The Short-term Effects of Thinning in Norway Spruce Stands in Sweden on Bilberry Flowering

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Abstract

Bilberry (*Vaccinium myrtillus*) is a foundation species in Swedish forests, providing forage for herbivores and fulfilling many services and functions in the ecosystem. However, bilberry cover has declined in recent decades in Sweden, partly due to dense and dark timber production stands. This study examines the short-term effects of different thinning treatments in Norway spruce (*Picea abies*) stands on the flowering of bilberry in southern Sweden. Three thinning treatments were applied: 60% basal area removal, 30% basal area removal - imitating standard silvicultural practices in Sweden, and a control with no thinning. Bilberry flowering was assessed before the treatments were applied, and one year after thinning. Data on the number of flowers and unopened flower buds was collected from 1,286 bilberry ramets across 66 plots distributed over nine different stands. According to expectations, one year after thinning, the number of flowers in plots with 60% thinning was significantly higher compared to the other treatments. Unexpectedly however, flowering was lower in general that year compared to the previous year, likely due to weather factors and interannual cycling in bilberry reproduction. Interestingly, the number of flowers in plots with 60% thinning did not significantly change between both years, while it drastically decreased in plots with 30% thinning and control treatment. The soil C:N ratio did not influence the flowering response. Only 11.5% of the variation in flowering could be explained by basal area, suggesting that other environmental factors, like microconditions, soil moisture, or understory competition, may play a role. These results show that standard thinning practices may not be sufficient to support bilberry populations in Norway spruce stands. Higher thinning intensities may help to support bilberry on the forest floor and by that also support biodiversity, improve forage availability for herbivores, and increase ecosystem services like berry picking.

Keywords: Vaccinium myrtillus, Picea abies, Phenology, Foundation species, Silviculture, Forest management

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Abbreviations

Abbreviation	Description
C:N ratio	Carbon to nitrogen ratio

1. Introduction

Bilberry (*Vaccinium myrtillus*) is a dwarf shrub species of the Ericaceae family and grows abundantly in Swedish forests. It is a semi light-demanding species that prefers to grow in forests dominated by Scots pine (*Pinus sylvestris)* (Bohlin *et al.* 2021). Bilberry thrives in acidic, relatively nutrient-poor soils. It grows and reproduces in ramets, which are clonal shoots that can function independently while being connected to the parent plant, and also by sexual reproduction (Zeidler & Banaš 2024). Bilberry provides different ecosystem services and is due to its abundance and role in the ecosystem considered a foundation species (Hedwall *et al.* 2014). Bilberry is an important food source for bears and birds, who feed on the fruits, but also for herbivore species like fallow deer (*Dama dama)*, red deer (*Cervus elaphus)*, roe deer (*Capreolus capreolus)* and moose (*Alces alces)*, that browse on the shrubs' leaves and fine stems (Obidziński *et al.* 2012; Schrempp *et al.* 2019). The growth of bilberry can be stimulated by browsing (Zeidler & Banaš 2024). It tolerates moderate herbivory and can recover from damage with the emergence of new ramets. (Zeidler & Banaš 2024). Bilberry provides important nectar to bumblebees and is dependent on insect pollinators (Bartholomée *et al.* 2024) Bilberry also plays a significant role in Swedish culture, with bilberry picking being a highly valued activity in the society (Sténs & Sandström 2013).

Research has shown that the cover of bilberry in Swedish forests have decreased drastically over the past half century, by 50% in southern Sweden (Hedwall *et al.* 2019). One reason for this could be the decline in habitats for the species with the increase of Norway spruce (*Picea abies*) plantations (Hedwall *et al.* 2019; Felton *et al.* 2020). The current standard forestry practices in Sweden focus mainly on production with rotational clear-felling. This includes planting even-aged stands with a relatively high density of seedlings, resulting often in a high basal area (m^2 ha^{-1}). 80% of the standing volume is composed of two native species, Norway spruce and Scots pine (Felton *et al.* 2020). In stands dominated by Norway spruce, the dense overstory is causing a low light availability on the forest floor (Felton *et al.* 2020), promoting shade-tolerant species on the ground cover (Tonteri *et al.* 2016), while ericaceous shrubs, like bilberry, have a lower abundance (Hedwall *et al.* 2019). After a clearcut, bilberry needs at least 80 – 100 years to recover (Kardell 1979; Hedwall *et al.* 2013). Most of the Norway spruce or Scots pine stands in southern Sweden are allowed to be harvested at an age between 45 and 65 years (Petersson *et al.* 2023), which means that the bilberry cover in these forests cannot recover completely after clearcutting (Hedwall *et al.* 2013). Previous studies have shown that with increasing basal area in Norway spruce stands, the ground cover and available forage biomass of bilberry decreases (Juvany *et al.* 2023). The decline in bilberry therefore also leads to a decreased food availability for browsers. This then results in herbivores feeding on alternative food sources, browsing more intensely on other forage plants, e.g. Scots pine seedlings (Felton *et al.* 2022). This raises an economic concern caused by browsing damage on seedlings in the forestry industry. To combat browsing pressure, forest owners in southern Sweden tend to replace Scots pine stands with Norway spruce, (Felton *et al.* 2020), which then decreases available forage for herbivores further and increases browsing pressure over the landscape.

