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Timing is everything: Within-plant flowering phenology impacts fruit production in the Arctic-Alpine cushion plant *Silene acaulis* (L.) Jacq.

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Cover photo: A hermaphrodite Silene acaulis in the High-Arctic site (Bjørndalen, Svalbard) photographed in late July 2020. Photo: Simen Hjelle.

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Master of Science in Biology – Northern Populations and Ecosystems
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Foreword

This thesis aimed to investigate flowering phenology and fruit production of *Silene acaulis* (L.) Jacq., but is also a part of several larger projects with wider scopes. Therefore, I contributed to the collection of a large quantity of data that is not presented in the final thesis. In the Low-Arctic, time-lapse cameras monitored plants every ten seconds throughout the season, and in the High-Arctic every minute, while only a subset of every 24 hours was used to study flowering phenology in the thesis. This was done to capture pollinator activity and to train machine learning algorithms first on flower stages, then on insect activity. Pitfall traps were established by each camera group to correlate image pollinator activity to ground arthropod activity.

In addition, I also collected data for this thesis that I will present less extensively. In addition to the time-lapse monitored plants, a large-scale population study was established in the Low Arctic site and all plot plants were photographed every third day throughout the flowering season. A similar population study was established in 2021 in the High-Arctic site, where plants were photographed every week. A preliminary study on cushion microclimate was also done at two sites in the High-Arctic. To keep the thesis focused and manageable within the given time frame, only an overview of the population study and one of the sites from the preliminary study are presented in sections “2.3 Study population”, “Appendix 1” and “Appendix 2”. Finally, at each site, a complimentary pollen limitation study was performed (Figure 1). However, the pollinator exclusion nettings were disturbed by reindeer in the High-Arctic site and small pollinators managed to get through the pollinator exclusion netting in the Low-Arctic site. The complementary pollen limitation studies will therefore not be included in the final thesis.

Figure 1 Research assistant Anne Bruls hand-pollinating flowers in the High-Arctic site. Such complementary pollen limitation experiments were performed in both sites but not included in the final thesis.

1 Abstract

Timing is everything for Arctic flowering plants. Early flowers might be destroyed by frost, while late flowers have less time and resources to mature fruit. With climate change, Arctic flowering phenology is shifting. Yet for many species, phenology studies only encompass the onset of flowering and lack baseline data on within-plant flowering times. I used the gynodioecious cushion plant *Silene acaulis* (L.) Jacq. to investigate how within-plant flowering phenology impacts fruit production in one growing season. In 2019, time-lapse cameras were used to daily observe flowers within two populations in the Low-Arctic (Narsarsuaq, Greenland in the Low-Arctic/Sub-Arctic transition zone; 7851 flowers, 21 plants) and the High-Arctic (Bjørndalen, Svalbard; 1587 flowers, 11 plants). Plants flowered for approximately three weeks, with a positively skewed peak floral display. In the Low-Arctic site, most investigated individuals were females dependent on pollinator visits for fruit production. Within these Low-Arctic females, flowers blooming during peak floral display had a higher probability of fruit set than flowers blooming outside peak floral display. In addition, flowers blooming before peak flowering were more likely to produce fruit than flowers blooming after peak flowering, both at the individual level and between individuals within the whole population. Hermaphrodites, however, can self-pollinate, and preliminary results indicate higher fruit set outside peak flowering within individuals and populations. In contrast to the Low-Arctic site, all plants in the High-Arctic site were females and a frost event occurred during flowering. Despite the frost event, females in the High-Arctic site had twice as high fruits per flower proportions as females in the Low-Arctic site. For flowers not exposed to frost, similarly to the Low-Arctic site, flowers blooming during peak floral display were more likely to produce fruit than flowers blooming outside peak floral display. Also similar to the Low-Arctic site, early flowers, both within individuals and the population, had a higher probability of fruit set than late flowers. For frost exposed flowers, however, the degree of frost damage was likely more important for fruit set than flower timing, indicating that late flowers can be part of a bet-hedging strategy. Altogether, these results portray how a long flowering period, combined with a peak floral display and early flowering, can be a strategy to ensure fruit production in the unpredictable Arctic growing season.

Keywords: *Silene acaulis*, phenology, within-plant flowering timing, floral display, fruit production, interspecific pollinator competition, gynodioecious, Arctic plant reproduction

2 Introduction

Reproduction is a challenge for Arctic plants. Due to the short growing season and low temperatures, Arctic plants have a short climatic window to grow and reproduce. This optimal climatic time is currently changing, with the Arctic warming twice as fast as other terrestrial regions (Box et al., 2019; Niskanen et al., 2019; Prevey et al., 2019). Moreover, many plants depend on pollinators to successfully reproduce. In the Arctic, plant-pollinator interactions have profound effects on plant diversity, distribution, and colonization (Alsos et al., 2015; Eidesen et al., 2017).

Plant-pollinator interactions are impacted by climate change, as temperature regulates both plant metabolism and pollinator activity (Høye & Forchhammer, 2008; Lafta & Lorenzen, 1995; Zoller et al., 2020). The weather during bloom can impact fruit production and early-season frost might destroy flowers and immature fruits (Arroyo et al., 1985; Bell & Bliss, 1980; Straka & Starzomski, 2015; Tuell & Isaacs, 2010). Clear days with higher bloom temperatures, on the other hand, could increase pollinator activity, pollinator visits to flowers, and subsequent fruit production (Corbet, 1990; Tuell & Isaacs, 2010). With current climate change, flowering patterns are changing, yet few studies focus on how within-plant flowering phenology impact plant-pollinator interactions under changing conditions (Ehrlen & Valdes, 2020; Fitter & Fitter, 2002; Høye et al., 2013; Iler et al., 2013).

Arctic pollinators are few and dominated by generalists (Coulson, 2007; Elberling & Olesen, 1999; Gillespie et al., 2020; Tiusanen et al., 2016). Successful pollination, therefore, depends on pollinator visits and pollinator fidelity (King et al., 2013; Mitchell et al., 2009). Pollinator fidelity is a measure of same-species flower visits, or pollinator specialization (Faegri & van der Pijl, 2013; Waser et al., 1996). Both pollinator visits and fidelity vary throughout the season (Gallagher & Campbell, 2020; Lefebvre et al., 2018). Pollinator numbers usually peak mid-season, when most flowers bloom and compete for pollinator visits (Gallagher & Campbell, 2020; Straka & Starzomski, 2015). Early-season pollinators, however, actively search for limited nectar resources on fewer flowering plants (Gallagher & Campbell, 2020; Kehrberger & Holzschuh, 2019; Mosquin, 1971). With fewer species flowering, early-season generalists might therefore be more effective by increased same-species visits (Ison et al., 2018; Kochmer & Handel, 1986; Munguia-Rosas et al., 2011).

To attract pollinators, many plants invest in large floral displays where many flowers open simultaneously (Harder & Johnson, 2005; Thompson, 2001; Wyatt, 1982). Fitness benefits of a large floral display, however, vary with plant sex as a large display might increase geitonogamy in hermaphrodites, or the pollen transfer among flowers of the same plant (Harder & Barrett, 1995; Zhu et al., 2020). Within plants, reproductive allocation generally decreases from the first to the last flower (Austen et al., 2015; Herrera et al., 2006; Thomson, 2010). Within populations, plants rarely flower for the same time, quantity, and duration due to abiotic and genetic differences (Elzinga, 2007; Figure 2). Pollinator activity could synchronize flowering, with simultaneous flowering able to attract more pollinators than single flowering plants (Ghazoul, 2006; Makino et al., 2007). Stochastic abiotic conditions, on the other hand, could select for more subsequent within-plant flowering, ensuring at least some flowers overlap with favorable climate and weather (Hall et al., 2018; Rodriguez-Perez & Traveset, 2016). Variable flowering times within populations could also limit the spread of floral herbivores and fungal diseases (Ågren & Ågren, 2019; Brody, 1997).

The early-flowering cushion plant *Silene acaulis* (L.) Jacq. provides a well-suited study system to investigate within-plant flowering phenology. *Silene acaulis* has a widespread, circumpolar distribution that was established before the most recent glaciations, with lineages surviving in different refugia during climatic oscillations and recurrent glaciations during the Pleistocene (Gussarova et al., 2015). Throughout its distribution, *S. acaulis* is a pioneer species thriving in early successional stages with fairly low levels of interspecific competition (Holway & Ward, 1965; Jones & Richards, 1962). Pollinators are attracted by abundant small, pink, sweet-scented flowers that are visited by bumblebees (Delph et al., 1999; Shykoff, 1988; Shykoff, 1992), moths, bees, ants (Delph & Carroll, 2001;

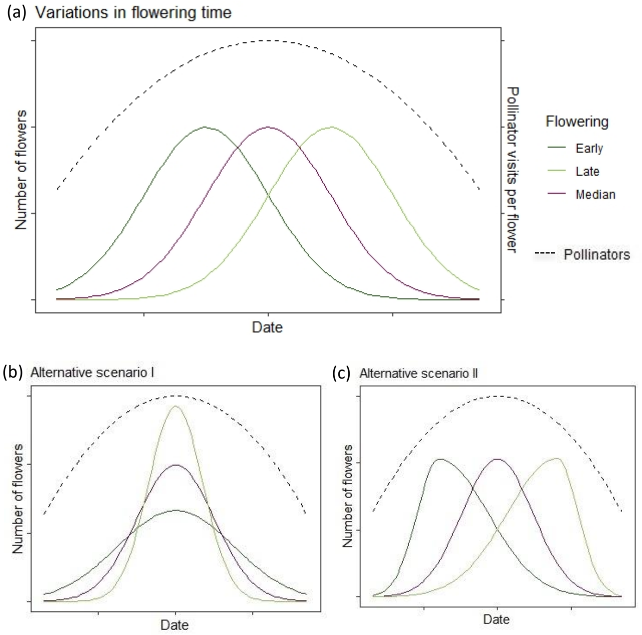


Figure 2 (a) Flowering time generally varies among individuals in a population. Alternative scenarios include variations in flowering (b) duration, kurtosis, and (c) skewness. Three possible flowering peaks are portrayed in (c): positive skewness (peak to the left), neutral skewness (peak in the middle), and negative skewness (peak to the right). In each figure, most flowers are predicted to bloom during the highest probability of pollinator visits per flower (dotted line).

Marr, 1997), flies (Delph & Carroll, 2001; Totland, 1994) and butterflies (Lortie & Reid, 2012). In the northern hemisphere, the south-facing sides of cushions receive more solar energy. In dome-shaped cushions, flowers on *S. acaulis,* therefore, open first on the southern side and later on the northern side. However, to my knowledge, no studies have thus far used the varied within-plant flowering phenology in *S. acaulis* to investigate fruit production.

Silene acaulis has a mixed breeding system with hermaphrodites and females (Delph et al., 1999; Shykoff, 1988). Such a breeding system enforces outcrossing in females while allowing hermaphrodites to self-pollinate. Females must thus have a fecundity advantage to persist in a population (Dufay & Billard, 2012). Several studies on *S. acaulis* show female advantage by higher capsule set, seed production, and seedling survival compared to hermaphrodites (Delph et al., 1999; Hermanutz & Innes, 1994; Shykoff, 1988). Svoen et al. (2019) and Phillip et al. (2009) found increased female frequency at higher latitudes, a correlation not fully understood but which could reinforce pollinator dependence further north. To better understand Arctic plant-pollinator dynamics, new methods in observational studies are rapidly developing.

Traditionally, flowering phenology studies have been based on in-field observations, many using the first open flower as a proxy for bloom time for entire plants (Elzinga et al., 2007; Kochmer & Handel, 1986; Molau, 1993; Ollerton & Lack, 1992; Primack, 1985). Today, new technology such as time-lapse cameras and machine learning may revolutionize observational studies (Høye et al., 2021; Lortie et al., 2012). The use of time-lapse cameras reduces observer bias in difficult field conditions, minimizes interferences, and allows detailed phenology analysis by timestamps (Lortie et al., 2012). Further, machine learning algorithms can be trained on manually analyzed images to automate image analysis in the future (Gogul & Kumar, 2017; Patel & Patel, 2019; Willi et al., 2018). In this thesis, I use time-lapse images to study thousands of individual flowers throughout one growing season to investigate how within-plant bloom time impact fruit at two different Arctic locations with contrasting climate and pollinator guilds.

2.1 Aims and hypotheses

My primary aim is to understand the dynamics of within-plant flowering phenology and its consequences on fruit production in *S. acaulis.* In particular, I investigate how (i) within-plant floral display, (ii) within-plant bloom time, and population bloom time impact fruit production in pollinator-dependent females, and if these relations vary with (iii) frost exposure. These aims are investigated by assessing four hypotheses:

(i) Pollinators are usually attracted to large floral displays and flowers blooming during peak floral display might receive more pollinator visits. Peak floral display is in this thesis defined as the observation day with the most blooming flowers within the growing season.

> **H_1:** Within females, flowers blooming during peak floral display (flowers blooming a few days away from the day with the most flowers) will have higher fruit production than flowers blooming outside peak floral display (flowers blooming many days away from the day with the most flowers).

(ii) Within individuals, resource allocation and time to mature fruit generally decrease from the first to the last flower. Within populations, there is more time and less pollinator competition early in the season. As a result, early flowers might receive more pollinator visits and produce more fruit than late flowers, both within individuals and whole populations.

> **H_2:** Within females, flowers blooming before peak floral display will have higher fruit production than flowers blooming after peak floral display.
> **H_3:** Within all females in a population, flowers blooming before peak population flowering will have higher fruit production than flowers blooming after peak population flowering.

(iii) However, flowers are vulnerable to frost, and frost exposure might destroy flowers before they can attract pollinators and mature fruit.

> **H_4:** In case of a frost event, H1-3 will not be present among flowers exposed to frost.

