capacity and snow manipulation treatments, which is similar to Saarinen et al (2016). However, the most flowers were recorded at Low site, this was unexpected as the niche optimum is expected to be close to the Medium site. The number of berries was equivalent to that of Medium site, which lead to a higher berry to flower ratio at Medium site (0,52), compared to Low site (0,22), suggesting greater fitness at Medium site. However, this could be due to soil moisture availability. As *V. vitis-idaea* showed rather rigid responses on site-level, it is possible that the berry to flower ratio was not high at Medium site, rather that it was lower than usual at the Low site, due to lack of moisture content during berry ripening (Gimenez-Benavides et al., 2007).

There was no change in growth for *V. vitis-idaea* from either site or treatment which was found significant in the analysis. There was a non-significant trend at Medium and High site. The changes at High site is likely due to the lack of data and should not be considered. The mass change at Medium site is however interesting as both removal and addition plots have marginally increased growth, which is similar to *V. myrtillus* at Medium site.

### 4.3 Comparison of the species

There is a stark difference between *V. myrtillus* and *V. vitis-idaea* in effect from treatments regarding growth and performance. All phenophases except shoot elongation were affected by the treatments in *V. myrtillus*, in contrast to *V. vitis-idaea* which only showed a weak response to the treatments on first flower emergence. There were some effects in reproduction in *V. myrtillus*, particularly for flower abundance at low site, *Vaccinium vitis-idaea* showed no effect from this, and the same goes for growth. It is clear that *Vaccinium vitis-idaea* is more robust, and it is questionable whether it shares species range with *V. myrtillus* to the degree as formerly believed (Grime et al., 1989; Wischmann et al., 1986).

The increased sensitivity in *V. myrtillus* is to some extent expected as it is an early flowering insect-pollinated plant, which often are more sensitive to frost (Hegland et al., 2009; Inouye, 2008; Selås, 2000).

*Vaccinium vitis-idaea* is also insect-pollinated, but emerges later (Grime et al., 1989). The effect found on *V. vitis-idaea* was however less prominent than expected, particularly at the expected niche periphery. (Kimball et al., 2014; Saarinen et al., 2016; Wipf et al., 2006). Still I believed that along an altitudinal gradient that there would be interactive responses between elevation and treatment in phenology and performance.

*Vaccinium vitis-idaea* was apparently only affected by altitude (site) in my results. This could be due to the manipulations not being strong enough (Wipf & Rixen, 2010), or that *V. vitis-idaea* is robust to the temperatures (Palacio et al., 2015) or that they are controlled by the photoperiod and phenology is not cued by effects related to snow cover change (Wipf et al., 2009). *Vaccinium vitis-idaea* was assumed to have a similar niche range to *V. myrtillus*. However, Low site clearly had the most flowers, but the same number of berries as Medium site (fig. 12b). It is possible that *V. vitis-idaea* has a higher fitness at Low site, but Low site was drier, which possibly halted the berry production (Gimenez-Benavides et al., 2007). If the Low site is closer to the optimum for *Vaccinium vitis-idaea*, the foundation for comparison is questionable.

The results of *Vaccinium vitis-idaea* suggests that it as a species is more controlled by the photoperiod or growing degree days as opposed to other environmental cues. Wipf and Rixen do suggest that this is often the case for dwarf shrubs (2010), but in dispute with Prevey et al. (2019); who by looking at tundra-species found that late flowering species respond stronger to warming than early flowering species. They suggest that early flowering species are often cued by photoperiod, while late flowering species often cued by temperature (Prevey et al, 2018). With climate change, it has been suggested that the time difference of flowering between early- and late flowering species is shortening (Prevey et al., 2019). However, there are differences in reaction to warming within early and late-flowering species (Hegland et al., 2009; Prevey et al., 2019; Wipf & Rixen, 2010). My results appear to correspond better with the analysis done by Wipf and Rixen (2010), which could further suggest that there are differences between biomes. That said, Prevey et al (2019) do state that they found several cases of conflicting trends, but that their conclusion is the general trend.