In Sweden, the current silvicultural practice for Norway spruce stands is to remove approximately 30% basal area in the first commercial thinning of the rotation. This enhances the growth of the remaining production trees in the stand and generates income for the forest owner (Agestam 2015). Thinning generally also increases light (Wallentin 2007) and water availability in the stand (del Campo *et al.* 2022). The aim of this thesis is to compare the short-term effects of three different thinning treatments in Norway spruce stands on the flowering of bilberry and to determine whether there is a difference in the data one year after treatment compared to pre-treatment conditions. The three different thinning treatments are approximately 60% removal of basal area, approximately 30% removal of basal area and a control treatment 0% removal of basal area. The growth of bilberry is sensitive to variation in soil nutrients which could influence the flowering (Zeidler & Banaš 2024). Therefore, I also looked at the soil productivity of the study sites, to see if that had an influence on the flowering, besides the thinning treatments. This study attempts to answer the following research question: What are the short-term effects of different thinning intensities on the flowering of bilberry ramets in Norway spruce forests in southern Sweden?

I will test two hypotheses. [1] The plots where a strong thinning of 60% removal of basal area was carried out are hypothesised to have more flowering, compared to the other treatments, and an increase in flowers when compared to pre-treatment. Therefore, the short-term effect of intense thinning will be likely seen in more thriving bilberry plants. [2] In contrast to that, plots where 30% of basal area was removed, which aim to imitate the current silvicultural practices in Sweden, are hypothesised to have no, or only a limited increase in the number of flowers compared to pre-treatment. The conclusions drawn can help to support bilberry populations in future Norway spruce forests.

2. Material and Methods

2.1 Study area

The studied sites are located near Osby in northern Skåne and Blekinge, and in the region around Växjö, in the Kronoberg county (Figure 1). The study area is part of the hemiboreal region with an mean annual temperature of 7.2 °C (SMHI 2021b) and an annual precipitation of 678.8 mm (SMHI 2021a). The experiment was established in the spring of 2023, and there has been ongoing data collection since. The study sites are distributed over nine stands dominated by Norway spruce, that are owned by Sveaskog, a state-owned forestry company. At the beginning of the experiment, the stands were around 30 years old and were mature enough for the first commercial thinning operation. Each stand contains six plots, except for two stands, which have 12 plots each. In total, there are 66 plots, each with a 10 m radius. The plots were chosen with an initial bilberry presence with no big gaps in the canopy and a comparable basal area of trees before applying the treatments. Each plot was divided into three to four subplots with a diameter of 60 cm (Figure 3). The subplots are fenced and marked with wooden poles (Figure 2). Five ramets in each subplot were tagged with an individual ID and used for the inventories. In total there are 1,286 individual ramets in 259 subplots that were tagged and followed since the beginning of the experiment.

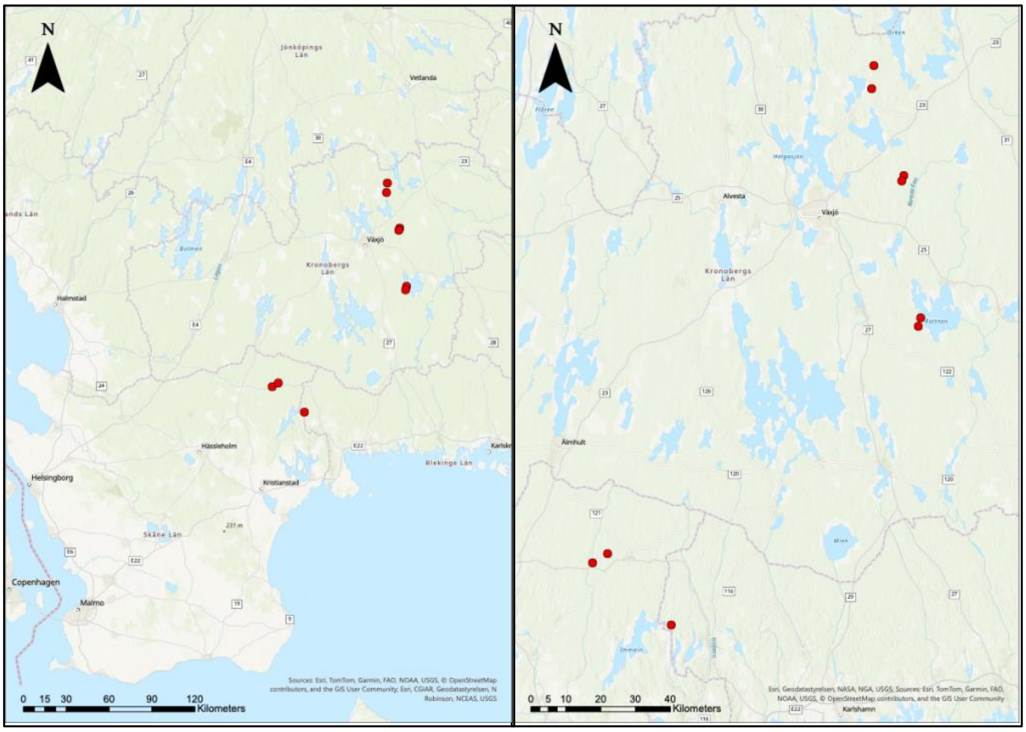

Figure 1. Map of Sweden displaying the positions of the stands, where the experiment was conducted. Each point represents one stand, on two different scales (left and right map). Map: ArcGIS Pro Version 3.4.0 (Esri 2024)

