Effects of Climate on Phenology, Flowering, and Berry Production of Boreal Forest Understory Plants

Shakhera Akter Shimu

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Shakhera Akter Shimu

Supervisor:	**Per-Ola Hedwall, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre**
Assistant supervisor:	Joan Diaz Calafat, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre
Examiner:	Jörg Brunet, Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre

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Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Southern Swedish Forest Research Centre

Abstract

Climate is changing faster than it was predicted before and consequently its impact is highly visible on many types of ecosystems globally. Effects of changing climate on forests and the environment are leading to threats for all sorts of ecosystems. Now the management of forests and decision making for environmental protection is following the trend of the impacts of climate change. Climate change is expected to affect plant and animal phenology. Phenological studies are a way to see how plants react to the changing climate. This study focused on this concept and tried to figure out the effects of climate on phenology, flowering, and berry production of four important boreal forest understory plants. Plant material was moved from colder locations (2-degree Celsius temperature difference) to three forest sites in southern, middle, and north Sweden. The potted plants were located in 10 different places at each site together with equally treated local plant material that served as a control. Sites used in the transplant experiment are from north to south: Tärnaby to Vindeln (northern Sweden), Idre to Siljan (middle of Sweden) and Tomtabacken to Vivarp (southern Sweden). For this experiment, the studied species were *Solidago virgaurea* L. (European golden rod), *Vaccinium myrtillus* L. (Billberry), *Vaccinium vitis-idaea* L. (lingonberry or cowberry) and *Fragaria vesca* L. (wild strawberry or woodland strawberry). Later, in the growing season, photos were taken of both provenances (cold provenance and warm provenance) in all three forest sites. This study aimed to find out translocation treatment effects for species-wise selected phenological traits. Finally, through image analysis considering selected phenological traits, this research has found strong treatment effects (at least at two sites out of three) for three phenological traits. DOY (day of the year) of first fruit development of *F. vesca* responded to the translocation treatment at Siljan and Vindeln. Again, DOY of seed setting and DOY of highest percentage of flowering of *S. virgaurea* responded to the translocation treatment at Vivarp and Vindeln. But, in most cases, no translocation treatment effects have been found for other phenological traits, and specifically for *V. myrtillus* and *V. vitis-idaea,* no treatment effects were found throughout this experiment which implies phenotypic plasticity. Absence of effects is an indication that these selected phenological traits would follow the effect of climate change through the adaptation process. This research work can be considered as a good reference for the phenology study of boreal forest understory plants, especially to know how studied phenological traits react to a translocation experiment with a temperature change, phenotypic plasticity and also to understand the change of phenology by climate change for above mentioned species.

Keywords: Climate change, plant phenology, phenological traits, phenology change, cumulative Temperature, phenotypic plasticity, genotypic variation.

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1. Introduction

Climate is changing faster than expected. Temperature has already increased by 1.5˚C compared to the preindustrial era with much larger increases in northern latitudes, causing devastating results in all parts of the globe (IPCC, 2021; Hermansen et al., 2021). Along with changes in precipitation patterns, this temperature increase is affecting the globe´s ecosystems (Roots, 1989). The resultant environmental stress is leading to changes in species distributions, local and global extinctions, altering forest management decisions with resultant impacts on biodiversity, as well as dramatically altering ecosystems' functionality and ecosystem services' delivery (Scholze et al., 2006). The prediction of ecosystem changes under increasing temperatures are, however, largely uncertain.

It is assumed that high latitude areas such as boreal forest, peatland and tundra will experience climate change impacts drastically in the future. Though in some cases rising temperature due to climate change contributes to carbon-sequestration and plant growth in boreal or temperate forests having sub-optimal temperatures (Antala et al., 2022). Boreal forests, also sometimes referred to as Taiga, is one of the largest land biomes in the world which spreads throughout Canada, China, Finland, Japan, Norway, Russia, Sweden, and the United States. The Taiga's species composition is generally dominated by coniferous trees such as pine (*Pinus* spp.), spruce (*Picea* spp.), and fir (*Abies* spp.), together with some broadleaf species such as poplar (*Populus* spp.) and birch (*Betula* spp.). Some understory species in boreal forests are different types of graminoids and forbs, while ericaceous dwarf shrubs play the role of foundation species in the understory of boreal ecosystems (Majasalmi & Rautiainen, 2020). Since deglaciation, boreal forests have been experiencing a variety of fluctuations in their climatic environment. Current warming trends received by Northern latitude and Artic regions are unprecedented. Ultimately resulting impacts are numerous and include the melting of permafrost, changes in plants growth rates, decreasing of nitrogen fixation, invasion of invasive species, increased incidences of wildland fire, and changes in the dynamics of pest and insect outbreaks (The International Boreal Forest Research Association, 1991; Renee Cho, 2022).

Overall plants' seasonal cycle and their development (phenology) are influenced by temperature, photoperiod, and precipitation (Koch et al., 2007). Climate change impacts the phenology of species and observing phenology is a significant tool to monitor climate change impacts which helps to see the following effects on vegetation, although there are other impacts of climate change besides phenology shifting (Koch et al., 2007): 1) shifting of ranges towards higher altitudes and polar regions, 2) changes in both species' composition and density of populations, 3) increasing length of growing seasons. All these events' occurring time are associated with climate conditions along with other global change components such as land use change, habitat fragmentation, pollution, and overexploitation (Koch et al., 2007; Matesanz, Gianoli, & Valladares, 2010). Plant phenological events can change due to climate change as well as other global change components. For example, advances in budburst of *Calluna vulgaris* were found due to nitrogen availability; delay of flowering date was also found for the plants growing in metal-contaminated soil. Matesanz, Gianoli, & Valladares (2010) reports that the ability of providing different phenotypes under different environmental conditions due to the responsible genotype is called phenotypic plasticity. Phenology may follow the changing climate due to phenotypic plasticity. For example, autumn phenology of *Populas trichocarpa* seedlings showed plastic response due to the combined effect of nitrogen addition and elevated CO_2 (Matesanz, Gianoli, & Valladares, 2010).

Observing plant phenology is one of the ways to monitor a plant's response to climate warming as the magnitude of changing climate can be visible through phenological shifts (Meier et al., 2021). Basically, plant phenology refers to some significant events of plants such as leaf unfolding, flowering, fruiting, fruit ripening, color changing of leaf and leaf fall. Evidence says these recurrent seasonal activities are changed due to climate change and these changes can affect whole ecosystem, ecosystem services, trophic chains and the entire dependency of human being and animals on plants (Denny et al., 2014; Nordt et al., 2021). Donnelly et al., (2012) clearly showed that the phenology of the trees *Prunus spinosa* and *Quercus robur* advanced with the spring temperature rise. Leaf phenology is changed with the shift of spring and autumn, and rising temperatures cause changes in the growing period of plants which is an indirect impact of climate change. On the contrary, changes of bioclimatic conditions of plants during growing periods is a direct impact of climate change (Meier et al., 2021).