3 Materials and methods

3.1 Study area

This study took place in two study sites; Narsarsuaq, South Greenland (61.1N, 45.40E; Figure 3a,c) and Bjørndalen near Longyearbyen, Svalbard (78.2N,15.15E; Figure 3b,d). Narsarsuaq is a settlement in the Narsaq region in southern Greenland and among the richest botanical provinces in Greenland, with slightly more than 300 native vascular plant species (Böcher, 1963; Feilberg, 1984). Narsarsuaq has been categorized as the Sub-Arctic/Low-Arctic transition zone between the northernmost part of the boreal zone and the southernmost part of the Arctic tundra (Daniëls, 2010; Karami et al., 2018). Average monthly temperature range between a July maximum of 14 ºC and a February minimum of -4 ºC (Weatherspark, 2019). Flowering and fruit phenology data at the site was collected from the 26th of May to 21th of August in 2019. In both 2018 and 2019, temperatures measured by the Narsarsuaq airport weather station about three kilometers from the study site, fluctuated from around 6ºC to 18ºC in June (*S. acaulis* flowering) and between 11 ºC and 16ºC in July (*S. acaulis* fruit development). The study site is located in the lower altitudinal zone, characterized by dwarf shrub or heath community dominated by *Salix glauca* and/or *Betula glandulosa* (Schofield et al., 2007). The pollinator community is dominated by flies (Diptera: Muscidae) and hoverflies (Syriphidae), but also include species of bumblebees (*Bombus sp.*; Gillespie et al., 2020)

The High-Arctic site Bjørndalen is located on the archipelago Svalbard, defined as bioclimatic zone C and dominated by tundra heath and open, exposed rock (Elvebakk, 2005; Walker et al., 2005). There are no bees in Svalbard, and pollination is dominated by Diptera (Coulson, 2007). Flowering and fruit phenology data at the site was collected from the 16th of May to the 23rd of August in 2019. In 2018, the Longyearbyen airport weather station recorded average July temperatures were 7.2 ºC but there was no frost event during *S. acaulis* flower timings. In 2019, temperatures ranged from 8.4 ºC (July average) to -11.1 ºC (February average) measured by the Longyearbyen airport weather station, about five kilometers from the study site (Yr, 2019). From approximately 2 am until 4 am on the 28th of June, weather station temperatures dropped to 0.2ºC, resulting in frost at the study site (Yr, 2019). Total rainfall was on average low, ranging from 6.2 mm in July and 39.5 mm in August. The field site is dominated by lichen, open rock, and biological crust, in addition to plant species like *Dryas octopetala*, *Saxifraga oppositifolia,* and *Silene acaulis.* In this thesis, I will refer to Bjørndalen as the High-Arctic site and Narsarsuaq as the Low-Arctic site. All concepts and definitions can be found in Table 1.

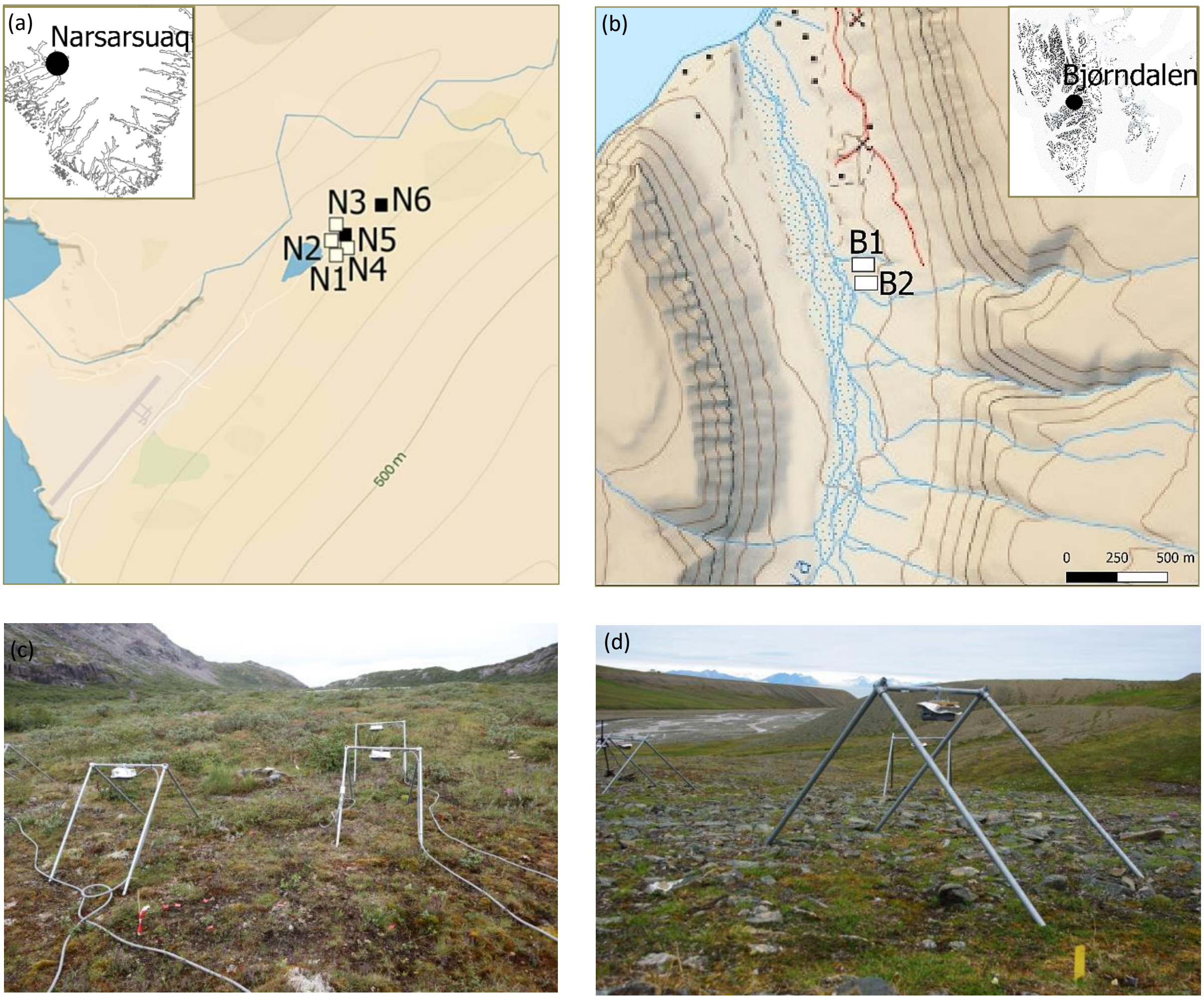


Figure 3 Map and habitat image from (a,c) the Low-Arctic site and (b,d) the High-Arctic site. In both maps, cameras positioned in well-drained habitats are marked as white squares, while cameras on the wetter ground are marked with black squares. (a,c) Map and image of camera groups N1-N6, located in the Low-Arctic site. The contour lines on the Low-Arctic map mark every 100 m. The map is acquired from Mapcarta. (b,d) Map and image of camera groups B1-B2, located in the High-Arctic site. The contour lines on the High-Arctic map mark every 50 meters. The map is acquired from TopoSvalbard. Photo (d) by Simen Hjelle.

Table 1 Concepts and definitions used in this thesis, grouped by level of observation: flower, individual, population, or site.

Level	Concept	Definition
Flower	Flower	The flowering stage with visible, elongated petals.
	Fruit	The presence of immature fruit (closed capsule) or mature fruit (open capsule) from an *S. acaulis* flower. Value is binary, either fruit or not fruit.
	Flower bloom	The date of the first visible elongated petals of a flower.
	Floral longevity	The number of days between flower bloom and withering.
	Frost exposed flower ❄	A flower blooming during the frost event on the 28th of June in the High-Arctic site.
	Within-plant floral display	The number of days between the flower bloom and the peak floral display.
	Within-plant bloom time	The number of days between the flower bloom and the first plant flower.
	Population bloom time	The number of days between the flower bloom and the first population flower.
Individual 🌱	Study plant	A plant under time-lapse monitoring.
	Flowering period	The days between the bloom of the first flower and the senescence of the last flower.
	Peak floral display	The day with the highest observed number of blooming flowers within the plant. If more than one day is possible, the first day is chosen as the peak floral display.
	Plant floral display	The maximum number of flowers open on the same day within the plant. If the peak floral display lasts over several days, the time in the middle is chosen.
	Fruits per flower proportion	The total number of flowers that produced fruit within each plant as a percentage. Calculated as (number of plant fruit/number of plant flowers*100) %.
	Flower increase	Flower increase per day before peak floral display. Calculated by dividing plant floral display by the number of days from the first flower to peak floral display.
	Flower decrease	Flower decrease per day after peak floral display. Calculated by dividing plant floral display by the number of days from the last flower to peak floral display.
	Hermaphrodite ⚥	An *S. acaulis* plant with the presence of pollen anthers inside its flowers.
	Female ♀	An *S. acaulis* plant without the presence of pollen anthers inside its flowers.
	Positively skewed flowering	A left-skewed cumulative flowering over the growing season, where most flowers bloom early and peak floral display is timed early within the flowering period. The term could also refer to population flowering, where most flowers bloom early within the whole population.
Population 🌱🌱🌱	Flowering season	The number of days between the first and last flower among all study plants.
	Population flowering peak	The day with the highest observed number of blooming flowers among all study plants.
	Study population	All plants included in one of the two complementary population studies presented in “3.3 Study population”
Site	The High-Arctic site	The study site in Bjørndalen, located in the High-Arctic archipelago Svalbard.
	The Low-Arctic site	The study site in Narsarsuaq, located in the Sub-Arctic/Low-Arctic transition zone in Southern Greenland.
	Open habitat	Habitat type dominated by well-drained, rocky soil.
	Closed habitat	Habitat type dominated by moss-dominated, moist soil.

3.2 Study species

Silene acaulis is an early-flowering Arctic-Alpine cushion plant characterized as a pioneer species in early successional plant communities (Holway & Ward, 1965; Jones & Richards, 1962; Svoen, 2014). Typical habitats are open tundra, rocky slopes, and wind-exposed ridges (Jones & Richards, 1962). *Silene acaulis* has been termed a foundation species and a nurse plant by facilitating the growth of other species with negative consequences on its own reproductive success (Antonsson et al., 2009; Molenda et al., 2012; Schöb et al., 2014)

One cushion is made up of rosettes sharing a single taproot and usually consists of a single individual that grows progressively in size as the plant ages with no clonal growth (Morris & Doak, 1998). *Silene acaulis* is long-lived and regularly exceeds 300 years of age (Morris & Doak, 1998). In warmer sites, plants are less compact to prevent damage from overheating, while in colder climates and higher elevations, *S. acaulis* form denser, more compact cushions that function as heat traps (Bonanomi et al., 2016; Hagen & Spomer, 1989). In the northern hemisphere, the south-facing sides of cushions receive more solar energy. Thus, dome-shaped cushions bloom earlier on the south-facing side than on the north-facing side – "thus the polar explorer can almost use the flower of *S. acaulis* as a compass" (Figure 6a; Jones & Richards, 1962). The seeds of the first flowers can already begin to ripen when the last flowers are opening (Jones & Richards, 1962).

Silene acaulis is primarily gynodioecious with female and hermaphrodites, but hermaphrodites have varying degrees of female function and some individuals can be classified as functionally male (Alatalo & Molau, 2001; Hermanutz & Innes, 1994; Philipp, 2009; Shykoff, 1988). Several studies have demonstrated female advantage concerning reproduction, establishment, and germination in *S. acaulis* (Delph et al., 1999; Delph & Mutikainen, 2003; Shykoff, 1988; Svoen et al., 2019). However, females are dependent on pollinators to reproduce, and female advantage may be counteracted in areas with pollinator deficiency as hermaphrodites can self-pollinate. An experiment performed in alpine Canadian tundra clearly showed that females had higher viability than hermaphrodites when pollen was not limiting, but females became less viable under reduced pollen loads (Reid et al., 2014). Additionally, a study from Greenland has found female frequency to increase with the harshness of the environment (Philipp 2009). Average female frequencies have also been found to increase along an altitude gradient in Northern Sweden (Alatalo & Molau 1995).

Silene acaulis has many small flowers commonly pink, and occasionally white (Jones & Richards, 1962). Flowering begins early and buds are pre-formed and overwinter before flowering (Hacker et al., 2011; Junttila & Robberecht, 1993). Pollination is done by flies (Figure 6b-c; Delph & Carroll, 2001; Totland, 1994), bumblebees (Delph et al., 1999; Marr, 1997; Shykoff, 1988; Shykoff, 1992), moths, bees, ants (Delph & Carroll, 2001; Marr, 1997), and butterflies (Lortie & Reid, 2012). Successful pollination is expected to cause flower senescence (Doorn, 1997; Primarck, 1985; Stead, 1992). Empty, aborted flowers can be easily distinguished from developing fruit capsules (Hall et al., 2018). Flowers and immature fruit are vulnerable to frost events, though internal cushion heat can protect shoots from short frost periods (Hacker et al., 2011). In addition, the anther-smut fungi *Microbotrum violaceum* can infect *S. acaulis* flowers (Bueker et al., 2016). The anther-smut fungi sterilize the infected plant by causing female structures to abort, thereby hindering reproduction for the plant (Alexander et al., 1996). Pollen in male structures is replaced with powdery, dark-colored fungal spores (Figure 6e). If the plant is female, it will start producing male structures after infection (Marr, 2006).

3.3 Study population

3.3.1 Whole population patterns

A population study was performed at both sites, and plants included in the two population studies will be collectively referred to as the study populations. In both study populations, flowers rotated uncorrelated to sun movement, and mature fruit capsules were observed to close during days with precipitation and high moisture levels. In the Low-Arctic site, the study population contained 68% female *S. acaulis* individuals (n=491 plants, methodology in Appendix 1). Plant sex ranged from pure females to hermaphrodites with varying degrees of fruit production. Measured flower size varied with plant sex, with female flowers having an average of 9.75 cm (±SD = ±7.8 cm; n=18 plants) for females and 10.9 cm (±SD = ±8.2 cm; n=15 plants) for hermaphrodites. Intrusive species percentage and dead areas varied with microhabitat.

In the Low-Arctic site, cushions in well-drained, rocky habitats had a lower average intrusive species (mean±SD = 3.6±5.4%; n=164 plants) and more average dead areas (mean±SD = 27.1±23.9%; n=164 plants) than wet, moss-dominated habitats (mean±SD = intrusive species 35.8±22.4%, dead areas 10.6±16.3%, n=182 plants). Nighttime Carabidae beetle (Coleoptera) activity was observed in the Low-Arctic study population (Figure 6d). Flowers around this area were gone the next day, indicating floral herbivory.

In the High-Arctic site, the *S. acaulis* study population contains 72% female *S. acaulis* plants (n=164 plants, methodology in Appendix 1). Plant sex ranged between female and hermaphrodites with varying female ovules. Gynomonoecy, the presence of both female and hermaphrodite flowers within one plant, was observed one kilometer further into the valley (Figure 6f). However, whether this is a case of separate plants grown together or a mutation in one individual is not confirmed. The average cushion size was 5.3 cm (±SD = ±4.4cm), average dead areas were 24.6% (±SD = ±29.8%) and 12.4% (±SD = ±16.6%) of the average cushion area were covered by intrusive species.

3.3.2 Within-individual patterns

In both study populations, cushions of *S. acaulis* were observed to flower first on south-faced sides and later on north-faced sides (Figure 4a-b). To get an impression of the temperature gradient within plants, two cushions in the Low-Arctic in 2019 and one cushion in the High-Arctic in 2018 were selected for temperature measurements (Methodology in Appendix 1). Surface temperatures were measured in the High-Arctic, while internal temperatures from the outer layer of cushions were measured in the Low-Artic. In both the Low-Arctic site and the High-Arctic site, the average logger temperature showed an approximately one-degree difference between the north and south-facing parts of the cushions (Figure 5a-b).