Figure 2. Pictures of one of the studied plots. Left: a fenced subplot marked with a wooden pole. Right: a plot with four fenced subplots. Pictures by author.

2.1.1 Study design and treatments

The study is designed with the Before-After-Control-Impact (BACI) design (Seger *et al.* 2021). With that, it is possible to monitor both the control plots and treatment plots both before and after the thinning treatments have been carried out.

Two different thinning treatments and one control treatment were applied in the stands. One treatment was intense thinning with 60% of basal area removed. The other had 30% of basal area removed, which is supposed to emulate the standard thinning treatment carried out by most forestry companies in Sweden. The control treatment had 0% basal area removed. In each stand there are two plots of each treatment (Figure 3), except for two stands, which have four plots of each treatment. In total there are 22 plots of each treatment. Hemispheric photos were taken to illustrate the density of the canopy cover after the thinning treatments (Figure 4).

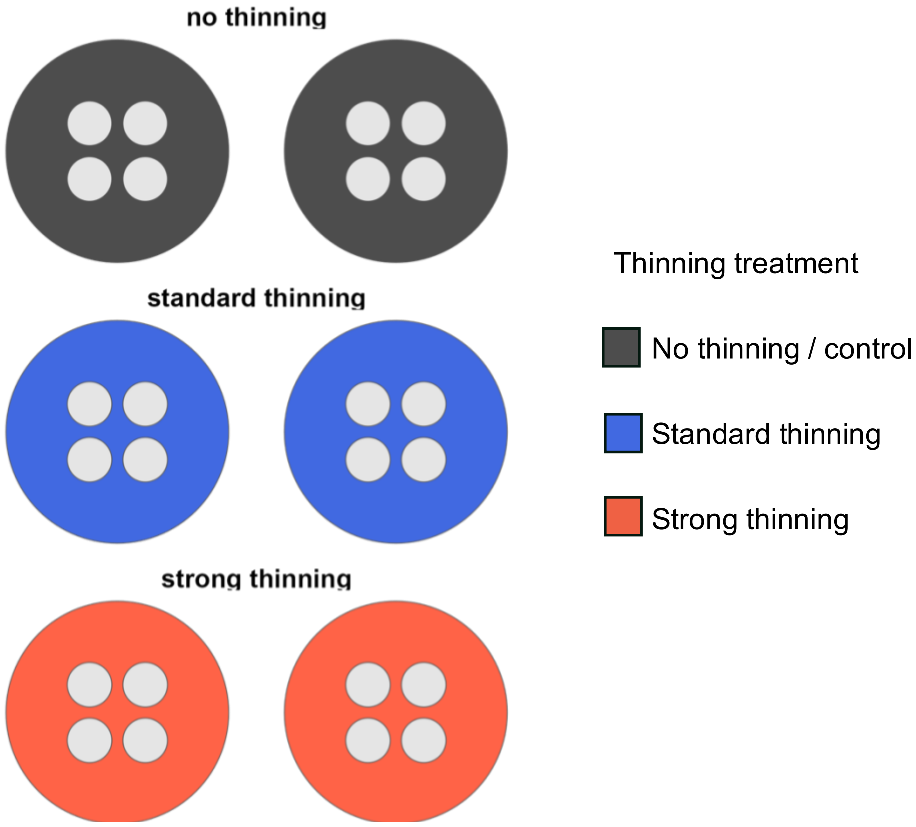

Figure 3. The three different thinning treatments in each stand: two plots with a strong thinning (60% removal of basal area), two plots with a standard thinning (30% removal of basal area) and two plots with no thinning (control). The large circles prepresent the plots. The white circles in each plot represent the four subplot in each plot. The radius of each plot is 10 m, and the diameter of each subplot is 60 cm. Figure made by Lukas Graf.

Figure 4. Hemispheric pictures of the forest canopy to visualise the effect of the thinning treatments. Control, 30% thinning, and 60% thinning (left to right). Pictures by Lukas Graf.

2.2 Data collection

At the beginning of the experiment, soil samples were collected in every plot to look at the soil carbon and nitrogen. From this data I calculated the C:N ratio for each plot, to determine whether the soil C:N ratio may also influence the response of the bilberries. Basal area measurements were done in each plot, before thinning was conducted. To estimate the basal area for 2024 post-thinning, I subtracted the percentage of the thinning intensities (30% and 60% respectively) from the original basal area values. As additional information, I also obtained data on annual precipitation and mean temperature for two nearby locations (Osby and Växjö) for the years 2022 to 2024 (Appendix 1). The thinning treatments were carried out in spring 2023, a few weeks before data collection. In that year, data on the number of flowers on every ramet tagged with a permanent ID (5 ramets per subplot), was collected, before seeing the effects of the different treatments, and is therefore treated as “before-data”. Data from 2024 is treated as “after-data”, because the bilberry ramets could show a response to the different treatments.