#### 4.4 Future predictions

Climate change is not a linear change in abiotic circumstances, but rather a multidimensional change with feedback mechanisms (Hannah, 2014). As the experiment is only done over one growth season, the results are not complete evidence of a future with more or less snow, but indicative of some aspects of climate change. The treatment effect on early phenology at Low site as well as reproductive capacity at

Low and Medium site suggests that less snow negatively affects *V. myrtillus*. The summer of 2018 is potentially a snapshot of the anticipated future summer season. This is in some ways similar to the snow removal study in Central Spain by Gimenez-Benavides (2007). They found that early snow melt led to soil moisture depletion as their study species had a photoperiodic phenology. *Vaccinium vitis-idaea* had a low rate of berries relative to flowers at low site. I believe that this is caused by the drought which was present in Western Norway during this study period (Grinde et al., 2019). Hence it appears that *V. vitis-idaea* is not vulnerable to frost, contrary to *V. myrtillus*. Results on *V. vitis-idaea* were indicative of vulnerability to drought because of the high abundance in flowers at Low site, but relatively low berry yield. If prolonged periods of drought become normal in Norway, this could significantly reduce the berry yield, which can further impact species of higher trophic levels, as their food resource is reduced.

Community shifts have been found after prolonged reductions of snow (Kreyling et al., 2012; Rixen et al., 2010) and a comparison of results from a one year of snow cover manipulation to 11 years found that the 11 year manipulation led to a significant reduction in the root system in both *V. myrtillus* and *V. vitis-idaea* (Blume-Werry et al., 2016). Blume-Werry et al (2016) state that short term studies underestimate the order of magnitude of the long-term effects. *Vaccinium myrtillus* and *V. vitis-idaea* are both regarded as relatively stress tolerant species which prefer deep snow packs (Gerdol et al., 2013; Grime et al., 1989; Kreyling et al., 2012; Rixen et al., 2010). And even though *V. vitis-idaea* showed little effect from snow cover manipulation in my study, as well as previous studies (Kimball et al., 2014; Saarinen et al., 2016; Wipf et al., 2006), they have been found to have high mortality rates from snow removal plots (Wipf, 2010). Both *V. myrtillus* and *V. vitis-idaea* has shown a reduction in cover from snow removal studies in long-term experiments (Blume-Werry et al., 2016; Kreyling et al., 2012).

The negative effects found in *V. myrtillus* could suggest an increase in local biodiversity as the parting of one dominant species leaves room for other species to colonise. Snow is unlikely to melt in a linear fashion upslope during spring due to microtopographic differences. That may leave preferential spots for *V. myrtillus* and *V. vitis-idaea* as snow melt occurs later due to natural variation in abiotic factors. Alternatively, more rain during winter, which is expected (Hanssen-Bauer I. et al., 2016; Marty, 2008) can significantly affect the snow cover properties and alter the insulating capacity (Sturm et al., 1997), nutrient cycling (Gavazov et al., 2017), ecosystem respiration (Bombonato & Gerdol, 2012) and the timing of soil water introduction in spring (Gimenez-Benavides et al., 2007). Such effects are large scale, and microtopography might not be able to halt such processes. In that case, it is possible that

particularly *V. myrtillus*, which was found to be less stress tolerant especially at low site, will see an altitudinal shift in the lower periphery of the niche.

This increased stress gives a specimen three ultimate options; to adapt with the changes, move or go extinct (Hannah, 2014). As both *V. myrtillus* and *V. vitis-idaea* can, and often do reproduce by clonal measures, they are generally thought to be quite robust to stress and have a wide niche (Grime et al., 1989). Consequently, environmental conditions which lead to reduction in performance as in growth might be a stronger control regarding the population turnover compared to phenology and reproductive capacity (Wipf, 2010). Even if the growth season of 2018 was initially cold then warm and dry, the growth at Low site did not seem strongly affected. Mortality has been found to be higher from snow removal compared to control plots for *V. vitis-idaea* (Wipf, 2010). I observed mortality in my plots but did not record this. Therefore, I am not able to compare this to other studies, or between plots. There will be interannual effects which have effects on performance, and potentially phenology of plants (Blume-Werry et al., 2016; Gerdol et al., 2013). Such effects are beyond the scope of this project.

If climate change leads to less snow and drought during the growth season, it is likely that both *V. myrtillus* and *V. vitis-idaea* will be negatively affected, but for slightly different reasons. This study argues that *V. myrtillus* is most affected by its weakness to frost, while *V. vitis-idaea* requires soil water availability during berry production. The snow line is likely to increase in altitude, which would be particularly negative to *V. myrtillus*. This is likely to be less harmful to *V. vitis-idaea*, but if coupled with little precipitation during summer, we might see an upward shift of the niche periphery of both species (Savage & Vellend, 2015).