Temperature averages were 13.1 °C and 14°C in the Low-Arctic and 9.3°C and 10.3°C in the High-Arctic for north-faced and south-faced sides of the cushions, respectively. Across the High-Arctic cushion, temperatures during clear days deviated strongly. On the warmest day (15th of July 2018), temperatures on the south-facing side of the High-Arctic cushion reached 36.7 °C, which was 22.9 °C higher than on the north-facing sides of the cushion. In 2019, the highest Low-Arctic temperature differences measured were 8.1°C, where the south-facing side of one of the cushions reached 32.2°C.

Temperature differences across dome-shaped cushions could result in differences in fruit production. Therefore, a preliminary study was performed in the High-Arctic in 2018, where cushions were more dome-shaped and differences in sun angle were the largest (n=63 plants; Figure 4c; Methodology and plot details in Appendix 1-2). Almost all fruits (99%) in the preliminary plots were produced by females (Figure 5c-d). Among these females, 54.4% of the fruits were produced in the south-facing parts of females and only 18.9% on the north-facing sides of cushions. Among hermaphrodites, the few fruits produced were mostly found in the top and south-facing parts of the cushions. These preliminary results in the High-Arctic indicated a relationship between within-plant flowering phenology and fruit production, which was further investigated in the main part of this thesis.

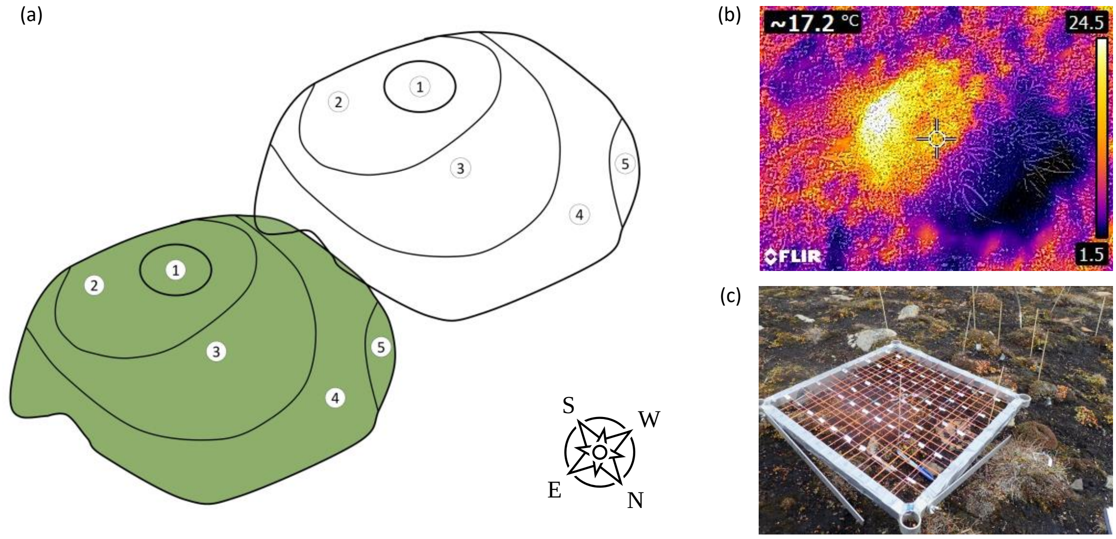


Figure 4 (a) Illustration of S. acaulis flowering (green) and subsequent fruit production (white). The numbering shows the sequence of flowering, with the bottom-right arrow marking cardinal directions in the figure. Illustration by Fanny Dommanget. (b) A thermal image of an S. acaulis cushion on a clear day shows a 23 °C temperature difference between the south and the north-facing sides of the cushion. (c) The grid system was used in the preliminary fruit production study in the High-Arctic. Fruits were counted within each grid to study fruit set differences in sun angle between north and south-facing parts of cushions.

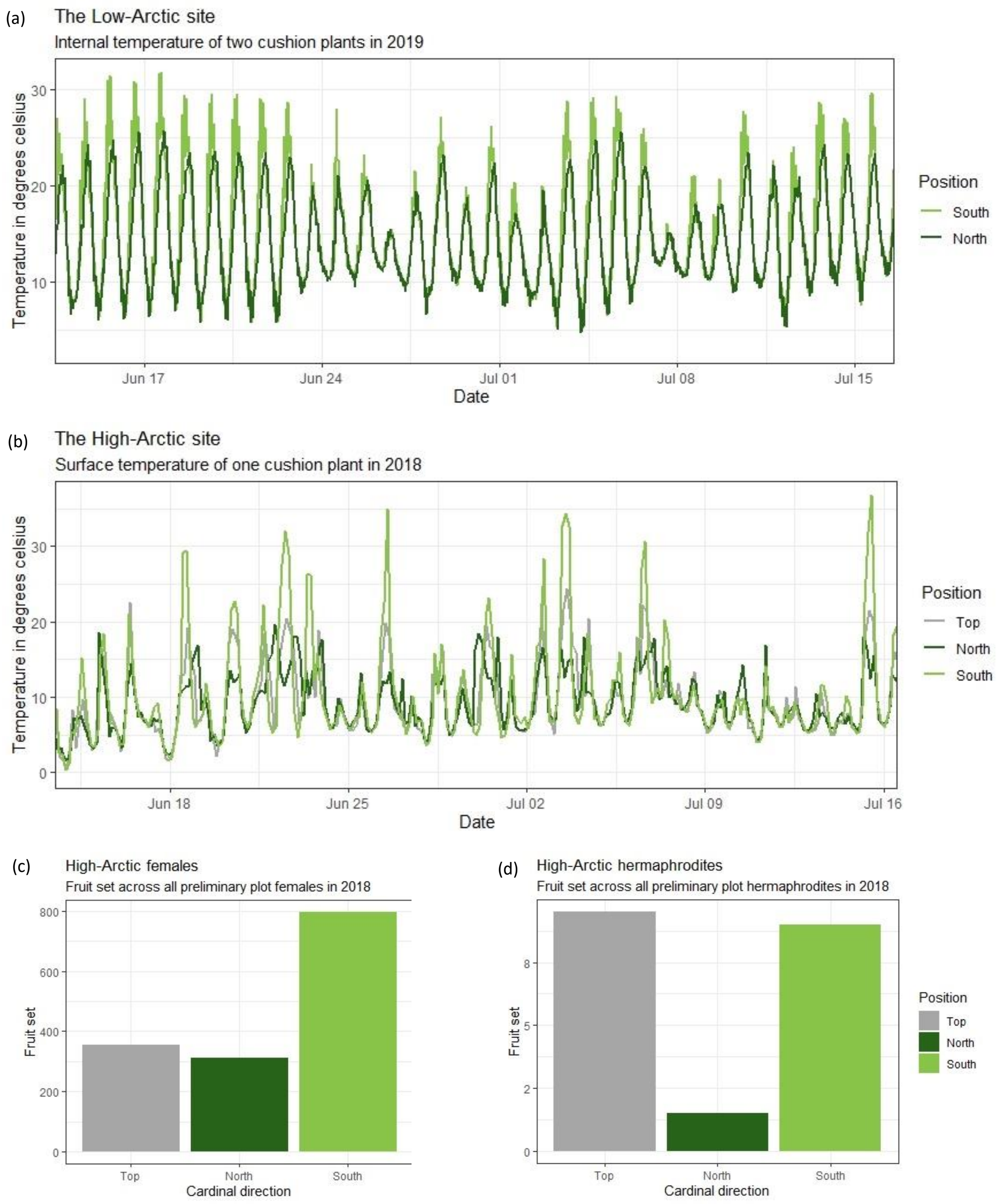


Figure 5 Preliminary results from (a) the Low-Arctic site in 2019 and (b-d) the High-Arctic site in 2018. The two upper panels show (a) internal temperature in the north and south-facing parts of two Low-Arctic cushion plants and (b) surface temperature in the north, top, and south-facing parts of one High-Arctic cushion plant. Finally, the two lower panels show fruit set across (c) females and (d) hermaphrodites in the preliminary plots in the High-Arctic site.

Figure 6 (a) A Silene acaulis cushion in the High-Arctic (Svalbard), flowering on the southern side at the beginning of the growing season. The next three panels show a fly (Diptera) likely pollinating (b) a female flower and (c) a hermaphrodite flower, and (d) a beetle (Carabidae, Coleoptera) likely feeding on a group of flowers. Finally, the two bottom images show (e) anther-smut fungi Microbotrum violaceum on a Low-Arctic study plant (PlantID NARS-46), and (f) two hermaphrodite flowers (top left and bottom right) in an otherwise female plant in the High-Arctic site. Photo (a) by Albert Michaurd; Photo (f) by Simen Hjelle.

3.4 Time-lapse monitoring

3.4.1 Study plant selection

To enable the establishment of long-term monitoring, study plants were chosen selectively among well-defined cushions with less than 10% intrusions or dead areas and placed on approximately the same slope. Intrusive species within the cushions and dead plant areas were observed by an approximate percentage of the total cushion area. It was not possible to quantify plant sex before flowering, so plants were selected without knowledge of plant sex. The aim of the plant selection was pollinator-dependent females which have the highest frequency among each site. However, if hermaphrodites were selected, they were included in the study as a comparison to females.

The study plants were compared with the surrounding study population. In both sites, the study plants were larger, with fewer dead parts, and contained a higher proportion of females, than the plants in the study population (Appendix 2). In the Low-Arctic site, study plants on average contained 13% fewer hermaphrodites and were 23 cm larger with 18% fewer dead areas and 2% less intrusive species than the plants in the study population. In the High-Arctic site, similarly to the Low-Arctic site, study plants on average contained 28% fewer hermaphrodites and were 10 cm larger, with 20% fewer dead areas and 4% less intrusive species than the plants in the study population.

3.4.2 Study plant monitoring

The waterproof time-lapse camera TimelapseCam Pro monitored the study plants throughout the season, adjusted to 60 cm above the ground (Detailed methodology in Appendix 3). Each camera included a temperature logger, which was compared to the local weather station at each site. In the Low-Arctic site, 15 camera traps were established in five clusters, all connected to a solar panel. The 15 cameras were distributed between two microhabitats: Seven cameras in two clusters in closed habitats and eight cameras in four clusters in open habitats (Figure 3a; Table 2). Open habitat was defined as well-drained ground dominated by gravel. Alternatively, microhabitats dominated by moss were defined as closed habitats. Four cameras encompassed more than one plant, which totaled 21 plants under time-lapse monitoring in the Low-Arctic site. In the High-Arctic site, eight time-lapse cameras were established in two clusters following a slight west-facing slope (Figure 3b). All plants in the High-Arctic site were in the approximately same habitat (Table 2).

Table 2 Habitat description of each plant under time-lapse observation in the Low-Arctic site (Narsarsuaq, Greenland) and the High-Arctic site (Bjørndalen, Svalbard). Species in each microhabitat are described, listed from the most proximate species to the least proximate plant species to the study plant position. Biological crust and graminoids were common in all microhabitats, but are excluded from the habitat description for readability.

Site	PlantID	Sex	Plot	GPS	Habitat	n	Microhabitat (1x1 meter underneath cameras)	Data collectors
High-Arctic	BJOR-01	F	B1	78.21664 015.33288	Open	1	Lichen, *Bistorta vivipara, Salix herbacea, Equisetum arvense,*	TL = SH; PS = REW, SH; IA=XB, REW
	BJOR-03	F	B1	78.21667 015.33257	Open	1	Lichen, *Salix herbacea, Bistorta vivipara, Equisetum arvense*	TL = SH; PS = REW, SH; IA=XB, REW
	BJOR-04	F	B1	78.21626 015.33277	Open	1	*Salix herbacea, Bistorta vivipara*	TL = SH; PS = REW, SH; IA=XB, REW
	BJOR-05	F	B1	78.21670 015.33270	Open	1	*Bistorta vivípara, Equisetum arvense, Dryas octopetala*	TL = SH; PS = REW, SH; IA=XB, REW
	BJOR-09	F	B2	78.21623 015.33313	Open	2	*Salix herbacea, Bistorta vivipara, Saxifraga cespitosa*	TL = SH; PS = REW, SH; IA=XB, REW
	BJOR-11	F	B2	78.21626 015.33347	Open	2	B*istorta vivipara, Salix herbacea, Dryas octopetala*	TL = SH; PS = REW, SH; IA=MH, REW
	BJOR-13	F	B2	78.21626 015.33277	Open	3	*Bistorta vivipara, Salix herbacea, Stellaria longipes, Equisetum arvense, Dryas octopetala*	TL = SH; PS = REW, SH; IA=REW
	BJOR-16	F	B1	78.21667 015.33190	Open	1	*Dryas octopetala, Equisetum sp., Salix herbacea,* moss and lichen	TL = SH; PS = REW, SH; IA=MH, REW
Low-Arctic	NARS-04	F	N1	61.18005 -45.37690	Open	3	*Dryas octopetala,* lichen, *Bistorta vivipara, Salix glauca, Betula pubescens, Potentilla sp.*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-14	F	N2	61.18225 -45.37675	Open	2	Moss, lichen, *Chamerion latifolium, Dryas octopetala, Bartsia alpina, Pinguicula vulgaris, Salix glauca, Bistorta vivipara, Thalictrum alpinum, Betula pubescens*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-20	F	N3	61.18242 -45.37677	Open	17	*Betula pubescens, Betula sp., Rhododendron lapponicum, Dryas octopetala, Vaccinium uliginosum, Salix herbacea, Salix glauca, Pinguicula vulgaris*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-21	F	N3	61.18240 -45.37679	Open	9	Moss, lichen, *Chamerion latifolium, Rhododendron lapponicum, Vaccinium uliginosum, Salix glauca, Betula sp.*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-24	F	N6	61.18408 -45.36749	Closed	1	Moss, *Saxifraga oppositifolia, Bistorta vivipara, Salix herbacea, Rhododendron lapponicum, Vaccinium uliginosum, Betula sp.*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-31	F	N6	61.18408 -45.36759	Closed	1	Moss, *Bistorta vivipara, Rhododendron lapponicum, Betula pubescens, Saxifraga oppositifolia, Vaccinium uliginosum, Tofieldia pusilla,*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-32	F	N6	61.18414 -45.36742	Closed	1	Moss, *Betula sp., Rhododendron lapponicum, Pedicularis sp., Bistorta vivipara, Vaccinium uliginosum, Dryas octopetala, Salix herbacea, Saxifraga oppositifolia*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-35	F	N4	61.18040 -45.37631	Open	3	Lichen, moss, *Taraxacum sp., Saxifraga oppositifolia, Potentilla sp.,*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-37	F	N4	61.18038 -45.37642	Open	4	Lichen, *Salix herbacea, Salix glauca, Chamerion latifolium,*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-40	F	N4	61.18029 -45.37646	Open	6	Lichen, *Chamerion latifolium, Saxifraga oppositifolia, Salix glauca, Taraxacum sp., Salix herbacea*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-43	F	N5	61.18186 -45.37710	Closed	9	Lichen, *Dryas octopetala, Saxifraga oppositifolia, Bartsia alpina, Bistorta vivipara, Vaccinium uliginosum, Betula sp., Chamerion latifolium*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-44	F	N5	61.18196 -45.37609	Closed	9	*Bartsia alpina, Bistorta vivípara, Salix glauca, Pinguicula vulgaris, Salix herbacea, Tofieldia pusilla, Potentilla sp., Pedicularis sp., Betula pubescens, Betula sp.*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-46	F	N5	61.18196 -45.37609	Closed	1	*Chamerion latifolium, Dryas octopetala, Pinguicula vulgaris, Betula pubescens, Bartsia alpina, Betula sp.*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-05	H	N1	61.18050 -45.37826	Open	3	*Dryas octopetala*, lichen, *Salix glauca*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-22	H	N3	61.18243 -45.37665	Open	10	Lichen, *Betula pubescens, Pinguicula vulgaris, Vaccinium uliginosum, Bistorta vivípara*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-36	H	N4	61.18041 -45.37640	Open	1	Lichen, moss, *Chamerion latifolium, Botrychium lunaria, Potentilla sp., Salix herbacea*	TL = REW, HMRM; PS = REW; IA= REW
	NARS-42	H	N5	61.18195 -45.37596	Closed	9	Lichen, *Bartsia alpina, Bistorta vivípara, Corallorhiza trífida, Saxifraga oppositifolia, Salix glauca, Pinguicula vulgaris*	TL = REW, HMRM; PS = REW; IA= REW