2.2.1 Field work

Each year during spring, data on the flowering of the bilberry was collected. To determine the optimal timeframe for this inventory, we used our own observations in similar habitats in the study region, and the bilberry flowering prognosis for the Asa research station, which is closely located to the northern study sites (Langvall 2025). Fieldwork was conducted in early May in 2023 and in late April in 2024. The data collection included counting the number of open flowers and flower buds on each ramet (hereafter referred to as 'flowers'). Only living ramets with intact ID tags were included in the counting.

2.3 Statistical analysis

All statistical analysis has been done in Microsoft Excel Version 16.89 (Microsoft 2025). The data was cleaned and sorted, with information on the stand, plot, subplot, conducted treatment, basal area, ramet ID, number of flowers, and the soil carbon and nitrogen. To assess the differences between treatments in bilberry flowering, I calculated the average number of flowers per ramet per plot for each treatment and year (total N = 66 per year). A Kruskal-Wallis test was used to compare the average number of flowers per ramet per plot between the three treatments in both years. The Dunn's post-hoc test with Bonferroni correction was performed to test the significant difference between treatment pairs in 2024. A paired t-test was used to compare the results of each treatment group between both years. A regression analysis was conducted to investigate the relationship between flower production in 2024 (one year after thinning) and the basal area resulting from the thinning treatments. A one-way ANOVA was used to compare the C:N ratio of the plots of different treatments. A significance level of $p < 0.05$ was used for all statistical tests.

3. Results

3.1 Average number of flowers per ramet per plot

The average number of flowers per ramet did not vary significantly among the treatments in 2023 (Kruskal-Wallis; $H = 0.02$, $df = 2$, $p = 0.99$, $N = 66$, $n = 22$), before the thinning treatments were conducted (Figure 5). In contrast to that, there was a significant difference in the average number of flowers per ramet among the treatments in 2024 (Kruskal-Wallis; $H = 16.11$, $df = 2$, $p < 0.001$, $N = 66$, $n = 22$). In 2024, plots with a 60% thinning treatment had the highest average of flowers and were significantly different to the 30% thinning treatment (Dunn's post-hoc; $z = 3.16$, $p = 0.002$) and the control treatment (Dunn's post-hoc; $z = 3.73$, $p < 0.001$), while both plots with 30% thinning treatment and control plots showed a lower average flower count. The results of the 30% thinning treatment and the control treatment in 2024 did not show a significant difference (Dunn's post-hoc; $z = 0.57$, $p = 0.57$). The average number of flowers per ramet in plots with a 60% thinning treatment did not vary significantly between the years 2023 and 2024 (t-test; $t = 0.36$, $df = 21$, $p = 0.72$, $n = 22$), while it did significantly vary between 2023 and 2024 in plots with 30% thinning (t-test; $t = 2.22$, $df = 21$, $p = 0.04$, $n = 22$) and control (t-test; $t = 2.37$, $df = 21$, $p = 0.03$, $n = 22$).