Most of the phenological observation-based work to see climate change impacts has been done on tree species rather than understory vegetation, despite that some of these species, especially dwarf shrubs, are a significant part of boreal forest ecosystems. Understory plant species are of supreme importance for climate change related research, especially for better understanding of the efficiency of climate change adaptation and mitigation strategies. Consequently, this project is focusing on how the development of forest understory plant species occurs under changing climate. This research will help us to think one more step ahead in these contexts. This work concentrates on four important understory species to see how their phenology reacts with the difference of 2-degree Celsius temperature span. This study selected species which are spread all over Sweden and overall common to boreal forest based on the following research question: How does temperature affect phenology, flowering frequency, and berry production?

Objective of the study:

- To increase our knowledge about how forest understory plant species may phenologically respond to increasing temperatures.

2. Methodology

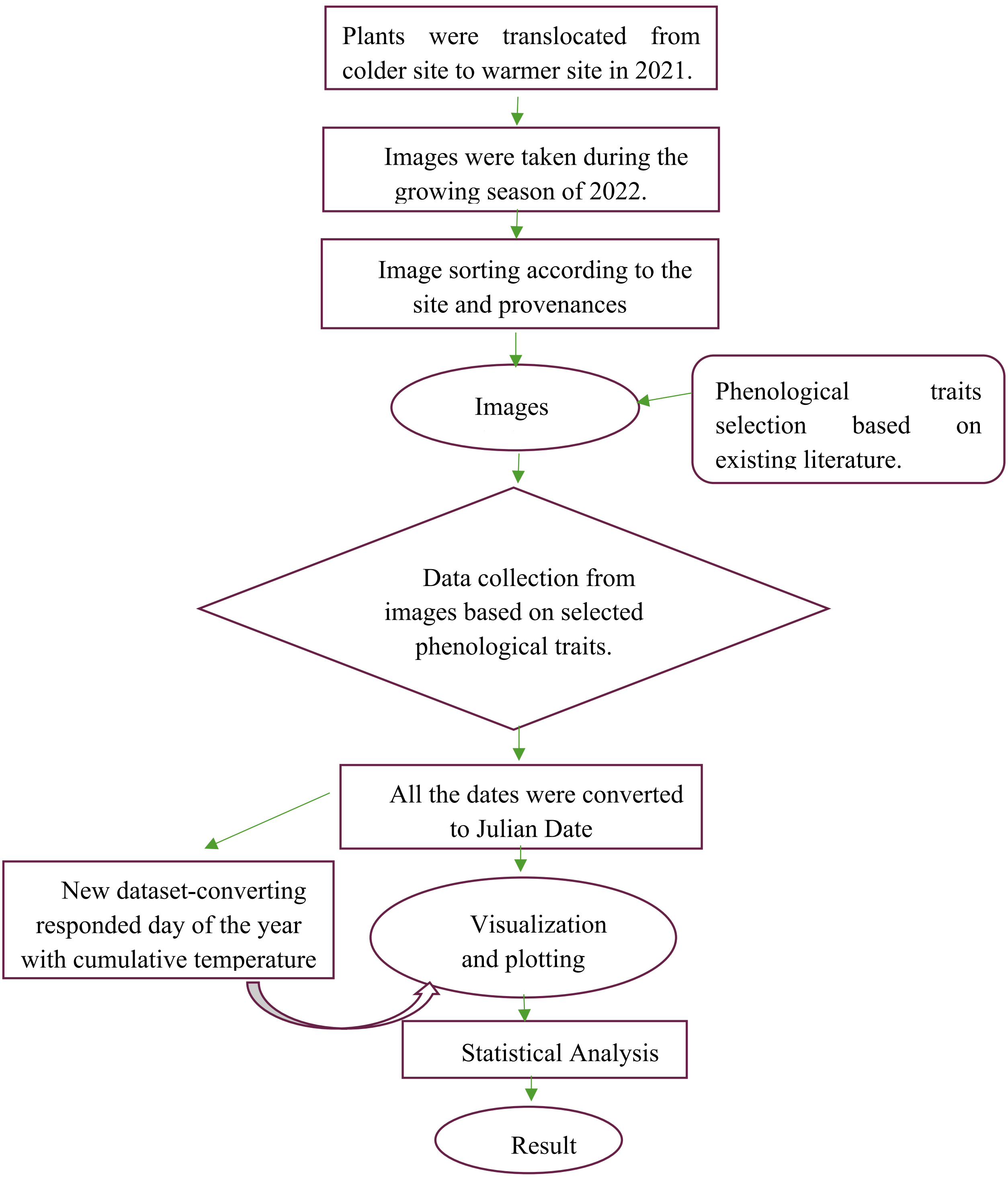

Figure 1. An overview of the whole work showing all the steps that were followed during this research work, especially after translocating the plant materials to the experimental site.

2.1 Species Selection with Short Description

The four species used in this thesis work are *Solidago virgaurea* L. (European golden rod), *Vaccinium myrtillus* L. (Billberry), *Vaccinium vitis-idaea* L. (lingonberry or cowberry) and *Fragaria vesca* L. (wild strawberry or woodland strawberry). These species were selected based on the following reasons:

1. Foundation species (*Vaccinium* sp.)
2. Spread all over Sweden.
3. Some are species with importance for human consumption and recreation.
4. They flower at different times.

Solidago virgaurea is from the Asteraceae family, *F. vesca* is from Rosaceae family and the two dwarf shrubs are from Ericaceae family and common in forest understories (Stewart and Folta, 2010; Turtiainen et al., 2016; Cao et al., 2018). In the following table (Table 1), a short description regarding appearance, distribution, flowering, and fruit harvesting time along with some important benefits to forest ecosystems is included.

Table 1. Short description of studied species regarding appearance, distribution, flowering, and fruits harvesting time along with some important benefits to forest ecosystems.