§ NARS = Narsarsuaq, Southern Greenland; BJOR = Bjørndalen, Svalbard; Plot = Camera cluster; Open = Well-drained, rocky ground, Closed = Wet, moss-dominated ground, n = Density of *S.* acaulis 1x1 meter under the cameras; TL = Time-lapse monitoring; PS = Population study; IA = Image annotations; REW = Rebekka Eriksen Ween; HMRM = Hjalte Mads Rosendal Mand; SH = Simen Hjelle; XB = Xenia Burthoft; MH = Maria Huntsar

3.4.3 Study plant measurements

Throughout the growing season, observations about flowering or fruit development were noted down. For each plant, sex was categorized as either female or hermaphrodite by the presence or absence of pollen anthers. Cushion size was measured as the average of the north-south and east-west axis. In addition, the surrounding species around each plant were noted down. Each plant was checked for any occurrence of the anther-smut fungi *Microbotrum violaceum* (Marr, 2006). One monitored plant in the Low-Arctic site was infested, produced no fruit, and with indeterminable sex due to the fungal infection. The infected plant was only included in preliminary investigations (NARS-46; Table 2) and was excluded from further analysis.

3.5 Image analysis

3.5.1 Image subset

Time-lapse images were analyzed manually using the program VGG Image Annotator 2.0.8 (Dutta & Zisserman, 2019). Images were taken at a higher frequency than needed to explore within-plant flower phenology. To establish an appropriate sampling interval, the average floral longevity of one randomly selected plant (NARS-14; Table 1) was calculated. In a preliminary annotation of all flowers every six hours, the average flower longevity was 7.7 days (95% CI: 7.5, 7.8; n=1066 flowers). Thus, an image subset was made every 24 hours for all time-lapse series to study flower development. In case of a missing image, the next available image was selected.

3.5.2 Image annotations

Each flower was annotated throughout the growing season (Figure 7; Detailed methodology in Appendix 4). A bud was defined as approximately round with no individual petals that could be distinguished, while a flower was defined by visible petals. Before flowering, all visible buds were marked and numbered, noting their position on the plant. Each shoot kept this number throughout the growing season. In sections with high flower density, some buds could not be spotted before flowering and were given a new number. If the shoot disappeared it was marked with “Gone”. Flowers were marked as withered when petals were visibly dried up and no longer elongated circles. Since petals might wither slightly after stigmas and anthers, the bloom time registered may be longer than the actual time flowers can receive or donate pollen. Fruit production was split into two phases: immature and mature fruit. An immature fruit was defined as a closed capsule, while mature fruit was defined as an open capsule. Immature fruit was in some images hard to distinguish. Therefore, the last image in each time series was used to classify whether flowers produced fruit so that each fruit observation was evaluated throughout the fruit development time.

3.5.3 Data cleaning

Each time-lapse series was checked for missing images and unexpected image annotations. From the image annotations, a full dataset and a reduced dataset were created. The full dataset was used for calculations of first plant flower, plant floral display, flower increase, flower decrease, and plant flowering time (section 3.1). This full dataset contained annotations of 7851 flowers in the Low-Arctic site and 1587 flowers in the High-Arctic site. The reduced dataset was created by removing flowers that disappeared or appeared from the image in the middle of flowering were removed. Specifically, flowers that were not marked as “Bud” before “Flower” were removed as these would not have an exact flower timing, and flowers marked as “Gone” in the last image were removed as these would not have an exact fruit set value. The reduced dataset was created to get precise calculations of floral longevity (section 3.1) and for the investigation of fruit set patterns (sections 3.2 and 3.3). This reduced dataset contained annotations of 7549 flowers in the Low-Arctic site and 1549 flowers in the High-Arctic site.

3.5.4 Data transformation

The annotation data was transformed into several flowering phenology variables. For each flower, flower bloom (the day of first observation of open petals) and flower longevity (the number of days between flower bloom and withering) were calculated. In the High-Arctic site, a frost event occurred and each flower observed open during the frost event was marked as a frost exposed flower. The image closest in time to the frost event included in the image subset was used for the frost exposure category.

For each individual, the first plant flower (the first observation of recognizably open petals within the plant), flowering period (the number of days between the first plant flower and the last plant flower), and peak floral display (the day with the highest observed number of blooming flowers) were noted down. In addition, the plant fruit set was observed as the total number of flowers that produced fruit within each plant, and the fruits per flower proportion as the plant fruit set relative to the total number of flowers. Finally, flower increase and decrease per day were calculated by the derivate of flowering before and after peak floral display.

For each population, the first population flower (the first observation of recognizably open petals within the population), and the flowering season (the number of days between the first population flower and the last population flower) were measured. All flowering phenology variables were assessed for outliers and deviating observations.

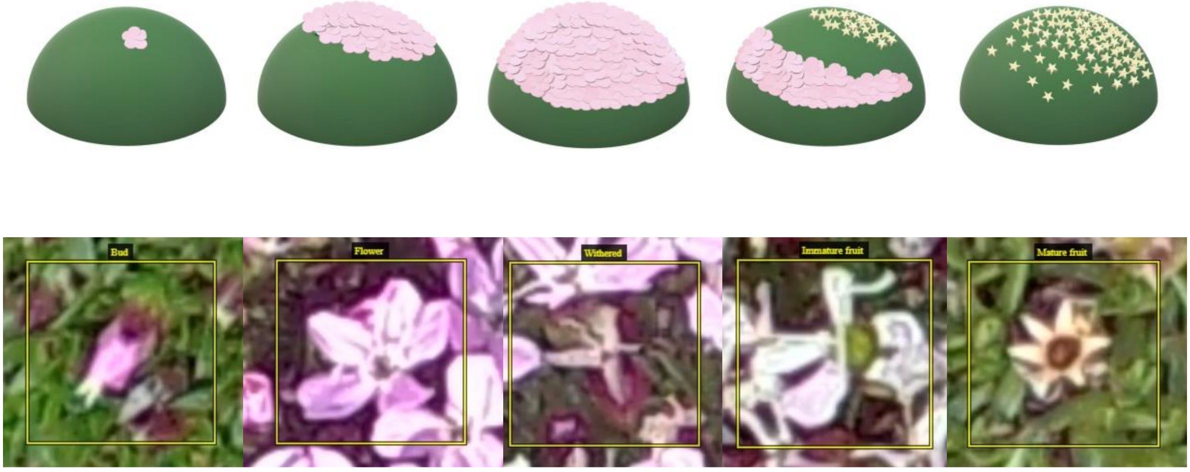


Figure 7 Illustration of S. acaulis flowering and subsequent fruit production throughout the growing season (higher panel) and examples from the time-lapse images of each annotation stage: bud, flower, withered, immature fruit, and mature fruit (lower panel).

3.6 Statistical analysis

All statistical analyses were done in the program R 3.5.2, using the *lme4* package for generalized linear and polynomial models (Bates et al., 2011), the gamm4 package for generalized additive models (Wood et al., 2017), and the *DHARMa* and *arm* package for the goodness of fit of the models (Gelman et al., 2013; Hartig & Hartig, 2017). All model parameters and predicted effects are reported by estimate (95% CI) unless otherwise stated. In figures 11-13, the best fitting models were compared to an empirical logit transformation of the fruits per flower proportions in the raw data. To enable empirical logit transformation, zero values were avoided by adding a small constant to all fruit proportions. For each figure, the constant chosen was half of the smallest nonzero value (Ekwaru & Veugelers, 2018).

3.6.1 Initial data exploration

As an initial exploration of the data, flowering phenology among individuals was investigated. In both sites, the relationships between plant size, flowering period, plant floral display, and fruits per flower proportions were explored. In the Low-Arctic site, the study population spanned two microhabitats. Therefore, in the Low-Arctic site, any habitat differences in the first plant flower and fruits per flower proportions were evaluated. In the High-Arctic site, all plants were in the approximately same microclimate and no habitat differences were therefore explored. Instead, any relationship between the amount of frost exposed flowers within plants in the High-Arctic site and fruit per flower proportion was explored. All relationships were assessed graphically and by linear regression with a Gaussian distribution, checking residuals for a mean of zero, outliers, constant variance, and an approximately normal distribution.

3.6.2 Phenological predictors of fruit set

To find the impact of within-plant flowering phenology on fruit sets, three standardized phenological predictors of fruit sets were created (Figure 8). All phenological predictors used flower bloom, the day of petal opening, as a proxy for within-plant flowering time. The first phenological predictor was termed within-plant floral display and was calculated by the days between each flower bloom and the peak floral display. The second phenological predictor was named within-plant bloom time and was calculated by the days between each flower bloom and the first plant flower. Finally, the last phenological predictor was termed population bloom time and was calculated by the days between each flower bloom and the first population flower.

3.6.3 Model assumptions

For each site, my study design was hierarchical with observations within plants as a nested effect. The model response variable (presence/absence of fruit) was binary represented by a Bernoulli distribution. Each model, therefore, used a logit-link with each plant as a random effect, and each phenological predictor was centered and scaled to better achieve numerical convergence (McMahon & Diez, 2007; Theobald et al., 2017). The three phenological predictors were correlated (Appendix 6). To avoid multicollinearity issues, the impact of the three phenological predictors on the fruit set was modeled separately in each site. For each model, the presence of any influential outliers was evaluated. Further, the assumptions of linearity between each phenological predictor and the logit response variable for the fruit set and approximately similar slopes within plants were assessed. A model with random slopes could not be fitted, thus approximately similar slopes within plants were evaluated by plotting relationships for each plant. Residuals of each model were investigated by using binned plots (Kumar & Duffull, 2011).

3.6.4 Model selection

The best-fitting hierarchical logistic regression model for each phenological predictor in each site was selected. In the Low-Arctic site, the most complex model included as fixed effects the interaction between plant sex (hermaphrodites and females) and the phenological predictors and the additive effects of plant sex and the phenological predictors. In the High-Arctic site, the most complex model included as fixed effects the interaction between frost exposure (frost exposed flowers and not frost exposed flowers) with the phenological predictors and the additive effects of frost exposure and the phenological predictors. All interaction terms were tested for significance and only included if significant differences in slopes were found between the groups.

In the Low-Arctic site, non-linear relationships between phenological predictors and the response on the logit scale were found. Therefore, I used polynomial and generalized additive models for each phenological predictor in both sites. For each site and phenological predictor, the polynomial term was assessed and only included if making a significant difference from the linear fitted model. The generalized additive model was evaluated by plotting the fitted model and assessing any differences in a linear or polynomial relationship between the phenological predictors and the response of the logit scale. In both sites, the generalized additive model closely resembled a linear or a polynomial model for each phenological predictor. Thus, generalized additive models will not be discussed further. In case of doubt between a linear and a polynomial model, both are presented.

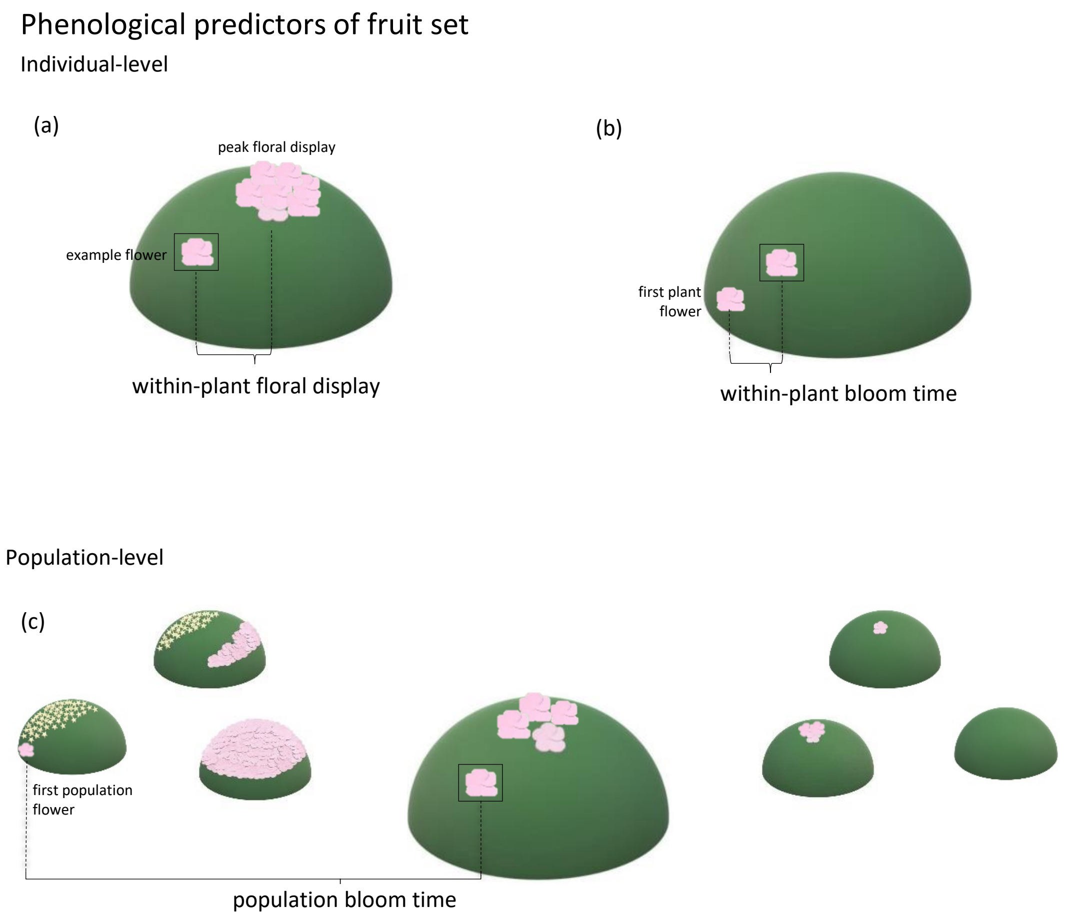


Figure 8 Illustration of the three phenological predictors of fruit set in this study. For each flower within the study plants, three standardized phenological predictors were calculated for flower bloom, or the date of petal opening, as shown for an example flower (black square) in the illustrations. For each flower in the study, three calculations were made: (a) within-plant floral display: the number of days between flower bloom and the peak floral display within the same plant, (b) within-plant bloom time: the number of days between flower bloom and the first flower within the same plant, and (c) population bloom time: the number of days between flower bloom and the first flower blooming within all study plants.