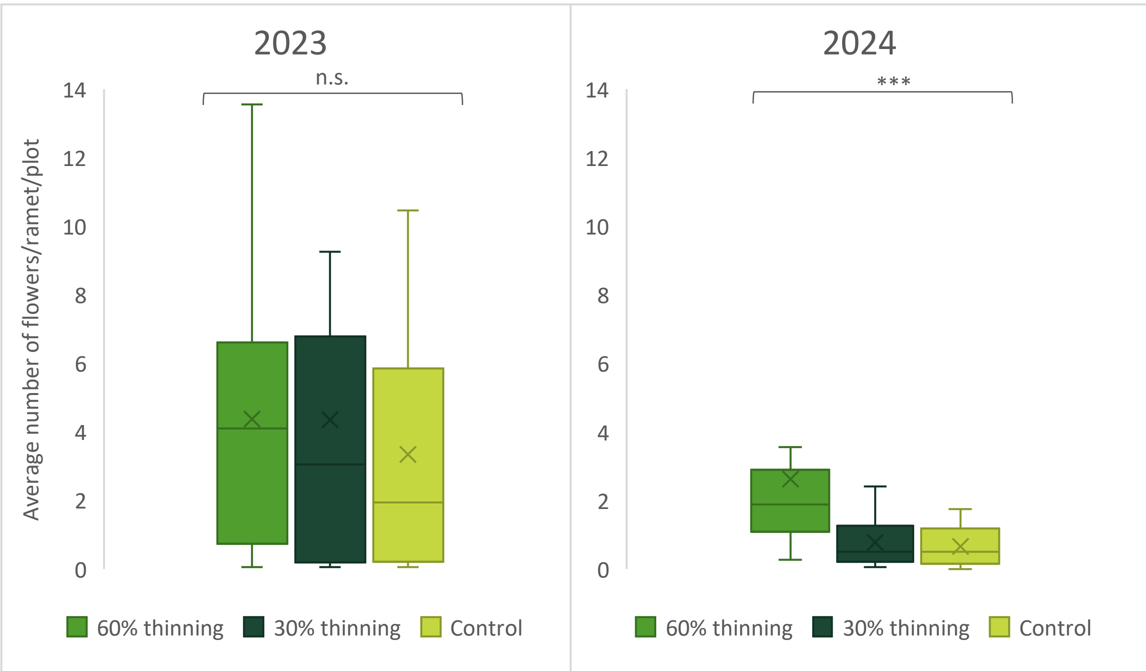

*Figure 5. Average number of flowers per ramet per plot (y-axis), divided into the three treatments and the years 2023 and 2024. "***" is p < 0.001 and "n.s." is p > 0.05 from a Kruskal-Wallis test. Box represents the interquartile range; line = median; whiskers = min/max; x = mean. All outliers and zero values were excluded from the figure.*

There is a negative relationship between the total basal area (m^2/ha) after each thinning treatment and the average number of flowers per ramet per plot in 2024 ($R^2 = 0.115$, SE = 1.85, n = 66). In total there are 22 data points per treatment, visualised by the dots in the figure and categorised by treatment (Figure 6). The regression line indicates a slight decrease in average number of flowers with increasing basal area. Plots that were thinned with 60% intensity, generally have a higher flower production with a lower basal area, compared to the control plots.

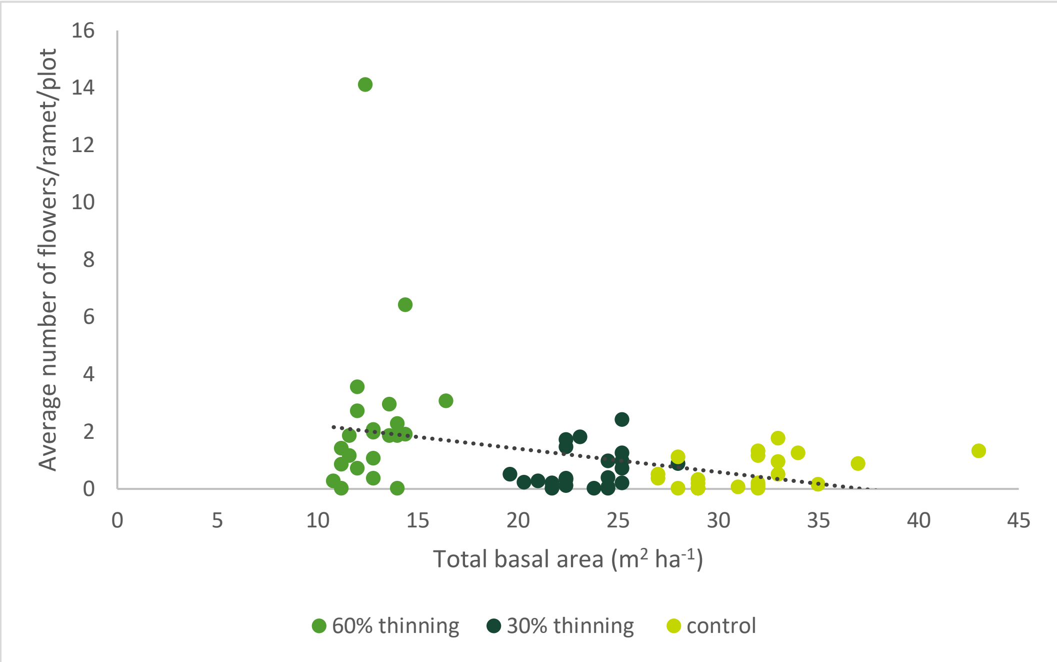

Figure 6. Average of flowers per ramet per plot in 2024 (y-axis) across the total basal area (m^2 ha^{-1}) (x-axis), divided into the three different treatments. Each dot represents one plot.

3.2 Soil C:N ratio

The soil C:N ratio did not differ significantly between the treatments ($p = 0.31$, $F(2, 63) = 1.20$), and I found no relationship between the average number of flowers per ramet per plot in 2024 and soil C:N ratio of each plot (Figure 7). The soil C:N ratios are ranging from 21:1 to 49:1, with the average being at 30:1.