Bilberry (Vaccinium myrtillus)	Cowberry (Vaccinium vitis-idaea)	Wild strawberry (Fragaria vesca)	Goldenrod (Solidago virgaurea)
 (Source: NCCIH) 1) Distributed in Europe, northern Asia, America. Bilberry grows in forests, heaths, moors, pristine and drained peatland (Turtiainen et al., 2016). 2) Flowering period starts from middle of May to end of May and fruits are harvested from mid-July in Sweden (Hjalmarsson, 2004). 3 Having anti-inflammatory and antioxidant effects, bilberries are good for human eyesight health (Bokelmann, 2021). A good habitat and important food source for wildlife, favorite to deer. Density of trees and light intensity in forests affect its production (Pires et al., 2021; Parlane et al., 2006).	 (Source: Depositphotos) 1) Distributed in Europe, north America, and northern Asia. Cowberries are native to boreal and subarctic regions and grow in forests, bogs, and other open habitats (Turtiainen, 2015). 2) Flowering period of cowberry in Sweden is May, June and fruiting starts in July (flowersinsweden.com) 3) Having the ability to avert low grade inflammation and diet related obesity in diabetic animals, lingonberries are also an important food source for wildlife (Kowalska, 2021). It plays a vital role to ecosystems being wildlife habitat, sequestering carbon, improving soil quality, and regulating water flows by increasing soil water retention and reducing erosion (Bohlin et al., 2021).	 (Source:Click & Grow) 1) Native to Europe and can be found growing in woodlands, meadows, and other open habitats (Stewart and Folta, 2010). 2) Flowering starts during May and the season lasts until July. (Lundblad, 2020). 3) Vitamin C and anti-inflammatory properties of strawberry fruits help to reduce chronic disease in the human body. Again, young leaves are advantageous as diuretic, laxative and tonic (Giampieri et al., 2015). This fruit is an important food source for wildlife. Strawberries play a vital role in soil conservation and habitat creation (Prior, 2003; Lundblad, 2020).	 (Source: myGarden.org) 1) Native to Europe and Asia. This species grows in forests, mountains, river sites, bogs and meadow vegetation and reaches into the alpine zone of the Scandinavian Mountain range (Bergsten, 2009). 2) Flowering period of goldenrod in Sweden is July-September (flowersinsweden.com) 3) For preventing diseases of the urinary system of the human body, this plant is used for its diuretic, antispasmodic, and analgesic properties (Budzianowski et al., 2021). It has ornamental values, soil stabilization capability, and a good source of nectar as well as pollinator habitat (source: Nature & Garden).

2.2 Study Area and Experimental Design

Study area and experimental design was set in 2021. Three experimental sites were selected following a sequence, northern Sweden, middle of Sweden and southern Sweden (warm locations). For each of these sites a corresponding site with 2-degree Celsius lower temperature was chosen (cold locations). Sites used in the transplant experiment are from north to south: Tärnaby (cold) and Vindeln (warm, northern Sweden), Idre (cold) and Siljan (warm, middle of Sweden), Tomtabacken (cold) and Vivarp (warm, southern Sweden) (Figure 2).

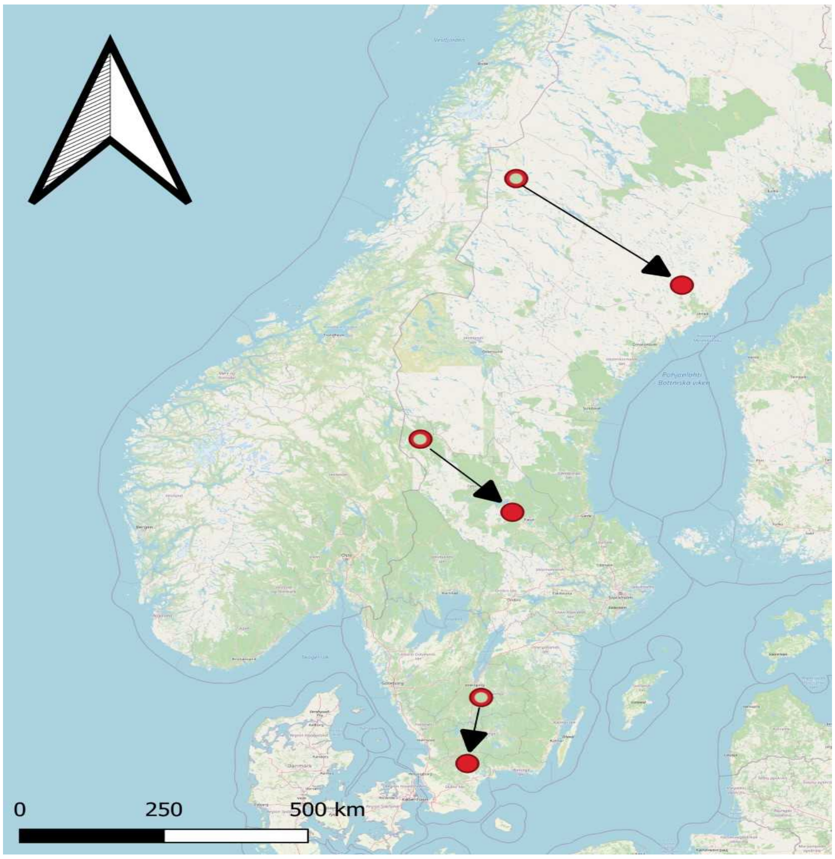

Figure 2. Sites used in the transplant experiment. From north to south: Sandsjö (Vindeln), Siljan and Vivarp. Rings correspond to the origins of the cold provenances from where plants were transplanted, whilst red full circles correspond to the warm sites, where all the material (both cold and warm provenances) was transplanted for the experiment.

Plant materials were collected in all sites (both warm and cold) and transplanted in the warm sites resulting in two provenances of each species in each warm site. Plant materials, for example ramets/seeds, were collected based on different strategies. Ramets of the dwarf shrubs and strawberry were collected at 2-4 sites/forest stands at each site. These sites were separated by at least 1 km. To avoid collecting ramets from the same clone these were collected with a distance of at least 7 m in-between. For goldenrod individuals, mature seeds were collected at each location and site/forest stand without taking the distance between individuals into account.

All the plant materials were collected during summer 2020. The dwarf shrubs and strawberry ramets were planted in container trays and kept in a garden at each warm location until replanting in bigger pots and placed in the forest in spring 2021. The goldenrod seeds were stored over winter and germinated and planted in container trays in spring and summer 2021 and placed in the forest in August 2021. Pots of 7.5 L size were used for planting collected plant materials. In each pot, four plant individuals were planted. The pots were inserted into the soil at the destination site with a spade. "Hasselfors P-jord" which is a soil type with medium pH was used for goldenrod and strawberry. On the contrary, "Hasselfors Rhododendronjord" which is a soil type with low pH was used for the dwarf shrubs (bilberry and lingonberry).