4 Results

Most image series were continuous throughout the growing season with only a few days lacking (Appendix 5). Outliers of flower longevity from 20-50 days were discovered in plants with many overlapping flowers, and the median instead of the average of floral longevity is therefore reported. Further, abnormally high values for camera temperatures were found in both sites, where the median camera temperature was on average 10ºC higher than local weather station temperatures. Therefore, camera temperatures were only used illustratively in Figure 7 and excluded from any analysis. In the Low-Arctic, females in open habitats flowered on average one day earlier. However, the average fruit set among females in different habitats was similar. In open habitats, the average fruits per flower proportions were 17.0% (95% CI: 5.6, 28.4%), while it was 15.7% (95% CI: 3.2, 28.2) in closed habitats. Thus, habitat differences will not be discussed further. Finally, no relationship between intrusive species or dead cushion areas and flowering phenology was found, and these plant measurements will not be discussed further.

4.1 Flowering phenology

4.1.1 Female flowering in the High-Arctic site

At the population level in the High-Arctic site, the flowering season among female study plants lasted for 39 days and most flowers bloomed early in the season (Figure 10). Flowering lasted from the 19th of June until the 28th of July and followed a bimodal pattern with the biggest peak on the 28th of June and a second, smaller flowering peak on the 16th of July. The first flowering peak coincided with a frost event on the 28th of June, and about half the flowers (n=800 flowers) within seven plants were exposed to frost (Table 4).

At the individual level, the average flowering period among females in the High-Arctic site was 22.9 days (95% CI: 20.2, 25.7 days), and plant floral displays ranged from 36 flowers to 329 flowers per plant, with an average of 144.3 flowers per plant (Table 3, Table 4). Among these females, there was no correlation between the onset of flowering and the size of the floral display. The plant size ranged from six cm to 22 cm, with an average of 13.2 cm. Within this size range, there was a clear correlation with flowering time but not plant floral display (Figure 9). For each cm increase in plant size among females in the High-Arctic site, the average plant floral display increased by 4.8 flowers (95% CI: -7.9, 17.5 flowers), and the average flowering time increased by 0.6 days (95% CI: 0.1, 1.0 days).

Within individuals, most female flowers in the High-Arctic site bloomed early. Within plants, flower increase (average of 18.3 flowers per day) was higher than flower decrease (average of 10.0 flowers per day). Therefore, plant flowering had a positive skew and the first flower within females bloomed closer in time to peak floral display (average of 8.4 days) than the last flower (average of 14.5 days). For flowers within females in the High-Arctic site, the median floral longevity was 9.0 days (95% CI: 7.0, 10.6).

4.1.2 Female flowering in the Low-Arctic site

The flowering season among females in the Low-Arctic population lasted for 37 days and started three weeks before the flowering season in the High-Arctic site (Figure 10). In the Low-Arctic site, the females flowered from the 27th of May until the 3rd of July, and similar to the High-Arctic site, most flowers bloomed early within the population. In the Low-Arctic site, contrary to the High-Arctic site, there was no frost event during the growing season. Flowering among the females in the Low-Arctic site followed an approximately unimodal pattern with a positively skewed peak population flowering peak on the 5th of June.

Females in the Low-Arctic site had on average larger plant floral displays, but a slightly shorter flowering period than females in the High-Arctic site. The average flowering period was 18.6 days (95% CI: 14.4, 22.9 days), while plant floral displays ranged from 1 to 1188 flowers with an average of 322.6 flowers per plant (Table 3, Table 4). Within this range, females with large floral displays bloomed earlier in the season than those with smaller plant floral displays. Female plant size ranged from 4 cm to 43 cm with an average of 19 cm and was correlated with plant floral display and plant flowering time (Figure 9). For each cm increase in female size, the average plant floral display increased by 32.3 flowers (95% CI: 25.1, 39.5 flowers), and the average flowering time increased by 0.6 days (95% CI: 0.4, 0.8 days).

Within females in the Low-Arctic site, similar to females in the High-Arctic site, most flowers bloomed early. Within plants, flower increase (average of 56.6 flowers per day) was higher than flower decrease (average of 27.9 flowers per day). As a result, the first flower within females bloomed closer in time to peak floral display (average of 7.6 days) than the last flower (average of 13.9 days). Among females in the Low-Arctic site, similar to females in the High-Arctic site, median floral longevity was 8.0 days (95% CI: 8.2, 8.4 days).

4.1.3 Hermaphrodite flowering in the Low-Arctic site

Within the Low-Arctic population, the four hermaphrodites started flowering on average 4.6 days earlier than the females. Flowering among these hermaphrodites spanned 32 days, from the 27th of May until the 28th of June, with a flowering peak on the 15th of June (Figure 10).

The flowering period varied greatly among the hermaphrodites in the Low-Arctic site, and the average flowering period was on average 19.6 days (95% CI: 2.4, 36.8 days; Table 3). These four hermaphrodites had on average 40 flowers more in their plant floral displays than females in the Low Arctic site and were on average 1.6 cm smaller (Table 4). The hermaphrodite plant floral displays ranged from 3 to 1171 flowers with an average of 900 flowers per plant and plant size ranged from 3 cm to 42 cm with an average of 24 cm. Within this range, for each cm increase in plant size among the hermaphrodites, the average plant floral display increased by 30 flowers (95% CI: 25.6, 34.4 flowers), and the average plant flowering time increased by 0.6 days (95% CI: 0.1, 1.0 days; Figure 9).

Similar to females in both sites, most flowers within the hermaphrodites in the Low-Arctic site bloomed early and flower increase (average of 77.3 flowers per day) was higher than flower decrease (average of 38.2 flowers per day). Within the hermaphrodites in the Low-Arctic site, therefore, the first flower bloomed closer in time to peak floral display (average of 6.3 days) than the last flower (average of 13.2 days). The median flower longevity among the hermaphrodites was on average 2 days shorter than for flowers among females in the Low-Arctic site, with a median of 6.0 days (95% CI: 5.0, 7.0 days). Finally, hermaphrodite flowers appeared to produce male stamens first, with the female carpels maturing later.

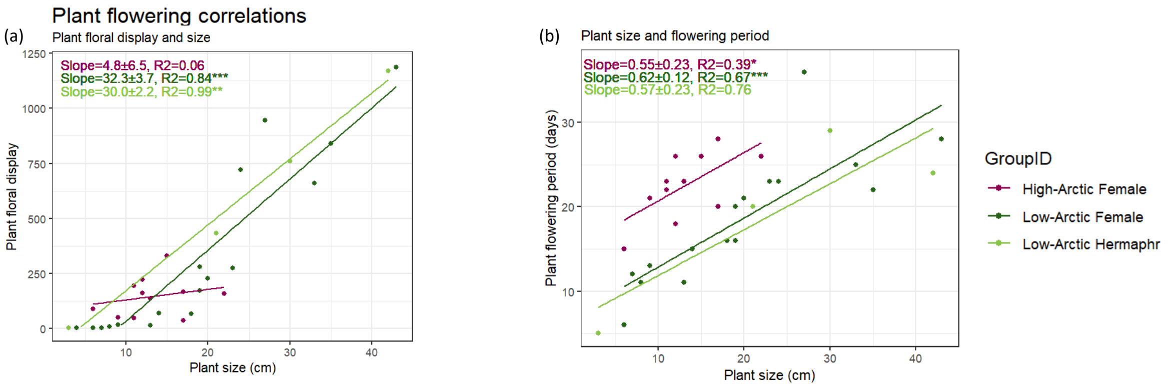


Figure 9 Relationship between plant size and (a) plant floral display and (b) flowering time for females in the High-Arctic site and females and hermaphrodites in the Low-Arctic. The fitted linear regression model and R^2 value with the significance of plant size on total plant floral display for each group are shown in colored text.

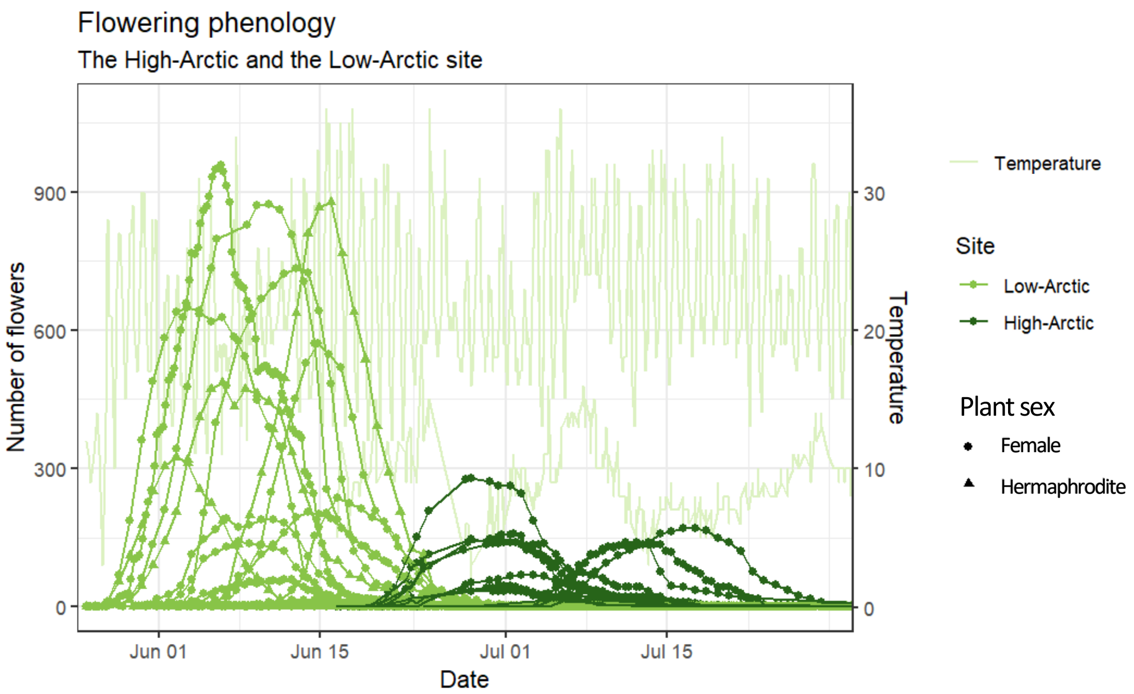


Figure 10 Flowering among females in the High-Arctic site (dark green) and females and hermaphrodites in the Low-Arctic (green). The temperature averages of each site (light green) are shown in the background of the plot. Detailed within-plant flowering phenology of all study plants can be found in Appendix 7.

Table 3 Population-level patterns for females in the High-Arctic site and females and hermaphrodites in the Low-Arctic site. For each group, the median floral longevity and the average first plant flower, plant flowering period in days, and fruit per flower proportions are shown.

			Average estimate		
Fecundity component	**Site**	**Sex**	**n**	**Estimate**	**95% CI**
Floral longevity (days)	High-Arctic	F	1549	9.0±3.4	7.0, 10.6
	Low-Arctic	F	5216	8.0±4.0	8.2, 8.4
		H	2333	6.0±3.4	5.0, 7.0
Flowering period (days)	High-Arctic	F	11	22.9±4.1	20.2, 25.7
	Low-Arctic	F	17	18.6±8.0	14.4, 22.9
		H	4	19.6±10.8	2.4, 36.8
First plant flower (DOY)	High-Arctic	F	11	173.5±9.0	167.4, 179.5
	Low-Arctic	F	17	154.6±5.6	151.6, 157.6
		H	4	150.0±3.8	143.9, 156.1
Fruits per flower proportion (% fruit)	High-Arctic	F	11	38.0±17.5	25.8, 50.1
	Low-Arctic	F	17	16.5±17.2	8.3, 24.7
		H	4	3.0±5.4	-2.2, 8.2

§ F=Female; H=Hermaphrodite; DOY= Day of Year; Estimate = Given as median±1 IQR (interquartile range) for floral longevity and mean±1 SD for all other fecundity components.

§§ All values are based on data from the full dataset

Table 4 Individual-level patterns for females in the High-Arctic site (PlantID BJOR) and females and hermaphrodites in the Low-Arctic site (PlantID NARS). Floral longevity is presented as median±interquartile range (IQR).