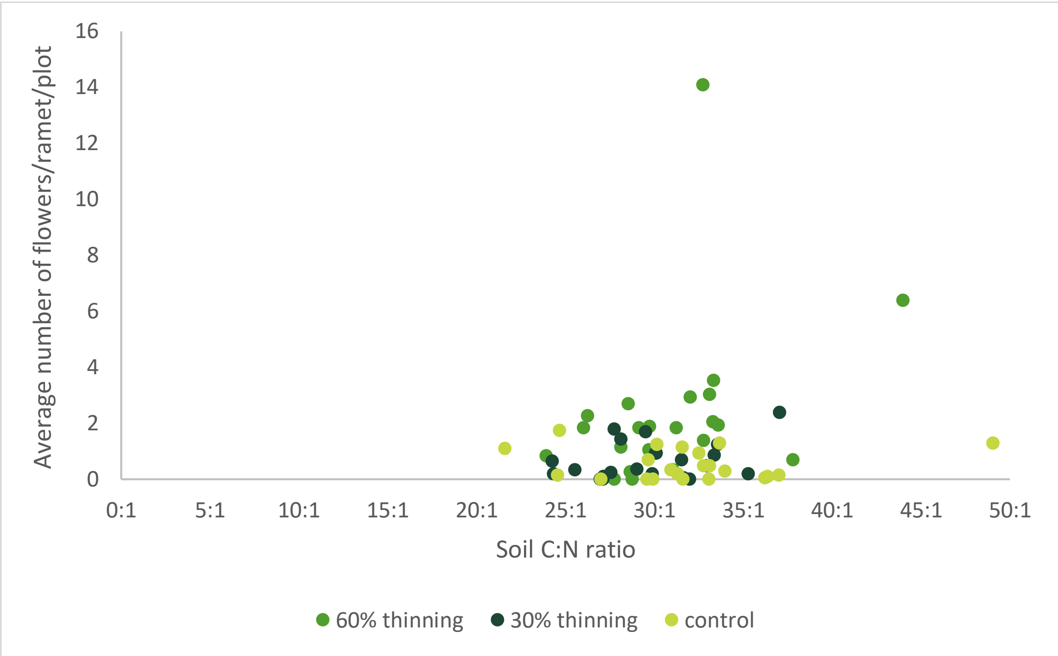

Figure 7. Average of flowers per ramet per plot in 2024 (y-axis) across the soil C:N ratio (x-axis), divided into the three treatments. Each dot represents one plot.

4. Discussion

The results show that heavy thinning has a clear and immediate effect on the flowering of bilberry compared to standard level thinning in Swedish spruce forests, providing support for my first hypothesis [1]. This suggests that high intensity thinning in Norway spruce stands does support bilberry flowering, likely resulting from higher water availability and more light reaching the forest floor. It also shows that the 30% thinning treatment was not sufficient to improve bilberry flowering when compared to pre-thinning data. This is supported by previous research which suggested that the decline of bilberry is partly due to dense and dark forest stands (Felton *et al.* 2020). I did not find support for my second hypothesis [2], since the flower production remained stable in plots with a 60% thinning between the years, while it notably declined in plots with a 30% thinning and control. However, the results are also pointing to other factors that influence the flowering besides basal area. These influencing aspects were not looked at in this study, but other environmental factors likely play an important part in the response of bilberry. In addition, the results show that the soil C:N ratio did not differ significantly between plots, indicating that nutrient availability was not influencing the flowering response.

Although thinning treatment had a clear effect, with more intense thinning generally leading to more flowers per plot, the results show that just 11.5% of the variation in flower numbers was explained by basal area. Other environmental factors, not measured here, are most likely influencing the shown results. These may be microconditions, specific light availability, soil moisture and water availability, differences in and influence of ramet height on flower production, and possible competition from understory vegetation. Besides that, another reason for the low explanatory power of basal area could be that the study only looks at the short-term response of bilberry. The investigation of these factors was outside the scope of this study but are important in order to gain complete understanding of bilberry responses to forest management. Contrary to expectation, I found no increase in flowering between year 2023 (pre-treatment) and 2024 (post-treatment) in plots with a 60% thinning treatment. Contrasting that, bilberry flowering declined drastically from 2023 to 2024 in plots with 30% thinning and control. This could be explained by climatic stressors, like low precipitation (Appendix 1), where bilberry ramets in intensely thinned plots could better allocate resources for flower production due to improved light and water availability. Thinning itself generally increases soil water content, due to increased rain throughfall, and reduces competition for water (del Campo *et al.* 2022), improving the drought resilience of the stand (Sohn *et al.* 2016). However, no increase in flowers was observed, suggesting that light and water availability may only partially compensate for climatic stressors. Previous studies have shown that climate seems to have an influence on bilberry flowering. For example, Boulanger-Lapointe *et. al* (2017) summarises previous findings on climate factors that seem to influence bilberry flower development. They found that bilberry primordia are influenced by the previous year's temperature and precipitation, flower bloom is influenced by spring snow cover, temperature, and precipitation, and frost influences the opening of flowers and can damage newly opened flowers. In this experiment, many of the studied bilberry ramets produced no flowers at all. Selås (2011) observed, that bilberry produces large seeds crops in 2-5 year intervals, highlighting the irregularity and unpredictability of bilberry flowering, which could help to explain the differences in flowering between the years, indicating the need for long-term data collection.

The results observed in this study are consistent with previous research, highlighting that the standard thinning regime done by most Swedish forestry companies is not sufficient to support bilberry populations in Norway spruce stands, and that a heavier thinning may help to maintain or improve bilberry flowering. Though, with regards to the irregular flowering cycles and influences of climate on bilberry, long-term data is needed to show clearer results and draw stronger conclusions. Future research should monitor bilberry flowering and growth over a longer timeframe and analysis should include more ecological variables that have the potential to influence the flowering dynamics.