The potted plants were located in 10 different places at each site. Later, in the growing season of 2022, photos were taken for both provenances (cold provenance and warm provenance) every 5th day (May 10, 2022, to August 12, 2022) at Siljan and Vindeln (May 20, 2022, to August 12, 2022), however at Vivarp images were taken more frequently (every 3rd to 4th day) than at the other two sites (April 24, 2022, to September 09, 2022). In total, approximately 6000 images (few examples in figure 3) were analyzed for the four species. Later, images were sorted and analyzed based on the selected phenological traits per species (Table 2). Acquired data from image analysis were used as response variables in a statistical framework together with Julian day and cumulative temperature. At first, all the responded dates were converted to calculated Julian day according to the Julian Calendar (data set 1). Furthermore, the number of flowers and the numbers of ripened fruits per observation day for *F. vesca* were counted. The average number of flowers per pot and the average number of ripe strawberries per pot were calculated. At Vivarp, all plants were protected from wild boar and browsing by a fence though other sites were not fenced.

Air temperature data at the macroclimate scale was downloaded from the ERA5-Land climatic model (Hersbach et al., 2020) for each forest stand. This data was downloaded through the ‘mcera5’ R package (Klinges et al., 2022), which applies a set of temperature range corrections to the raw data. Data was downloaded hourly, averaged daily and then the cumulative temperature was calculated for the vegetation period of each site. We understand the vegetation period as that one in which the temperatures are warm enough to allow vegetation growth. The vegetation period was considered to start after daily mean temperature surpassed 5C for at least five consecutive days. This was on the 10^{th} of April 2022 in Vindeln, 17^{th} of April 2022 in Siljan, and on the 13^{th} of April 2022 in Vivarp. Finally, these cumulative temperatures were matched with the corresponding Julian days of phenological events and used in the following analyses.

Fragaria vesca

Solidago virgaurea

Vaccinium myrtillus

Vaccinium vitis-idaea

Figure 3. Four images of four species among analyzed total 6000 images of studied species.

2.3 Selected Phenological Events

After reviewing literature and Wikipedia, including standard protocols for phenological traits observation (Meier et al., 2021; Denny et al., 2014; Sandor et al., 2021; Nordt et al., 2021; Montgomery et al., 2020, Koch et al., 2007), the traits in Table 2 were selected. Furthermore, the day of the year (DOY) for each phenological event was recorded by analyzing all the photos.

Table 2. Species wise selected phenological traits for image analysis.

Name of the Species	***Solidago virgaurea* (European goldenrod)**	***Fragaria vesca* (wild strawberry or woodland strawberry)**	***Vaccinium myrtillus* (Bilberry)**	***Vaccinium vitis-idaea* (lingonberry or cowberry)**
Selected Phenological Traits	First emergence of petals	Flower bud development	Starting day of first leaf	Flower bud development
	Flower bud development	First emergence of petals	Flower bud development	Ending flowering period
	Highest number of flowers	Number of flowers	Ending flowering period	
	Ending flowering period	Ending flowering period		
	Seed setting day	First fruit development day		
	Remaining percentage of flowers after stopping image taking	Number of ripen fruit		

2.4 Statistical Analysis

R programming language (R Core Team, 2021) was used for data analysis. In the beginning, lubridate package was used for converting the response date (DOY of Gregorian calendar) to Julian date (Julian calendar). Later, data assumptions' tests (Shapiro's test to see the normal distribution of data and Levene's test to see the homoscedasticity of error variance) were completed to check whether the data fulfill the assumptions of ANOVA (Analysis of Variance) or not. However, it was found that more than half of the number of response variables did not satisfy the assumptions of ANOVA even with the log and square root transformation. Therefore, the Kruskal-Wallis test was used for all the response variables. Finally, to test for treatment effects between provenances within site, the Dunn´s test was used for the significant (P value <0.05) variables that were found with the Kruskal-Wallis tests. Finally, for visualization, box plots were created with the variables which had largest treatment effects (at least for two sites out of three sites) and also visualization was made to compare the flower and fruit production of *F. vesca* between provenances of three sites using ggplot2 package.

3. Results

3.1 *Fragaria vesca* with Julian Date

According to the Kruskal-Wallis test, P-values for all the variables are <0.05. Therefore, Dunn's test was implemented to test for differences between the provenances within site. However, there are no significant differences between provenances for *F. vesca* (Table 3).

3.2 *Fragaria vesca* with Cumulative Temperature Data

According to the Kruskal-Wallis test, except variable DOY of the ending flowering period, P-values for other three variables are <0.05. Therefore, Dunn's test was implemented to those significant variables to test for differences between the provenances within site. For the variable DOY flower bud development and DOY of first petal emergence, there is significant treatment effect at Siljan (middle of Sweden). On the contrary, in the case of DOY of first fruit development, there are significant treatment effects in both Vindeln (north) and Siljan (south) (Table 4 and figure 4).

Table 3. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Fragaria vesca (Julian Date). Here, N (north, Vindeln), M (middle, Siljan), S (south, Vivarp), C= Cold provenance and W= Warm Provenance.

Variable	Kruskal-wallis two-way interaction (site and pot) and treatment effect						
Flower Bud Development	Kruskal wallis chi-squared = 46.6, df = 5, p-value <0.01						
	Treatment effect						
	Group1	Group 2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	-0.461	0.647	ns
	M C	M W	9	9	-1.81	0.699	ns
	S C	S W	10	10	0.31	0.760	ns
First Petal emergence	Kruskal-Wallis chi-squared = 45.3, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	0.32	0.749	ns
	M C	M W	9	9	-1.27	0.205	ns
	S C	S W	10	10	0.78	0.437	ns
Ending Flowering period	Kruskal-Wallis chi-squared = 17.9, df = 5, p-value = 0.003						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	1.03	0.304	ns
	M C	M W	9	9	0.45	0.653	ns
	S C	S W	10	10	0.78	0.439	ns
First Fruit Development	Kruskal-Wallis chi-squared = 37.8, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group1	N1	N2	Statistics	P-value	Significance
	N C	N W	9	10	1.15	0.252	ns
	M C	M W	5	9	-1.51	0.133	ns
	S C	S W	10	10	0.00	1.000	ns

Table 4. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Fragaria vesca (Cumulative Temperature).