		Plant measurements				Number of flowers		Fruit set		Flowering phenology						Other
Site	**PlantID**	**Sex**	**Size**	**Invasion**	**Dead**	**Flowers (-)**	**Frost (-)**	**Fruit**	**%Fruit**	**Floral longevity**	**First flower**	**Peak display**	**Last flower**	**Flowering**	**First fruit**	**Image**
High-Arctic	BJOR-01	F	11	10	5	192 (3)	0 (0)	35	0.19	10.6±2.2 days	05.07.2019	17.07.2019	28.07.2019	22.6 days	21.08.2019	
	BJOR-03	F	12	0	10	154 (7)	0 (0)	54	0.37	7.0±2.6 days	03.07.2019	02.07.2019	22.07.2019	18.6 days	08.08.2019	
	BJOR-04	F	12	10	0	219 (3)	137 (2)	50	0.23	9.0±2.3 days	20.06.2019	29.06.2019	17.07.2019	26.6 days	06.08.2019	
	BJOR-05	F	17	5	0	35 (1)	0 (0)	20	0.59	6.0±3.0 days	04.07.2019	08.07.2019	25.07.2019	20.7 days	09.08.2019	
	BJOR-09-A	F	17	5	0	166 (0)	124 (0)	106	0.64	10.0±2.5 days	19.06.2019	01.07.2019	18.07.2019	29.0 days	04.07.2019	
	BJOR-09-B	F	11	15	0	48 (0)	37 (0)	7	0.15	9.0±2.5 days	22.06.2019	30.06.2019	13.07.2019	21.5 days	30.06.2019	Crop
	BJOR-11-A	F	6	0	0	87 (1)	52 (0)	23	0.27	7.8±2.0 days	24.06.2019	27.06.2019	09.07.2019	15.0 days	12.08.2019	Crop
	BJOR-11-B	F	15	5	10	324 (5)	278 (5)	83	0.26	8.8±1.8 days	19.06.2019	27.06.2019	16.07.2019	27.0 days	19.07.2019	
	BJOR-13-A	F	22	30	0	149 (9)	139 (8)	57	0.41	12.0±3.0 days	19.06.2019	01.07.2019	15.07.2019	26.0 days	01.07.2019	Crop
	BJOR-13-B	F	9	5	0	42 (7)	33 (0)	21	0.60	9.4±3.9 days	20.06.2019	01.07.2019	11.07.2019	21.0 days	11.07.2019	
	BJOR-16	F	13	5	0	133 (2)	0 (0)	61	0.47	10.5±2.5 days	03.07.2019	13.07.2019	27.07.2019	24.0 days	26.07.2019	
Low-Arctic	NARS-04	F	7	40	0	3 (0)	0 (0)	2	0.67	9.0±3.7 days	04.06.2019	12.06.2019	17.06.2019	12.5 days	27.06.2019	
	NARS-14	F	43	15	0	1066 (122)	0 (0)	81	0.09	7.8±3.3 days	27.05.2019	06.06.2019	25.06.2019	29.0 days	20.06.2019	Crop
	NARS-20-A	F	19	5	10	263 (17)	0 (0)	38	0.15	7.0±4.0 days	30.05.2019	06.06.2019	19.06.2019	20.0 days	07.06.2019	Crop
	NARS-20-B	F	14	15	15	67 (1)	0 (0)	13	0.20	7.0±3.0 days	02.06.2019	11.06.2019	17.06.2019	15.0 days	16.06.2019	
	NARS-20-C	F	19	25	0	171 (0)	0 (0)	25	0.15	7.0±3.0 days	30.05.2019	07.06.2019	16.06.2019	17.0 days	15.06.2019	
	NARS-21-A	F	33	15	0	640 (19)	0 (0)	65	0.11	6.0±2.0 days	05.06.2019	14.06.2019	30.06.2019	25.0 days	25.06.2019	Crop
	NARS-21-B	F	13	30	0	13 (0)	0 (0)	1	0.08	5.0±5.0 days	07.06.2019	13.06.2019	17.06.2019	10.0 days	26.06.2019	Crop
	NARS-24	F	18	20	0	65 (0)	0 (0)	5	0.08	7.0±1.0 days	04.06.2019	12.06.2019	19.06.2019	15.0 days	17.06.2019	
	NARS-31	F	20	10	0	219 (8)	0 (0)	6	0.03	9.0±5.5 days	04.06.2019	13.06.2019	25.06.2019	21.0 days	18.06.2019	Crop
	NARS-32	F	23	35	0	263 (12)	0 (0)	26	0.10	6.0±3.0 days	09.06.2019	16.06.2019	02.07.2019	23.0 days	05.07.2019	
	NARS-35	F	24	10	0	716 (5)	0 (0)	88	0.12	10.0±4.0 days	27.05.2019	03.06.2019	20.06.2019	24.0 days	08.06.2019	
	NARS-37	F	27	5	0	927 (18)	0 (0)	122	0.13	11.0±2.0 days	28.05.2019	05.06.2019	03.07.2019	36.0 days	10.06.2019	Crop
	NARS-40	F	4	0	0	1 (0)	0 (0)	0	0.00	7.0±0.0 days	04.06.2019	07.06.2019	11.06.2019	7.0 days	NA	
	NARS-43-A	F	6	5	0	3 (0)	0 (0)	0	0.00	6.0±5.0 days	15.06.2019	17.06.2019	19.06.2019	4.0 days	NA	
	NARS-43-B	F	9	0	0	15 (1)	0 (0)	7	0.50	7.0±2.0 days	09.06.2019	13.06.2019	21.06.2019	12.0 days	21.06.2019	
	NARS-43-C	F	8	0	0	7 (2)	0 (0)	1	0.20	5.0±4.5 days	11.06.2019	15.06.2019	23.06.2019	12.0 days	02.07.2019	Crop
	NARS-44	F	35	20	0	777 (64)	0 (0)	137	0.19	9.0±2.0 days	01.06.2019	12.06.2019	24.06.2019	23.0 days	14.06.2019	Crop
	NARS-05	H	3	30	10	3 (0)	0 (0)	0	0.00	4.5±2.1 days	31.05.2019	31.05.2019	04.06.2019	4.5 days	NA	
	NARS-22	H	30	5	0	733 (26)	0 (0)	74	0.11	7.0±3.0 days	27.05.2019	06.06.2019	26.06.2019	29.8 days	07.06.2019	Crop
	NARS-36	H	21	5	10	433 (0)	0 (0)	1	0.00	5.0±2.0 days	27.05.2019	02.06.2019	16.06.2019	20.0 days	11.06.2019	
	NARS-42	H	42	15	0	1164 (7)	0 (0)	12	0.01	6.0±2.0 days	04.06.2019	15.06.2019	28.06.2019	24.0 days	15.06.2019	Crop

§ H = Hermaphrodite plant; Size = Average between north-south and east-west axis in centimeter; Invasion = Percentage cushion covered by invasive species; Dead = Percentage of the cushion being dead; (-) = Flowers that were removed due to imprecise bloom time or fruit set; %Fruit = Percent fruits per flower; Flowering = Flowering period in days flowers are blooming within plants; NA = Not Applicable; Crop = A part of the study plant is outside the camera frame.

4.2 Female fruit set without frost exposure

The average female fruits per flower proportions in the High Arctic site were higher than in the Low-Arctic site (Figure 11). The average female fruits per flower proportion among females was 16.5% (95% CI: 8.3, 24.7%) in the Low-Arctic site and 38.0% (95% CI: 25.8, 50.1%) in the High-Arctic site. Among females in both sites, plants with larger floral displays produced more fruit in total. However, no impact of larger floral display on the average fruits per flower proportion was found in either site.

4.2.1 Within-plant floral display ♀🌱

In both sites, the logit of fruit set within females was highest in flowers during peak floral display and decreased in flowers that bloomed further outside peak floral display (Table 5; Figure 12a-b). In the Low-Arctic site, the logit of fruit set decreased with -0.264 (95% CI: -0.368, -0.161) for every day a flower within individuals bloomed away from peak floral display. In addition, there was some evidence for a non-linear effect in the Low-Arctic site. Specifically, a second-order polynomial model fitted better for two plants (NARS-20-A; coefficient for day^2 -1.21; 95% CI; -0.06, -2.38; and NARS-20-B; -0.83; 95% CI: -0.06, -1.60). In the High-Arctic site, similar to the Low-Arctic site, the logit of fruit set among flowers not exposed to frost decreased linearly by -0.463 (95% CI: -0.681, -0.244) for every day a flower bloomed away from peak floral display. However, in the High-Arctic site, in contrast to the Low-Arctic site, a linear decrease in the probability of fruit set with distance to peak floral display was the best model fit and the decrease was approximately equal for all days of flower bloom away from peak floral display.

4.2.2 Within-plant bloom time ♀🌱

The logit of fruit set in both sites was highest for early flowers within females and decreased in late flowers (Table 5; Figure 12c-d). In the Low-Arctic site, the logit of fruit set showed an approximately linear decrease of -0.296 (95% CI: -0.401, -0.191) for every day a flower bloomed later within plants. In addition, there was some evidence of a non-linear relationship in the Low-Arctic site. In particular, a second-order polynomial model fitted better for one plant (NARS-37; coefficient for day^2 -0.21, 95% CI: -0.13, -0.50), where the logit decreased slowly in early blooming flowers and then decreased more rapidly in later blooming flowers. In the High-Arctic site, similar to the Low-Arctic site, the logit of fruit set among flowers not exposed to frost decreased linearly with -0.469 (95% CI: -0.691, -0.246) for every day a flower bloomed later within females. In the High-Arctic site, however, there was no evidence for a non-linear relationship between the logit of fruit set and within-plant bloom time.

4.2.3 Population bloom time ♀🌱🌱🌱

Within populations in both sites, the logit of fruit set was higher for flowers blooming early than late within the population (Table 5; Figure 12e-f). In the Low-Arctic population, the logit of fruit set decreased by -0.384 (95% CI: -0.560, -0.228) for every day a flower bloomed later in the population. However, in the Low-Arctic site, the logit of fruit set showed a non-linear relationship to population bloom time where the fruit set odds of flowers remained high for early and peak floral display flowers, then rapidly decreased for late flowers within the population. In the High-Arctic site, similar to the Low-Arctic site, the logit of fruit set was highest in flowers blooming early within the population and decreased in flowers blooming later. Specifically, the logit of fruit set among females in the High-Arctic site decreased by -0.338 (95% CI: -0.643, -0.133) for every day a flower bloomed later within the population. In the High-Arctic site, in contrast to the Low-Arctic site, there was no evidence of a non-linear relationship between the logit of fruit set and population bloom time.

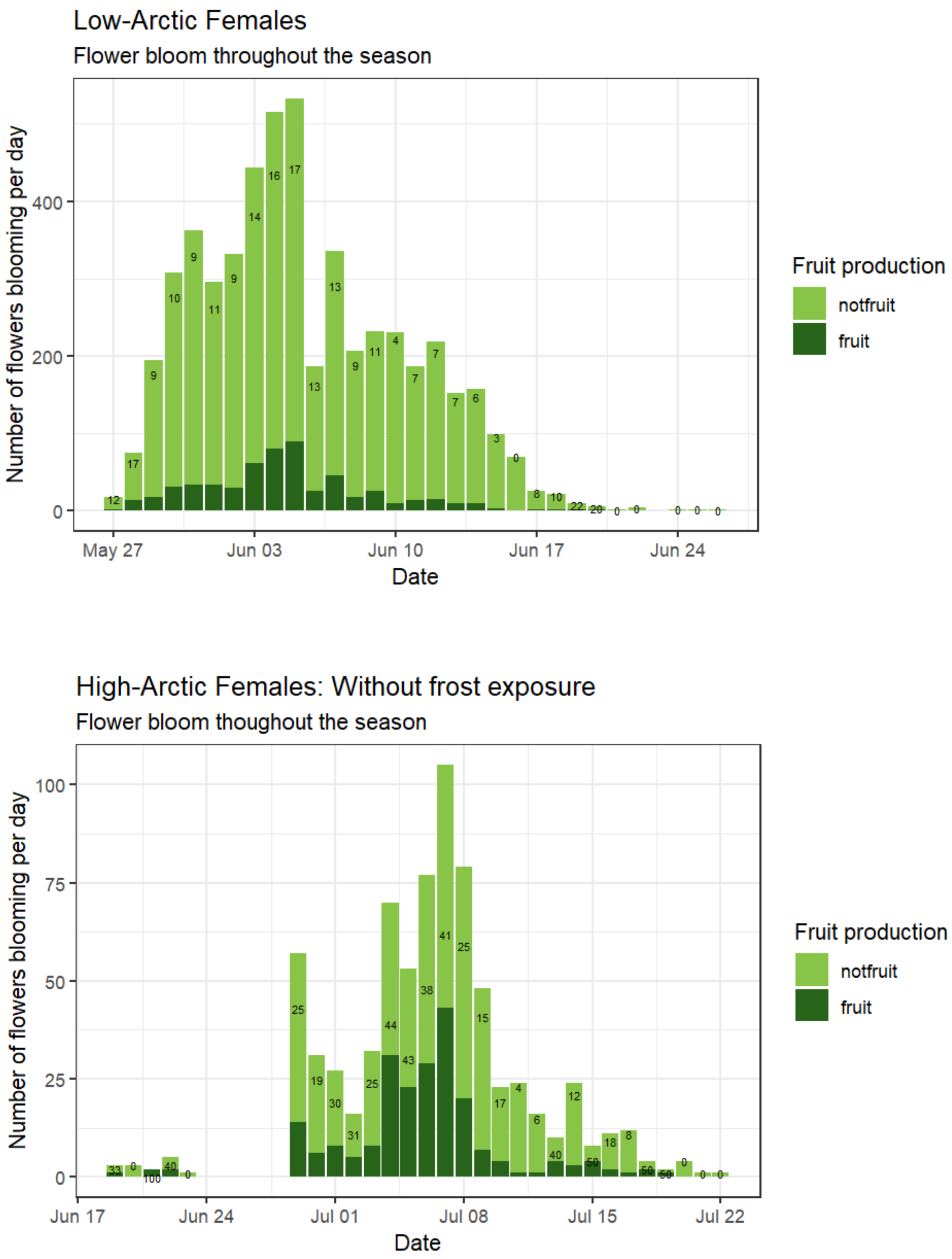


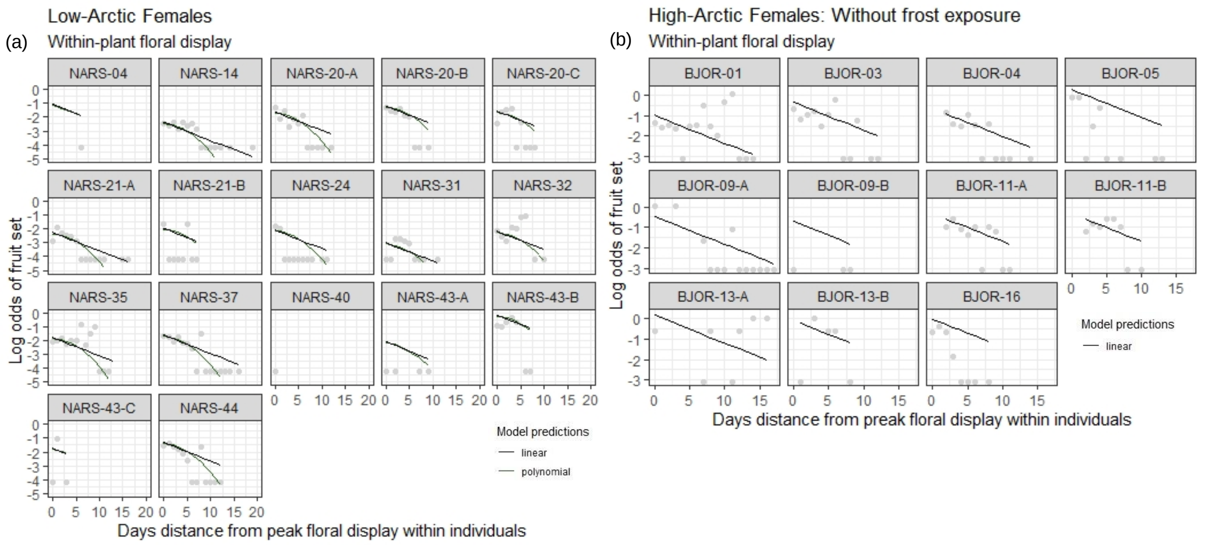
Figure 11 Female fruit set patterns in the Low-Arctic site (upper panel) and the High-Arctic site (lower panel) among flowers not exposed to frost. Each panel shows the proportion of flowers that set fruit (dark green bar) and that did not set fruit (light green bar) in each site, with the percentage of flowers that produced fruit in numbers on each column. At the High-Arctic site, there was a frost event on the 28th of June 2019. Flowers exposed to frost are not presented here, and are instead treated in the section "4.3.1 High-Arctic site: Frost exposure".