4.1 Limitations

Several limitations should be considered when looking at the results. The irregular flowering pattern of bilberry makes it difficult to draw strong conclusions from this short-term study. The stands surrounding the studied plots of this experiment were thinned with 30% intensity, at the same time as the thinning treatments for the experimental plots. Since each plot had a 10 m radius, it is likely that in some cases, more light than planned entered the control plots. This could have reduced the contrast between the treatments. Variation in the timing of flowering between the plots of different stands made it difficult to date the timeframe for data collection. Furthermore, the exact basal area measurements for each plot after thinning were not available, which was limiting in seeing a clear effect of basal area on bilberry flowering.

5. Conclusions

The key finding of this study is that higher thinning intensities in stands dominated by Norway spruce, result in higher levels of flowering in bilberry compared to the level of thinning that is routinely conducted in Sweden today. By performing more intense thinning practices, forest owners might reach a better balance between browsing pressure and forage availability, while also making their stands more resilient to drought. An increase in bilberry cover in the understory could reduce browsing pressure on trees, as bilberry can serve as an alternative forage source. Additionally, a thriving bilberry population can improve the habitat for biodiversity, where bilberry functions as a foundation species in the ecosystem. Increased berry production also increases food resources for other wildlife and enhances the ecosystem service of berry picking.

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For this thesis, I used Elicit (https://elicit.com/), an AI research assistant, to search for literature.

Appendix 1

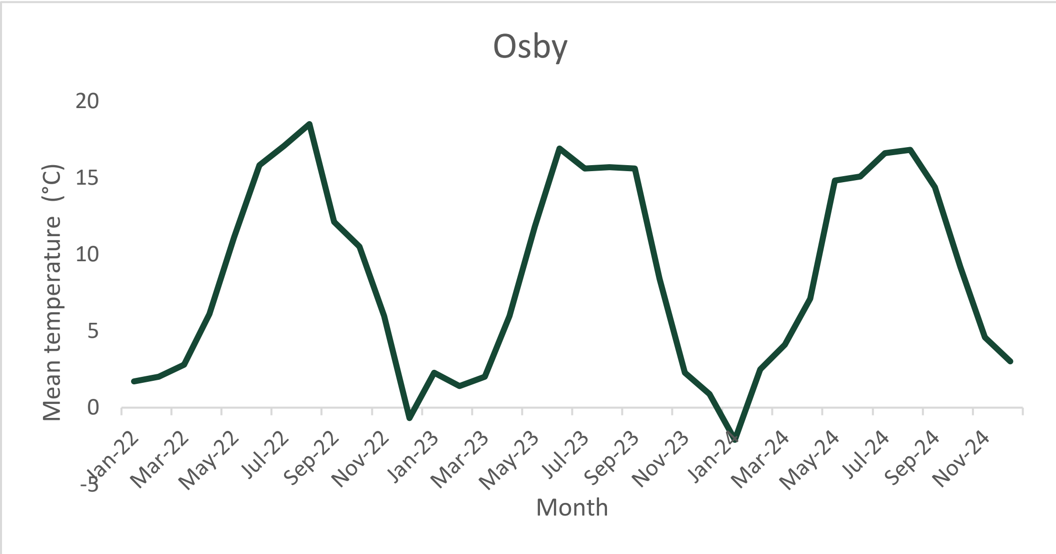

Figure 8. Monthly mean temperature (°C) in Osby from January 2022 to December 2024 (SMHI 2025).

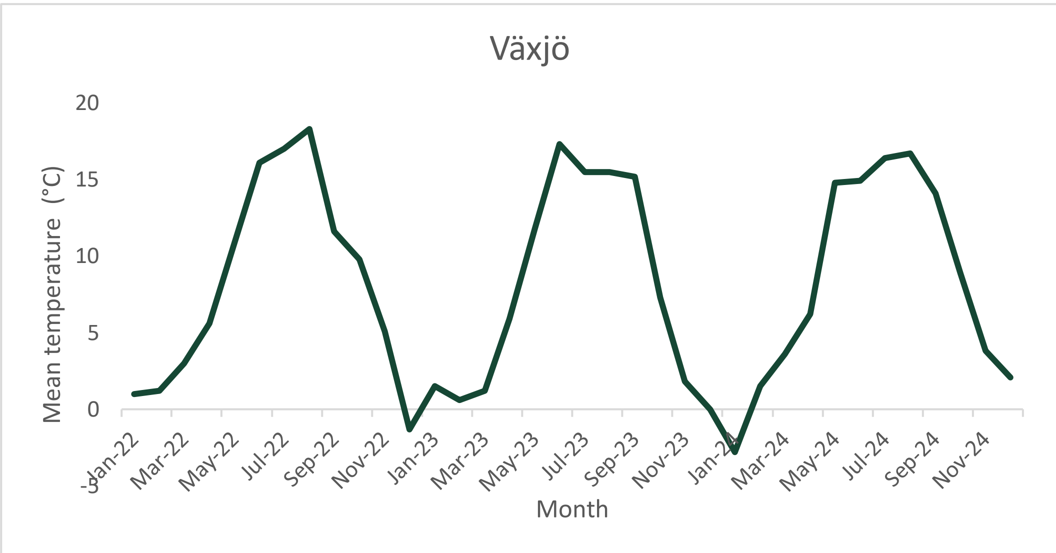

Figure 9. Monthly mean temperature (°C) in Växjö from January 2022 to December 2024 (SMHI 2025).