Variables	Kruskal Wallis two ways interaction (site and pot) and treatment effect					
Flower Bud Development	Kruskal-Wallis chi-squared = 21.9, df = 5, p-value = 0.0005					
	Treatment Effect					
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	-0.65	0.515	ns
	M C	M W	9	9	-3.09	0.002	**
	S C	S W	10	10	0.52	0.474	ns
First Petal Emergence	Kruskal-Wallis chi-squared = 17.2, df = 5, p-value = 0.004					
	Treatment Effect					
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	0.56	0.577	ns
	M C	M W	9	9	-1.96	0.049	*
	S C	S W	10	10	1.56	0.120	ns
Ending Flowering Period	Kruskal-Wallis chi-squared = 2.1, df = 1, p-value = 0.148					
First Fruit Development	Kruskal-Wallis chi-squared = 11.9, df = 5, p-value = 0.036					
	Treatment Effect					
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	9	10	2.11	0.035	*
	M C	M W	5	9	-2.21	0.027	*
	S C	S W	10	10	0.10	0.919	ns

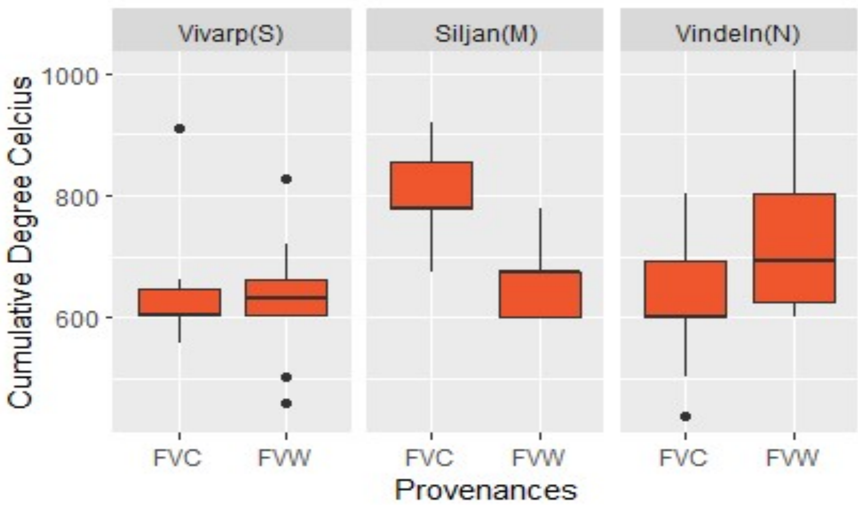

Figure 4. Day of the year (DOY) cumulative temperature of first fruit development in different sites. Here, FVC and FVW represent F. vesca at cold and F. vesca at warm sites respectively.

3.2.1 Calculated Average Number of Flowers and Fruits of *F. vesca.*

The average number of flowers and fruits of *F. vesca* were calculated during image analysis (Table 5). All the data assumptions' tests (Shapiro's test to see the normal distribution of data and Levene's test to see the homoscedasticity of error variance) and later Kruskal-Wallis test was performed for calculated average number of flowers and fruits also. However, no significance was found with the statistical tests. It is visible from the table 5 and figure 5 that there were differences in average number of flowers between cold and warm provenances in Vivarp and Siljan. But no variation was found at Vindeln. In the case of the average number of fruits, the highest difference was found at Vivarp (Table 5 and Figure 5). In figure 6, the number of flowers and fruits' distribution in different sites are also visible.

Table 5. Average number of flowers and fruits of Fragaria vesca.

Provenances	Sites	Average no of flower	Average no of fruit
FVC	Vivarp(S)	4.17	3.61
FVW	Vivarp(S)	3.76	2.09
FVC	Siljan(M)	3.75	3.25
FVW	Siljan(M)	4.81	3.08
FVC	Vindeln(N)	2.56	3.15
FVW	Vindeln(N)	2.58	3.35

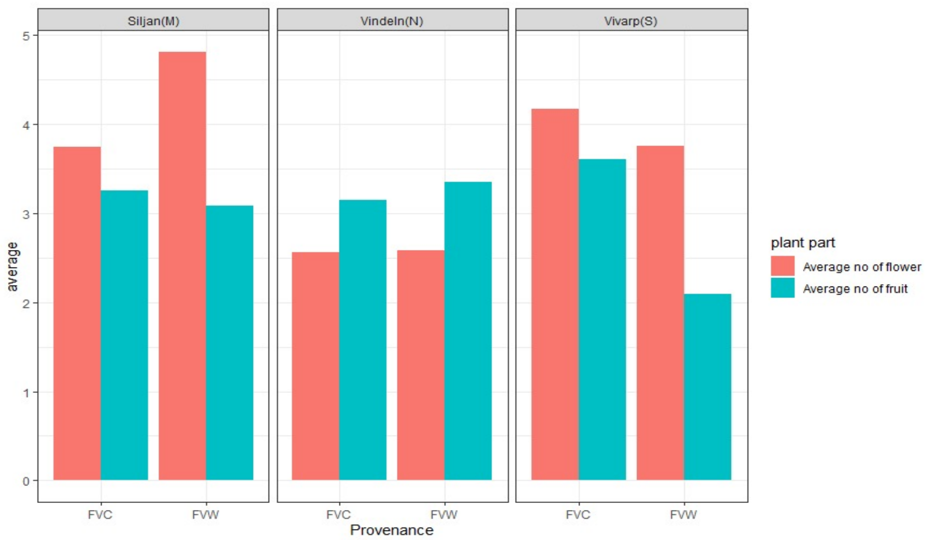

Figure 5. Average number of flowers and average number of fruits of F. vesca in different sites.

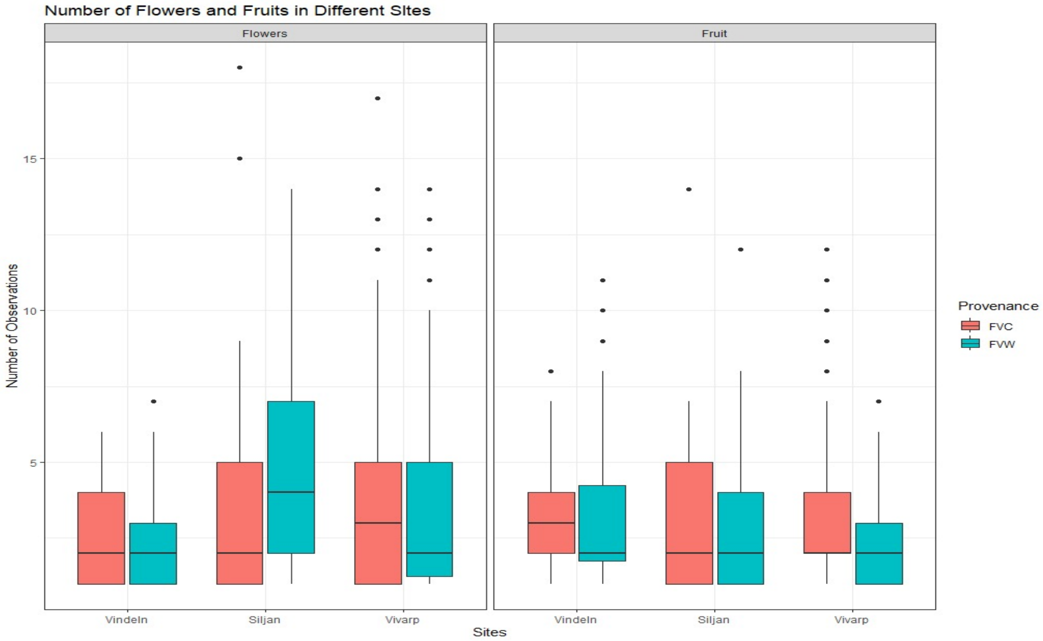

Figure 6. Number of flowers and fruits of F. vesca in different sites.