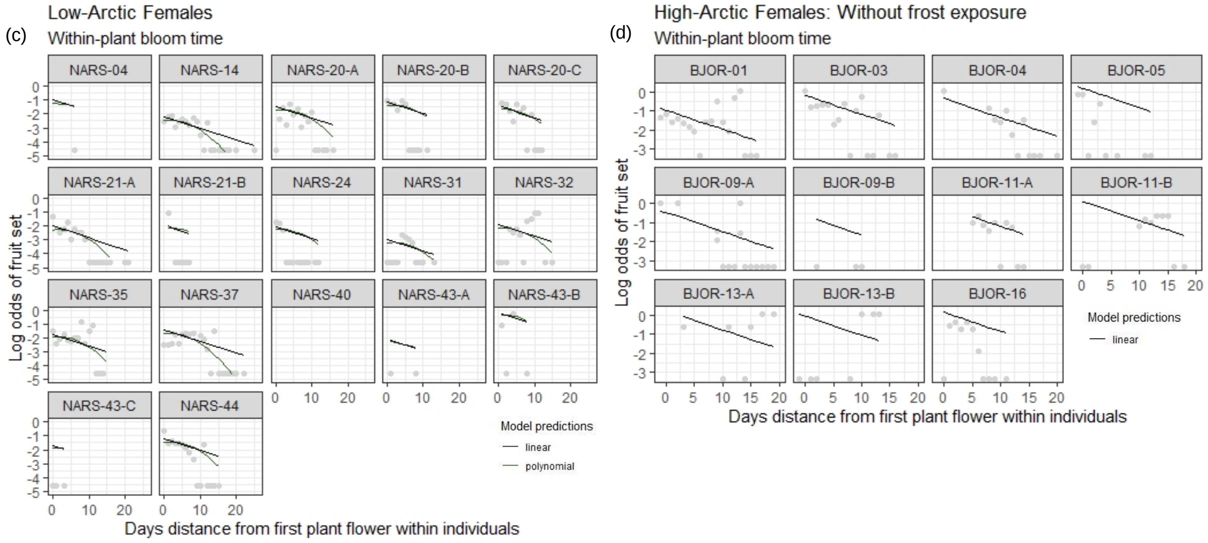
Table 5 Hierarchical logistic regression for the effect of three phenological predictors: within-plant floral display, within-plant bloom time, and population bloom time on the logit response variable of the fruit set. The best-fitting model is presented for each group. In the case of doubt between a non-linear and a linear relationship, both models are presented.

						Model estimates for the logit of fruit set								
						Within-plant floral display			**Within-plant bloom time**			**Population bloom time**		
Site	**Sex**	**Frost**	**df, Gr**	**Model**	**day**	**Est**	**95% CI**	**Z value**	**Est**	**95% CI**	**Z value**	**Est**	**95% CI**	**Z value**
Low-Arctic	F	No	5216, 17	\	x	-0.264	-0.368, -0.161	-5.0***	-0.296	-0.401, -0.191	-5.5***	-0.384	-0.560;-0.228	-4.8***
				∩	x	-0.230	-0.343, -0.117	-4.0***	-0.225	-0.351, -0.100	-3.5***	-0.365	-0.531, -0.198	-4.3***
					x^2	-0.095	-0.178, -0.012	-2.3*	-0.096	-0.188, -0.003	-2.02*	-0.206	-0.326, -0.085	-3.4***
	H	No	2333, 4	/	x	0.131	0.081, 0.181	5.1***						
				U	x				-0.507	-0.775, -0.239	-3.7***	0.083	-0.155, 0.322	0.7
					x^2				0.293	0.194, 0.392	5.8***	0.495	0.283, 0.708	4.6***
High-Arctic	F	No	749, 11	\	x	-0.463	-0.681, -0.244	-4.2***	-0.469	-0.691, -0.246	-4.2***	-0.388	-0.643, -0.133	-3.0**
	F	Yes	800,7	/	x							0.183	0.016, 0.351	2.1*
				U	x	0.049	-0.113, 0.221	0.6	-0.120	-0.296, 0.056	-1.3			
					x^2	0.240	0.094, 0.386	3.2**	0.258	0.050, 0.466	2.4*			

§ F = Female; H = Hermaphrodite; Frost = Frost exposure of flowers; Df = Degrees of freedom; Gr = Groups for the random effect variable; day = Whether estimate of coeficient is for a first-order parameter (x = day) or a second-order parameter (x^2 = day^2); Est = Estimate; . = p-value>0.1; * = p-value<0.05, ** = p-value<0.001, *** = p-value<0.0001.

§§ Model estimates represent effects on the logit scale and all predictors are standardized.





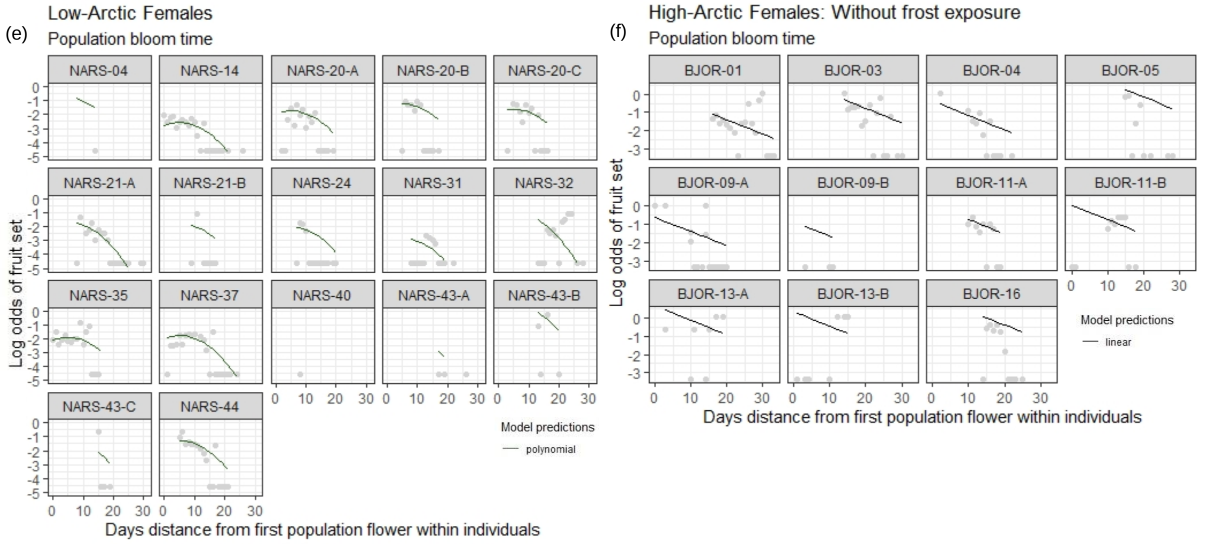


Figure 12 Fruit set probabilities among flowers not exposed to frost in the Low-Arctic site (right panels) and the High-Arctic site (left panels). Each panel portray the best fitting linear (black line) and/or a second-order polynomial (green line) model response between the logit of fruit set and (c,d) within-plant floral display, (e,f) within-plant bloom time, and (g,h) population bloom time. In the background of each plot, grey dots show the empirical logits of the raw data.

4.3 Site-specific fruit set patterns

4.3.1 High-Arctic site: Frost exposure ♀❄

Among females in the High-Arctic site, frost exposed flowers (n=800 flowers) produced 5.3% fewer fruits per flower than flowers not exposed to frost (n=749 flowers). However, 24.3% of frost exposed flowers did produce fruit (Figure 13a). No relationship was discovered between fruits per flower proportions and the amount of frost exposed flowers within females. In contrast to flowers not exposed to frost, relationships between the logit of fruit set for frost exposed flowers and the three phenological predictors were weak (Table 5; Figure 13b-d). A slight linear relationship was discovered between fruit set and population bloom time, where flowers blooming later in the population appeared to have a bit higher logit of fruit set. Specifically, the logit of fruit set among frost exposed flowers seemed to increase linearly by 0.183 (95% CI: 0.016, 0.351) for every day a flower bloomed later in the population. Between the logit of fruit set and the two other phenological predictors, within-plant floral display and within-plant bloom time, some evidence for non-linear relationships was found.

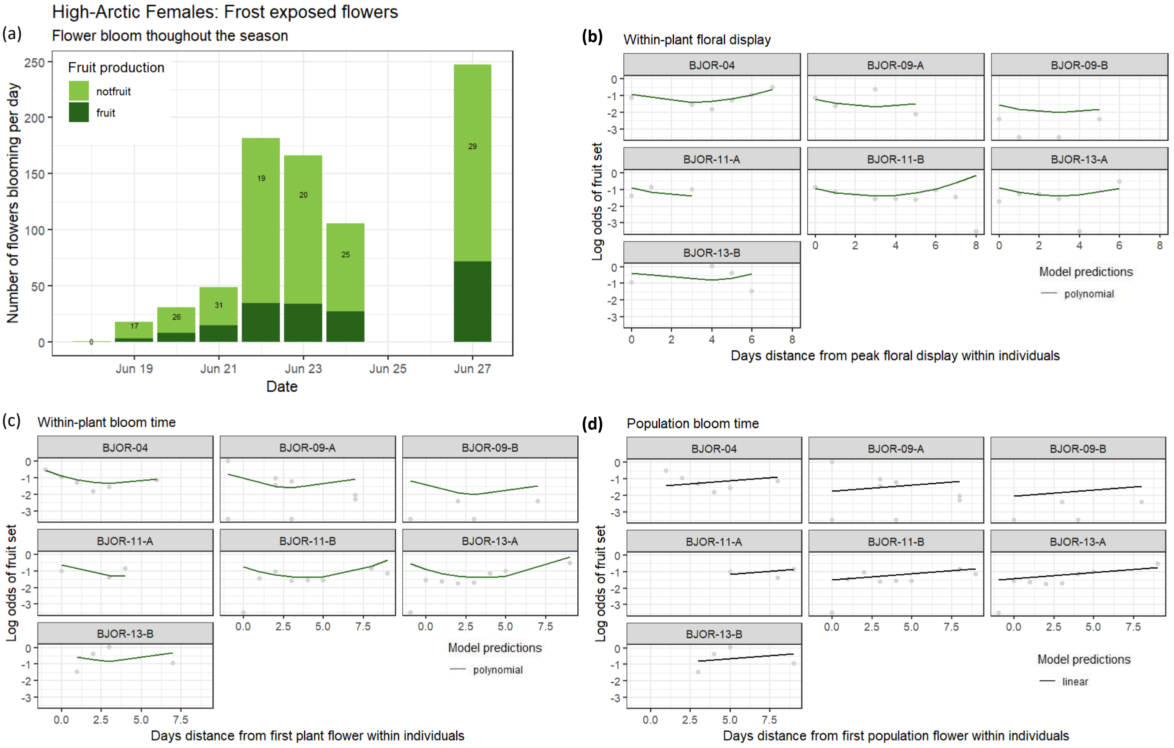


Figure 13 Female fruit set patterns among frost exposed flowers in the High-Arctic site. The upper left panel show (a) the proportion of flowers that set fruit (dark green bar) and that did not set fruit (light green bar). The other three panels show the log-odds of fruit set for each phenological predictor: (b) within-plant floral display, (c) within-plant bloom time, and (d) population bloom time. The best-fitting model for each predictor is shown with a linear (black line) and/or a second-order polynomial (green line). In the background, grey dots show the empirical logits of the raw data.

4.3.2 Low-Arctic site: Hermaphrodites ⚥

In the Low-Arctic site, the few hermaphrodites produced many flowers (n=2252 flowers) but few fruits (n=81 fruits; Figure 14a). The average hermaphrodite fruits per flower proportion was on average 3.0% (95% CI: -2.2, 8.2%), which was 13.5% lower than the average among females in the Low-Arctic site. However, fruit production greatly varied among the hermaphrodites. Three hermaphrodites produced under 1% fruits per flower each, while the fourth hermaphrodites produced 11% of fruits per flower. Within these hermaphrodites, the logit of fruit set was higher in early and late flowers, both at the individual level and within the whole population (Table 5, Figure 14b-d). Within hermaphrodites, the logit of fruit set linearly increased with distance from peak floral display, increasing by 0.131 (95% CI: 0.081, 0.181) for every day a flower bloomed further before or after peak floral display. For within-plant bloom time, a second-order polynomial relationship was found, with a higher logit of fruit set in early and late blooming flowering within hermaphrodites. A similar polynomial relationship was found between the logit of fruit set and population bloom time, with a higher logit of fruit set in early and late flowers than flowers blooming in the middle of the season.