#### 4.5 Limitations of the study, and thoughts for future studies

The timing of plot allotment is perhaps the most fundamental flaw in this project, as there was too much snow at High site, and choosing plots there was aborted. This made analysis difficult and has compromised the results, particularly for *V. vitis-idaea* as there is only one snow removal plot with the species. Due to few data points at the High site, some models gave singular fit, forcing a simplified model which did not ask exactly the question of interest, such as growth for *V. myrtillus*.

Snow cover manipulation during different phases of winter could lead to different pathways regarding ground temperature, plant stress and other effects (Cooper, 2014). This project attempted to only affect the spring snow melt timing, while keeping other variables the same at each site. As Wipf and Rixen (2010) has pointed out, the reason for less effect found due to snow melt delay in snow cover

manipulation studies can be due to the intensity in labour connected to it. My project did not provide big variances in snow melt dates (See table 2). Other options are snow fences and reflective tarps to delay snow melt timing (Wipf & Rixen, 2010). Snow fences do however require windy locations which two of my sites were not, to get the wanted effect. A tarp can affect the nutrient flux in the snowpack. It does seem more sensible to do manipulation through digging, then introducing a tarp at a later stage, but removing it when the added snow is starting to melt. I suspect that there are differences in plasticity in plants in relationship with the snow climate. Different snow regimes have significantly different properties. Maritime and transient snow climates such as that of Western Norway can have great interannual variations in snow cover, which plants may become robust too. Many studies performed are in areas with continental snow regimes such as Northern Sweden (Krab et al., 2018; Kreyling, 2010; Kreyling et al., 2012), Northern Finland (Saarinen et al., 2016), Central Alaska (Wipf, 2010; Wipf et al., 2006; Wipf et al., 2009), while others are performed in the high European Alps (Gerdol et al., 2013; Rixen et al., 2010). The different snow climates could impact the required amount of change needed to perform snow cover manipulation to exceed natural interannual variations.

The size of the snow cover manipulation plots was 1.5m<sup>2</sup>, which is possibly too small due to the extensive root system which these plants can have (Flower-Ellis, 1971). It is not known if *V. myrtillus* or *V. vitis-idaea* communicates between specimen or even within specimens. As budburst was observed before snow had melted fully, it is possible that the whole specimen reacts when parts of it is free from snow.

The summer temperatures were record breaking, which must affect the results. The growth in *V. myrtillus* is higher for both snow removal and snow addition plots compared to the control, supporting Gerdol et al (2013) and Rixen et al (2010) which both found that warm temperatures enhanced growth from both treatments. Hence, the warm and dry summer weather has clearly had an impact on my results. The soil moisture content was found to be 5-10% higher in Medium site compared to Low and High site. Two removal plots at Medium site were allotted in proximity to ephemeral spring streams. This was not seen while deciding on the position of the plots during the prior autumn. This has possibly affected the results as the removal plots did not receive the full effect of reduction in snow cover as that could have led to reduced soil moisture content. Soil moisture data was not tested in the data analysis due to time scope of this project. However, as the snow manipulations were only done in small designated patches, the surrounding area still had the normal amount of snow. This will obviously affect the soil moisture everywhere.

This project only spans one growth season, processes which affect phenology and performance over the altitudinal gradient may present themselves better over longer study periods. On top of this, studies which compare two similar study sites with big differences in snow cover extent could also highlight thresholds of snow cover manipulation which are needed within different snow climates.

## 5. Conclusion

This study has investigated how phenology, reproductive traits and growth in *Vaccinium myrtillus* and *Vaccinium vitis-idaea* responds to snow cover manipulation along a climate gradient.

Altitude was the main control on phenology in both species. The study found that there were interactive responses from elevation and treatments in the early-flowering deciduous *V. myrtillus*, but not in the later-flowering evergreen *V. vitis-idaea*, in that snow cover manipulation led to significantly different responses in *V. myrtillus* along the gradient. The responses differed in low elevations, compared to other altitudes. The negative responses in phenology and reproductive traits are mainly allocated to frost damage in *V. myrtillus*. Phenological traits had translational effects in reproductive capacity of *V. myrtillus* at Low site.