3.3 *Solidago virgaurea* with Julian Date

According to the Kruskal-Wallis test, P-values for all the variables are <0.05. With the implementation of Dunn's test, significant treatment effects for both DOY flower bud development and DOY of first petal emergence have been found at Vivarp, however, no treatment effects have been found in other two sites. For DOY of highest percentage of flowers and DOY of seed setting, there are significant treatment effects in both Vindeln (north) and Vivarp (south), not at Siljan. Finally, for DOY of ending flowering period, there is only significant treatment effect at Vindeln (north) (Table 6).

Table 6. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Solidago virgaurea (Julian Date).

Variables	Two ways Kruskal Wallis interaction and treatment effects						
Flower Bud Development	Kruskal-Wallis chi-squared = 41.9, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	1.02	0.309	ns
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	3.23	0.001	**
First Petal Emergence	Kruskal-Wallis chi-squared = 42.1, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	1.87	0.061	ns
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	2.68	0.007	**
Highest percentage of Flower	Kruskal-Wallis chi-squared = 47.6, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	2.45	0.014	*
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	2.54	0.011	*
Seed Setting	Kruskal-Wallis chi-squared = 35.1, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	2.85	0.005	**
	M C	M W	10	10	0.00	1.00	ns
	S C	S W	10	10	2.94	0.003	**
Ending Flowering Period	Kruskal-Wallis chi-squared = 27.6, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	4	1	2.35	0.019	*
	M C	M W	7	7	-0.43	0.670	ns
	S C	S W	10	4	1.26	0.209	ns

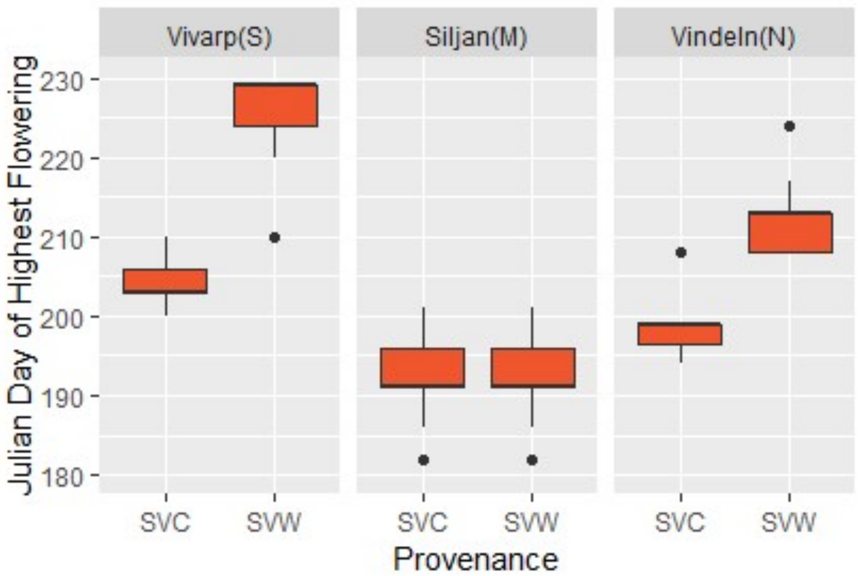

Figure 7. Response of Julian DOY (day of the year) of highest percentage of flowering. Here, SVC and SVW represent S. virgaurea at cold and S. virgaurea at warm sites respectively.

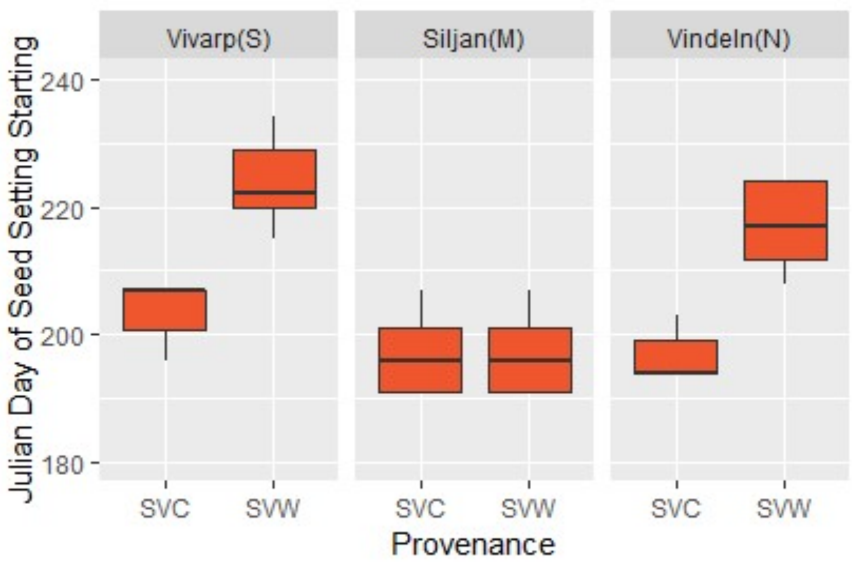

Figure 8. Response of Julian DOY (day of the year) of seed setting starting in different sites. Here, SVC and SVW represent S. virgaurea at cold and S. virgaurea at warm sites respectively.

In figures 7 and 8, it is visible that the highest flowering percentage and seed setting starting need less average Julian days in the cold provenance and more average Julian days in the warm provenance in both Vivarp and Vindeln. However, at Siljan, the time is almost same for both phenological traits to respond.

3.4 *Solidago virgaurea* with Cumulative Temperature Data

According to the Kruskal-Wallis test, P-values for all the variables are <0.05. With the implementation of Dunn's test, except DOY of ending flowering period, all other variables have significant treatment effect in northern site (Vindeln) (Table 7).

Table 7. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Solidago virgaurea (Cumulative Temperature Data).