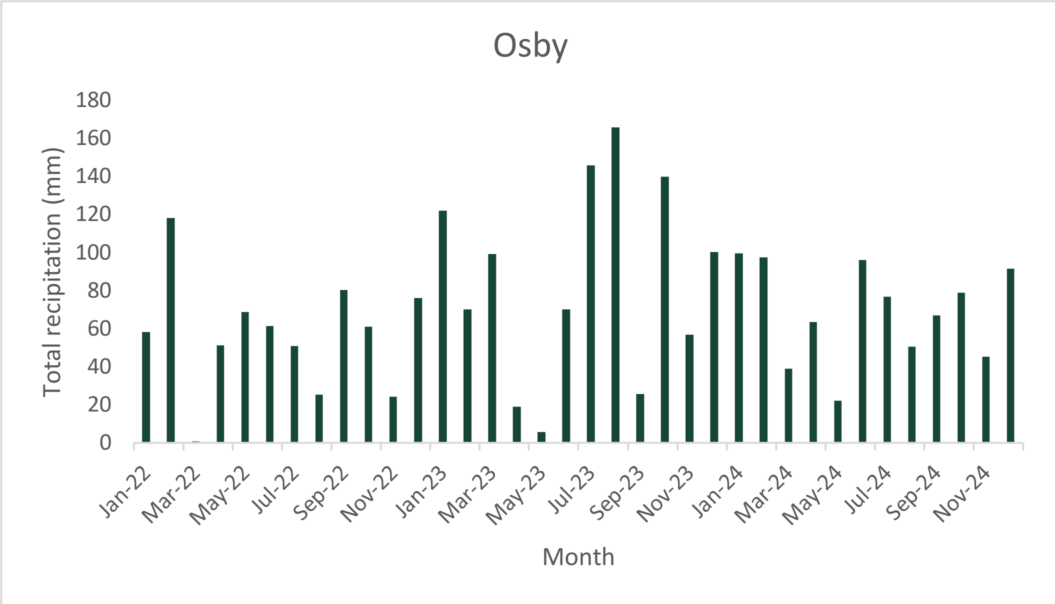

Figure 10. Total monthly precipitation (mm) in Osby from January 2022 to December 2024 (SMHI 2025).

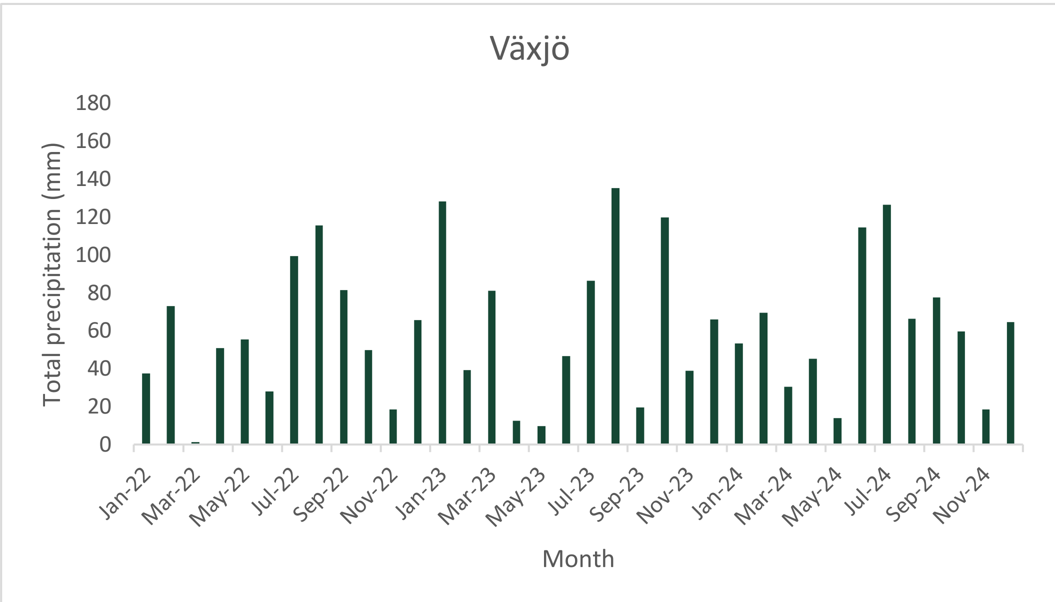

Figure 11. Total monthly precipitation (mm) in Växjö from January 2022 to December 2024 (SMHI 2025).

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