*Vaccinium vitis-idaea* did not show any significant interactive effects and was found to be robust to the snow cover manipulations done in this experiment. There was only marginal effect from treatments in phenology, and no effect detected in reproductive traits or amount of biomass change. *Vaccinium vitis-idaea* is thus thought to be robust to changes in the winter climate. There are noteworthy indications of soil water availability being an important environmental control on berry formation in *V. vitis-idaea*.

*Vaccinium myrtillus* appeared to react to several environmental cues, with snow melt timing being important during phenophase initiation. *Vaccinium vitis-idaea* was apparently controlled by growing degree days or photoperiod, which could prove detrimental if the hydrological conditions during the summer changes from what it is accustomed to.

From this, I argue that some differences and similarities between the dwarf shrubs have been highlighted. It is likely that with ongoing climate change, including warmer temperatures, lower ground temperatures during winter and less frost protection in spring; *V. myrtillus* will see increased stress in lower elevations in Western Norway. 2018 was an abnormal year with deep snow cover, rapid spring transition and an extremely warm and dry summer. This may be an image of the future norm. These

concluding remarks should be tested further so that interannual variations become highlighted, as well as years with more pleasant weather.

This project has been an attempt to increase the resolution on differences in fitness of dwarf shrubs, focussing on *V. myrtillus* and *V. vitis-idaea* along an altitudinal range from manipulating the spring melt timing. Dwarf shrubs which has been elusive to generalising trends are presented in this study, showing a dichotomy between the deciduous early flowering *Vaccinium myrtillus* and the evergreen later flowering *Vaccinium vitis-idaea*.