Variables	Two ways Kruskal-Wallis interaction and treatment effects						
Flower Bud Development	Kruskal-Wallis chi-squared = 42.4, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	2.27	0.023	*
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	1.59	0.112	ns
First Petal Emergence	Kruskal-Wallis chi-squared = 44.1, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	2.22	0.027	*
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	1.27	0.205	ns
Highest percentage of Flower	Kruskal-Wallis chi-squared = 47.9, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	9	2.64	0.008	**
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	1.36	0.173	ns
Seed Setting	Kruskal-Wallis chi-squared = 44.6, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	7	8	2.87	0.004	**
	M C	M W	10	10	0.00	1.000	ns
	S C	S W	10	10	1.69	0.089	ns
Ending Flowering Period	Kruskal-Wallis chi-squared = 28.9, df = 5, p-value < 0.01						
	Treatment Effect						
	Group1	Group2	N1	N2	Statistics	P value	Significance
	N C	N W	4	1	1.46	0.145	ns
	M C	M W	7	7	-0.34	0.736	ns
	S C	S W	10	4	1.25	0.213	ns

3.5 *Vaccinum myrtillus* with Julian Date

According to the Kruskal-Wallis test, P value is significant (<0.05) for only DOY of first leaf. With the Implementation of Dunn's test, no treatment effect was found (Table 8). All the plant materials of *V. myrtillus* at Siljan died before being placed to the experimental site. Therefore, data analysis had to be restricted to the available data from the other two sites (Vivarp and Vindeln). In tables 8 and 9, the green colored row indicates unavailability of data from site Siljan.

3.6 *Vaccinum myrtillus* with Cumulative Temperature Data

According to the Kruskal-Wallis test, P value is significant (<0.05) for only DOY of first leaf. With the Implementation of Dunn's test, no treatment effect was found (Table 9).

Table 8. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Vaccinum myrtillus (Julian Date). Green colored row indicating no data. At Siljan, all the plants died before being established.

Variables	Two ways Kruskal Wallis interaction and treatment effects						
First leaf	Kruskal-Wallis chi-squared = 44.4, df = 4, p-value < 0.01						
	Treatment effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	-0.02	0.988	ns
	M C	M W					
	S C	S W	10	10	-0.40	0.684	ns
Flower Development	Kruskal-Wallis chi-squared = 5.7, df = 3, p-value = 0.129						
Ending Flowering Period	Kruskal-Wallis chi-squared = 3.1, df = 2, p-value = 0.220						

Table 9. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Vaccinum myrtillus (Cumulative Temperature Data).

Variables	Two ways Kruskal Wallis interaction and treatment effects						
First leaf	Kruskal-Wallis chi-squared = 13.9, df = 4, p-value = 0.008						
	Treatment effect						
	Group1	Group2	N1	N2	Statistics	P-value	Significance
	N C	N W	10	10	-0.02	0.988	ns
	M C	M W					
	S C	S W	10	10	-0.41	0.684	ns
Flower Development	Kruskal-Wallis chi-squared = 3.1, df = 3, p-value = 0.382						
Ending Flowering Period	Kruskal-Wallis chi-squared = 3.1, df = 2, p-value = 0.220						

3.7 *Vaccinum vitis-idaea* with Julian Date

According to the Kruskal-Wallis test, P value is significant (<0.05) for only DOY of flower bud development. With the Implementation of Dunn's test, no treatment effect was found (Table 10). During image analysis, no phenological response was found for the trait DOY of flower bud development from the images of site Siljan. In table 10, green colored row indicates data unavailability for that specific site.

3.8 *Vaccinum vitis-idaea* with Cumulative Temperature Data

According to the Kruskal-Wallis test, P-values for all the variables are >0.05. Therefore, the Dunn's test has not been implemented to see the treatment effect (Table 11).

Table 10. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Vaccinum vitis-idaea (Julian Date). Green colored row indicating no data.

<table>
<tr><th>Variables</th><th colspan="7">Two ways Kruskal Wallis interaction and treatment effects</th></tr>
<tr><td rowspan="6">Flower Bud Development</td><td colspan="7">Kruskal-Wallis chi-squared = 9.9, df = 4, p-value = 0.042</td></tr>
<tr><td colspan="7">Treatment Effects</td></tr>
<tr><td>Group1</td><td>Group2</td><td>N1</td><td>N2</td><td>Statistics</td><td>P-value</td><td>Significance</td></tr>
<tr><td>N C</td><td>N W</td><td>4</td><td>2</td><td>-0.69</td><td>0.491</td><td>ns</td></tr>
<tr><td>M C</td><td>M W</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>S C</td><td>S W</td><td>6</td><td>5</td><td>-0.52</td><td>0.603</td><td>ns</td></tr>
<tr><td>Ending Flowering Period</td><td colspan="7">Kruskal-Wallis chi-squared = 7.4, df = 3, p-value = 0.060</td></tr>
</table>

Table 11. Results from Kruskal-Wallis (Omnibus test) and Dunn's (pairwise comparisons) tests of different variables of Vaccinum vitis-idaea (Cumulative Temperature Data).

Variables	Two ways Kruskal Wallis interaction (Site and pot)
Flower Bud Development	Kruskal-Wallis chi-squared = 5.6, df = 4, p-value = 0.239
Ending Flowering Period	Kruskal-Wallis chi-squared = 3.5, df = 3, p-value = 0.324

4. Discussion

As response to changing climate, plants generally may shift their ranges to the favorable condition, adjust their phenotype with the plastic nature or adapt to the different environments with their standing genetic variation (Matesanz & Ramírez-Valiente, 2019). Finding or not finding translocation treatment effects indicate two different responses, phenotypic plasticity, and genotypic variation, respectively. Showing different phenotypes in different environments due to responsible genes is called phenotypic plasticity. Phenotypic plasticity is one of the fastest mechanisms to respond to the changing climate. Plastic response allows plants to alter their developmental stages instead of altering genetic composition when there is environmental difference. More specifically, this phenotypic plasticity is a more short-term response than genetic adaptation to continue plant's survival in changing environment (Donnelly et al., 2012). Plasticity could be adaptive in heterogeneous environment and these adaptive plastic responses allow plants to maintain functional activities and keep fitness to varied environments (Sultan, 2000; Matesanz, Gianoli, & Valladares, 2010). In this study, the lack of significant provenance effects in many cases indicates that the cold provenance has adapted to the warmer site by phenotypic plasticity meaning probably they are able to tackle a 2-degree warming and adapt quickly as their phenology is plastic. With this special ability, plants generally withstand environmental stress to maintain growth and fitness in the short term or long term (Donnelly et al., 2012). However, the type of plasticity shown by plants depends on the type or level of pressure that comes from different environments. Plants also show survival and recovery mechanisms (high level plasticity due to extreme environmental events) to withstand environmental stress. For example, *Polygonum persicaria* has strong phenotypic plasticity for functional and fitness traits in different environments (contrast light availability, nutrients, and moisture level) (Sultan, 2000).

Following the results of this thesis work, there weren't many effects of translocation which has both positive and negative sides. In a positive way, these low translocation effects must be considered good as it indicates that phenology will follow temperature change through the ability of altering behavior in different environmental conditions. Matesanz, Gianoli, & Valladares (2010) listed the adaptive plastic nature of phenological (functional) and morphological traits of a number of species due to the global change components. When no translocation treatment effects are found it denotes that species show the phenotypic plasticity and with that ability, phenology follows the temperature change. *Vaccinum myrtillus* and *V. vitis-idaea* are highly common in all over Sweden, especially in the north. Almost in every stand the availability of these dwarf shrub species is visible. Therefore, it could be assumed that the dwarf shrubs may have less genetic variation and local adaptation due to their abundance. Also, the mortality of *V. myrtillus* at Siljan restricted data analysis to the available data from the other two sites (Vivarp and Vindeln).

Genotypic variation or gene involvement is a reason behind translocation treatment effects found by recent studies. Studies claim that specific genes could be responsible for showing different phenological responses. A European study found phytochrome B2 (*phyB2*) gene's involvement is responsible in controlling photoperiodism and light responses. Another experimental translocation study of *Larix europea* and *Pinus mugo* based on an altitudinal gradient found genetic diversity and genetic responses (Donnelly et al., 2012). In this research, among all the four species, *S. virgaurea* only showed strong translocation treatment effects which could be because of genetic variation or specific gene involvement. Effects of different genotypes probably lead this species to show differences between provenances. Either they need lower temperature sums and thus flower earlier at the warm site, or that they are restricted to a certain (later) time period from their (cold) home site and then flower later at the warm sites compared to the warm provenance.

However, there could be some negative effects anyway if pollinator communities don't respond the same way since *S. virgaurea* responded strongly to translocation. Therefore, it could be assumed that the two origins faced quite different pollinator communities. Resulting seed production and seed quality are largely unknown, and more research is needed to sort that out. Evidence says that rising temperature plays a vital role in shifting phenology such as for *S. canadensis*, rising temperature leads to early flowering and fruiting along with the change of species distribution (Cao et al., 2018). However, during this research work, some weaknesses have been identified for *S. virgaurea*. For example, variation among plots in case of protection from browsing as it is already mentioned that, only at Vivarp, species were protected from browsing effect. Therefore, browsing effects were found in other sites during image analysis. Also, low picture quality was a problem during data analysis (especially in Siljan). Taking photos of *S. virgaurea* was difficult as this plant is tall and has a bushy structure. In choosing phenological traits, initially it was decided to count berries to get assumption on berry production. But from images, counting bilberries was difficult and considering that would lead to controversial data. So, this trait was excluded.

Forest layer has a great potential impact on phenology. A recent study in the Black Forest National Park, Germany, shows that flower buds, fruit abundance and overall fruit production of *V. myrtillus* is increased with greater canopy openness. Even under the sun, seed setting is highest, influenced by higher pollinator activities (Eckerter et al., 2019). Initially, the plan was to consider the forest layer/canopy type's effect in phenology analysis. The variability in light conditions among the sites where the replicate pots were located may have lowered the chance of getting significant differences between the provenances. However, considering the time frame and length of this work, analysis of light conditions had to be excluded. Transplanting plants to a 2-degree Celsius warmer location and studying the response of appropriate phenological traits considering pollinator communities' behavior and forest structure could be considered realistic for understory plants, especially if the naturally temperature rising scenario is observed. In Sweden, according to SMHI (the Swedish Meteorological and Hydrological Institute), the average temperature has increased around 1.9 degree Celsius compared to 1800s (SMHI, 2022). Therefore, a greater knowledge about how phenology is reacting to this rising temperature and what is the total change, could be identified through this type of transplanting experiments.

5. Conclusion

Focusing on the changing climate and its impact on forest understory plant species, this study analyzed the effects of climate on phenology, flowering, and berry production of four important forest understory species. In most cases, this study couldn't find any translocation treatment effects, however for some phenological traits, significant treatment effects of translocation have been found. For example, DOY of first fruit development of *F. vesca;* DOY of seed setting and DOY of highest percentage of flowering of *S. virgaurea* showed strong significant treatment effect (at least in two sites out of three). A few other phenological traits showed significant treatment effects at one site. Reasons behind these results could be both phenotypic plasticity and genotypic variation. It can be assumed that having less translocation treatment effects describe that the phenology will follow temperature changes with the ability of adaptive phenotypic plasticity which is positive. Again, due to genotypic variation, getting translocation treatment effects of phenological traits is possible. However, different pollinator communities' behaviour also could cause treatment effects on seed production and seed quality. Therefore, in the future these issues need to studied in more detail. However, no significant treatment effects have been found for *V. myrtillus* and *V. vitis-idaea*. Treatment effects on phenological traits for these two species may have been detected if variation in forest density (light conditions) would have been considered for this study. Also, if the number of fruits could have been counted, this research could see the effect on the total berry production.

6. Recommendation

To get better response for *V. myrtillus* and *V. vitis-idaea*, more phenological traits such as counting number of berries, and number of flowers can be considered in future research. Furthermore, instead of using photos, direct counting of flowers and fruits at the site is suggested. Future research can find out whether there is any genotypic variation behind having treatment effects or not in *S. virgaurea*. Again, to avoid the weakness of image quality issue, videos can be made, and more images can be captured carefully. Also, browsing effect should be avoided by fencing all the species in all sites to get representative results. Including canopy structure and ensuring the identical behavior of pollinator communities are also recommended. Overall, considering these issues, more research is recommended, building on the results and experiences gained by this research work.

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Popular science summary

Temperature rises and environmental change: How flowering, fruiting and different types of berry production can be affected?

Leaf unfolding, flowering of plants, fruiting, fruit ripening, color changing of leaf, leaf fall and so on are referred to plant phenology. For the entire ecosystem, these phenological traits are highly important for example, food chain can be altered if these phenological traits get disturbed. Recently, climate change and global warming have become the most familiar words. It is unpleasant to hear that plant phenology is affected by climate change. Phenological traits react to the changing climate. This research work tried to figure out the responses of different phenological traits to the rising temperature for four important understory plants that are available in Sweden. These studied plant species are wild strawberry, blueberry or bilberry, lingonberry or cowberry, and European golden rod. This research also tried to see how berry production gets hampered due to temperature rise. To do that, this work followed a transplanting method where all the plant materials of studied species were established in warm sites from cold sites along a 2-degree Celsius temperature difference. Later, in spring (plant's growing season) 2022, pictures were taken in both cold and warm sites to continue the study. Some phenological traits were selected to examine those photos based on some previous research guidance. For getting some responses following a method, it was decided to use Julian days. Later, another comparison was also done following the temperature data to see how phenology changes against temperature. Surprisingly, this study found few phenological traits responding. Therefore, the results mainly indicate that the studied plant populations can cope with a 2-degree temperature difference by their inherent phenotypic plasticity. Finally, considering a few methodological weaknesses, improvements for future research are suggested.

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