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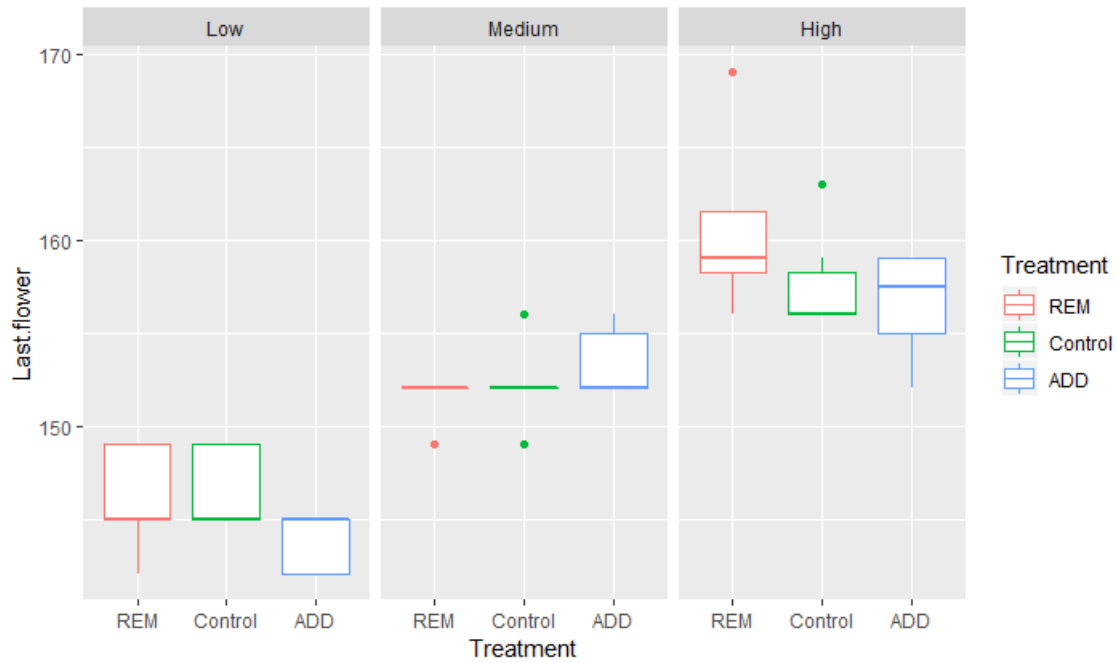
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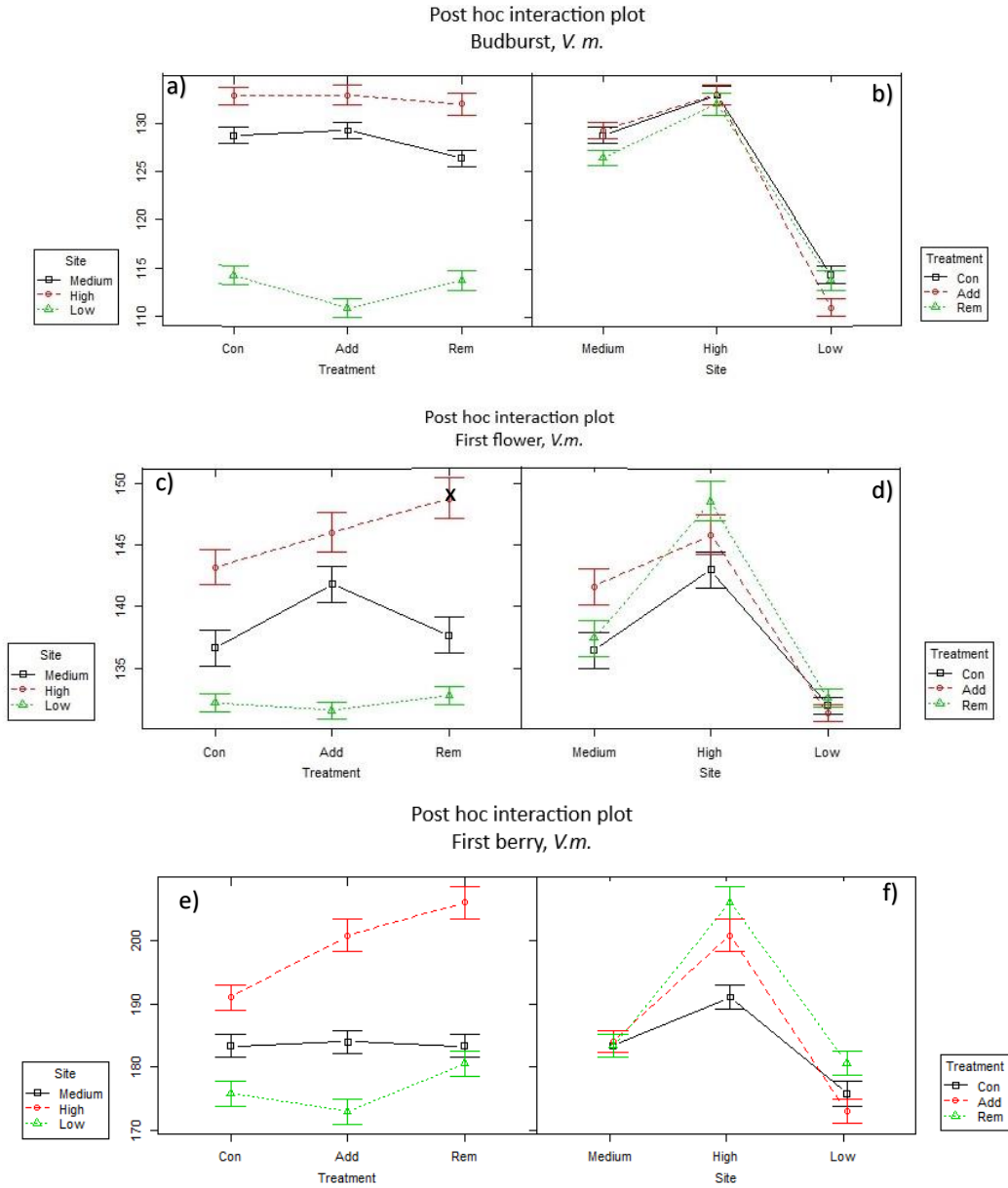
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## 7. Appendix



**Figure 14:** Figure of last flower in *V. myrtillus*. Last flower was only affected by Site ( $F=76,69$ ,  $p<0,01$ ) Treatment<sup>1</sup> and the interaction<sup>2</sup> was not significant ( $F^1=1,21$ ,  $p^1=0,31$  and  $F^2=2,01$ ,  $p^2=0,11$ ).



**Figure 15:** Post hoc interaction plot of first berry (phia). Take note that Control and Medium are to the left on the x-axis. A) shows budburst with comparison of treatments at all sites. B) shows all treatments per site of budburst. C) shows the first mature flower with comparison of treatments at all sites. High site removal is annotated with an x to signify that it was removed from the statistical model. D) shows all treatments per site of first mature flower. E) shows the first ripe berry with comparison of treatments at all sites. F) shows all treatments per site of first ripe berry. The y-axis is the day of emergence in Julian day.