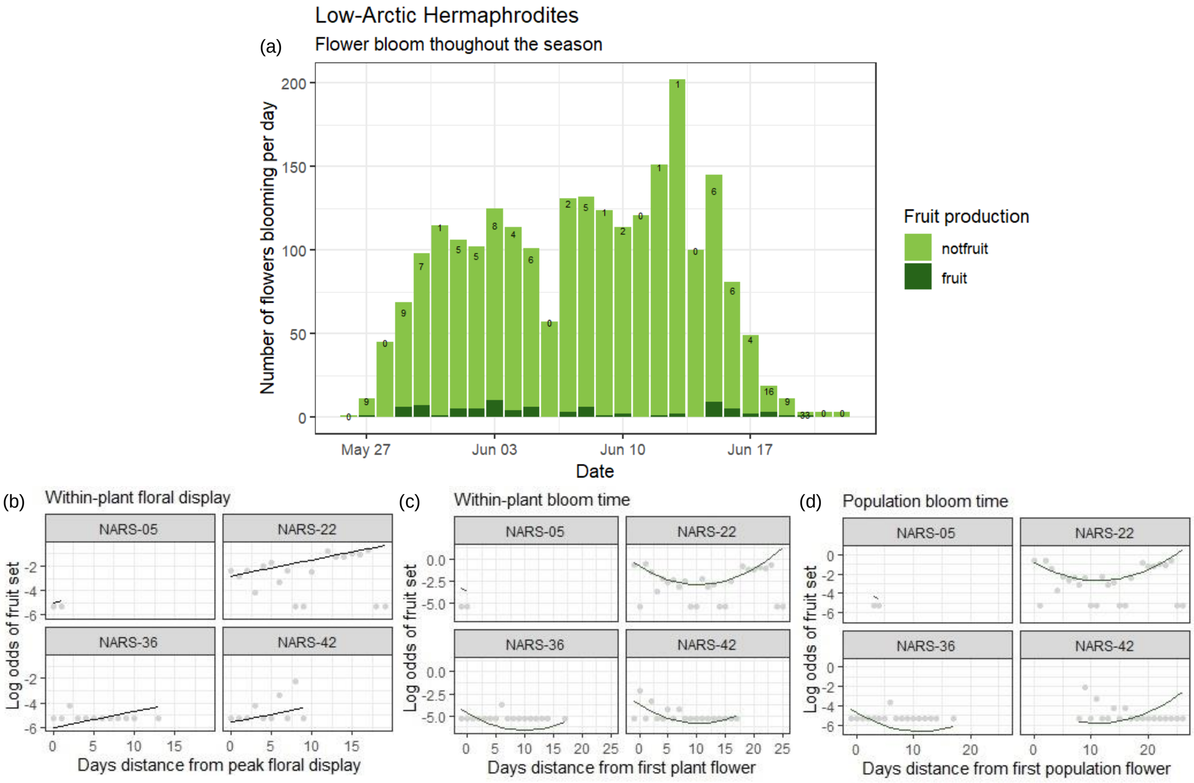


Figure 14 Hermaphrodite fruit set patterns in the Low-Arctic site. The upper panel show (a) the proportion of flowers that set fruit (dark green bar) and that did not set fruit (light green bar). The three lower panels show the logit of fruit set for each phenological predictor: (a) within-plant floral display, (b) within-plant bloom time, and (c) population bloom time. The best-fitting model is shown with a linear (black line) and/or a second-order polynomial (green line). In the background of each plot, grey dots show the empirical logits of the raw data.

5 Discussion

The primary aim of this study was to understand the dynamics of within-plant flowering phenology and its consequences on fruit production in the early-flowering pioneer species *S. acaulis. Silene acaulis* is a long-lived cushion plant that flowers in different abiotic and biotic conditions each year. These findings are based on data from one season, thus annual variation is not addressed. However, data were collected from two locations belonging to different weather and bioclimatic zones, thus common trends in both locations are therefore less likely to be influenced by seasonal variations.

In both sites, the average plant flowering period was around three weeks and most flowers bloomed early, both at the individual level and within whole populations. Among female flowers not exposed to frost, the probability of fruit set was higher in flowers that bloomed during peak floral display than outside peak floral display. In addition, flowers blooming early within individuals and populations were more likely to set fruit than late flowers.

In the High-Arctic site, there was a frost event and among frost exposed flowers, the degree of frost exposure was likely more important than bloom time for fruit production. In the Low-Arctic site, four study plants were hermaphrodites. Preliminary results from these hermaphrodites showed the opposite pattern of females, where the probability of fruit set was highest in late flowers blooming outside peak floral display, both at the individual level and within whole populations.

5.1 Flowering phenology

5.1.1 Female flowering in both sites

Silene acaulis is an early-flowering cushion plant with a long flowering period and floral longevity. This study found an average flowering period of approximately three weeks, with floral longevity of about one week. The females in the Low-Arctic site flowered around three weeks before the females in the High-Arctic site, likely due to earlier snowmelt in the Low-Arctic site. Interestingly, flowering was positively skewed and most flowers bloomed early, both at the individual level and in whole populations (Figure 15b-c). In the Low-Arctic site, in contrast to the High-Arctic site, plants that started flowering early had the largest floral displays. At the High-Arctic site, however, a frost event occurred and flowering among the females was bimodal, with the first largest peak during the frost event and then a second, larger peak afterward. Other studies have found similar flowering periods and floral longevity for *S. acaulis* (Alatalo & Totland, 1997; Hall et al., 2018; Marr et al., 1997; Table 6). A positively skewed flowering where most flowers bloom early within plants has also been found in other early-flowering species in Arctic-Alpine plants (Brown & McNeil, 2006; Forrest & Thomson, 2010). *Silene acaulis* is known to be early-flowering, and these results indicate that both the onset of flowering and peak floral display is timed early in the season. To my knowledge, this study is the first to propose a positively skewed flowering of *S. acaulis* throughout the growing season, both at the individual level and within populations.

5.1.2 Hermaphrodite flowering in the Low-Arctic site

Silene acaulis has a mixed breeding system with pollinator-dependent females and hermaphrodites able to self-pollinate (Hermanutz & Innes, 1994; Shykoff, 1992). This study included four hermaphrodites in the Low-Arctic site as a preliminary comparison to females in both sites. These four hermaphrodites, similarly to females in both sites, had positively skewed flowering where most flowers bloomed early. In addition, hermaphrodite flowers were protandrous, maturing male stamens before female carpels. Shykoff (1992) also found that hermaphrodite *S. acaulis* flowers are not as early receptive to pollen as females. Protandy has also been found in other *Silene* plants (Buide & Guitián, 2002; Talavera et al., 1996). Interestingly, the median floral longevity of hermaphrodite flowers was two days shorter than for female plants in the Low-Arctic site. Other studies have found shorter floral longevity in hermaphrodites than in females in gynodioecious plants (Elzinga & Varga, 2017). For another gynodioecious species (Campanulaceae), Wang et al. (2021) experimentally showed that during pollen-limitation, protandrous hermaphrodite flowers expand the male phase of flowers at the expense of the female phase and subsequent fruit production. The same pattern could be happening in the Low-Arctic site, where hermaphrodites might expand the male flower phase under pollen-limitation, and only produce fruit under sufficient pollen donation to pollinators. However, experimentally testing varying degrees of pollen limitation on a larger number of hermaphrodites will be needed for further evidence. Overall, these preliminary results suggest hermaphrodite flowers as protandrous and highlight the need for further studies on hermaphrodite investment in male and female flower phases under different pollinator conditions.

Table 6 Plant traits recorded of S. acaulis in other studies. For temperature measurements, the date of logging is also presented.

Plant trait	**Estimate**	**Location**	**Study**
Floral longevity (days)	6.8-10.5	Niwot Ridge, USA	Hall et al., 2018
	5-7	Pennsylvania Mountain, USA	Marr, 1997
	6.7±0.3	Pennsylvania Mountain, USA	Shykoff, unpublished, 1988
First flower (DOY)	177.6	Latnajavagge, Sweden	Alatalo & Totland, 1997
	169.3	Finse, Norway	Alatalo & Totland, 1997
	171-183	Niwot Ridge, USA	Hall et al., 2018
	177.6	Pennsylvania Mountain, USA	Shykoff, unpublished, 1988
	181	Endalen, Svalbard	Ween & Eidesen, unpublished, 2018
	173	Hotellneset, Svalbard	Ween & Eidesen, unpublished, 2018
Plant bloom time (days)	~28	Latnajavagge, Sweden	Alatalo & Totland, 1997
	~28	Finse, Norway	Alatalo & Totland, 1997
	11.7±0.8	Pennsylvania Mountain, USA	Shykoff, unpublished 1988
	15	Endalen, Svalbard	Ween & Eidesen, unpublished, 2018
Self-heating of plants (°C)	17.06.2010 - 07.09.2010 Outside: 7.5±3.8 Inside: 7.6±3.9	Endalen, Svalbard	Ween & Eidesen, unpublished, 2010
Surface temperatures across plants (°C)	06.11.2018 – 04.08.2018 North: 7.2±2.8 South: 7.9±4.2	Endalen, Svalbard	Ween & Eidesen, unpublished, 2011
	08.06.2018 – 23.08.2018 North: 9.0±3.6 South: 10.3±6.4	Hotellneset, Svalbard	Ween & Eidesen, unpublished, 2018

§ Self-heating of plants lists temperature on the outside (top) of a cushion and within five cm inside the same plant; Temperature gradient across plants lists temperature outside the north and south of a cushion.
§§ The estimates are given in mean±1 SD if available.

5.2 Female fruit set without frost exposure

5.2.1 Within-plant floral display ♀🌱

Silene acaulis has a varied within-plant flowering phenology, but with a peak floral display to attract pollinators. Within females, flowers that bloomed during peak floral display were expected to produce more fruit than flowers that bloomed outside peak floral display (Hypothesis H1). For flowers not exposed to frost, this study supports this hypothesis and found higher fruit set probabilities in flowers blooming during peak floral display. In both sites, a linear decrease of the logit of fruit set was found as flowers bloomed further away from peak floral display. In another study on *S. acaulis,* Hall et al. (2018) found that pollinator visits increase with floral display size and that plants with larger floral displays produced more fruits per flower proportion, despite less synchrony with conspecifics. Other studies have found a similar positive impact of increased local flower density, with increased pollinator visits and fruits per flower proportions within the *Silene* genus (Buide, 2006) and in other plant families (Braun & Lortie, 2019; Diggle, 1995; Vamosi et al., 2007). Makino & Sakai (2007) also found more sequential visits and a higher proportion of returning pollinators in plants with large floral displays. Interestingly, this study found positive impacts of floral display within plants, yet plants with larger floral displays did not have higher fruits per flower proportions than plants with small floral displays. Some studies indicate that pollinators visit a declining proportion of individual flowers in plants with large floral displays and that proportions of fruits per flower proportion thus remain approximately equal despite higher pollinator visits (Mitchell et al., 2004; Robertson & Macnair, 1995; Thomson, 2010). Future studies will be required to relate the positive effects of the within-plant floral display to whole populations with varying floral display sizes.

In the Low-Arctic site, there was also some evidence of a non-linear pattern between the logit of fruit set and within-plant bloom time. Specifically, two plants in the Low-Arctic site showed a second-order polynomial decrease in the logit of fruit set due to a rapid decline in fruit set probabilities after peak floral display. These two plants were positioned close to a large *Rhododendron lapponicum* (Table 2). *Rhododendron lapponicum* has large, fragrant flowers that are possibly more attractive to pollinators than flowers on *S. acaulis* (Bergman et al., 1996; Berry & Geeta, 2019). Possibly, only numerous flowers blooming synchronously were able to attract pollinators in these microhabitats with high levels of interspecific competition. Altogether, these findings highlight the importance of within-plant floral display as a strategy among early-flowering plants to attract pollinators in the Arctic growing season.

5.2.2 Within-plant bloom time

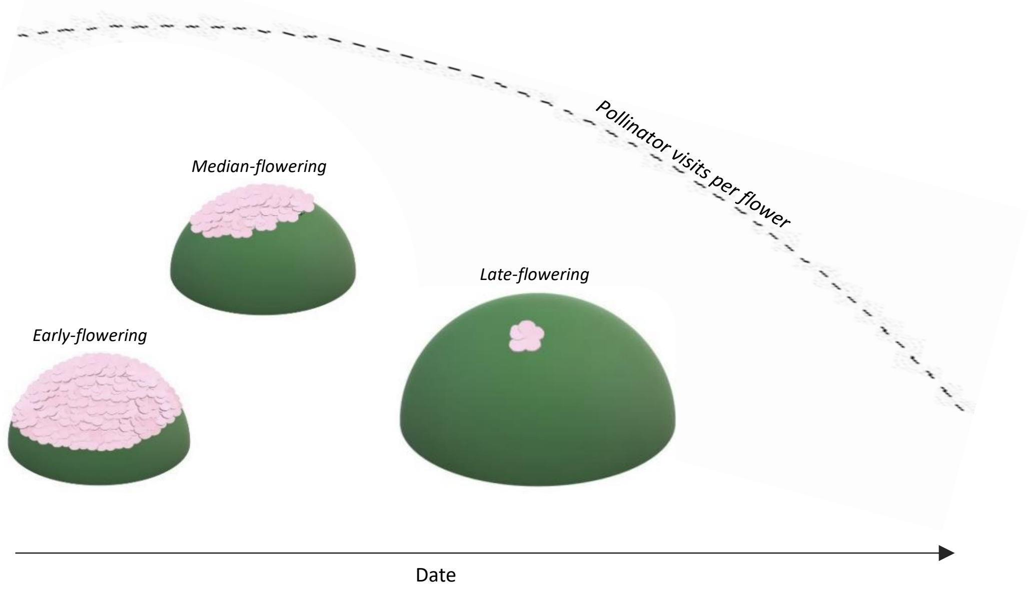
The Arctic growing season is short and *S. acaulis* flowers have a limited climatic window to attract pollinators and mature fruit. Within females, early flowers were expected to have more time and resources, and thus have higher fruit production, than late flowers (Hypothesis H2). For flowers not exposed to frost, this study supports this hypothesis and found higher fruit set probability in early flowers within plants than in late flowers. In both sites, a linear decrease of fruit set probabilities was found for each day a flower bloomed later within plants. Other studies have found that resource allocation within inflorescences often decreases from the first to the last flower (Diggle, 1995; Kliber & Eckert, 2004). In addition, several studies have found that floral arrangement and within-plant temperature patterns can influence pollination and fruit set (Bell & Bliss, 1980; Kilkenny & Galloway, 2008; Nicholls, 1987; Wyatt, 1982). In the northern hemisphere, dome-shaped cushions of *S. acaulis* receive sunlight at a higher angle on the south-faced sides of the cushions, which generally bloom before the north-facing sides (Jones & Richards, 1962). Early flowers on the south-facing sides of cushions might thus have higher cumulative temperatures to attract pollinators and to mature fruit. Forrest & Thompson (2010) found that late flowers were only capable of equal seed production as early flowers if early ovules were prevented, and argued that late flowers serve a bet-hedging function. In *S. acaulis*, early flowers might generally have more time, resources, and higher temperatures to attract pollinators and mature fruit. In case of a frost event, however, a long flowering period could ensure some flowers overlap favorable conditions and mature fruit. These results suggest an advantage of early flowers within *S. acaulis*, while late flowers could be a bet-hedging strategy in case of unpredictable events.

In the Low-Arctic site, some evidence for a non-linear relationship between fruit set probabilities and within-plant bloom time was found, suggesting a link between within-plant bloom time and floral display. In the Low-Arctic site, a second-order polynomial relationship between fruit set probability and within-plant bloom time was a better fit for one large plant. Within this large plant, peak floral display was eight days after the onset of flowering (Table 3), and the positive effects of peak floral display might have resulted in the polynomial relationship observed. Within all plants, flowering was positively skewed and the peak floral display was closer to the first flower than the last flower. Altogether, these findings indicate that due to most flowers blooming early within *S. acaulis*, early flowers might create larger floral displays and attract more pollinators than late flowers.

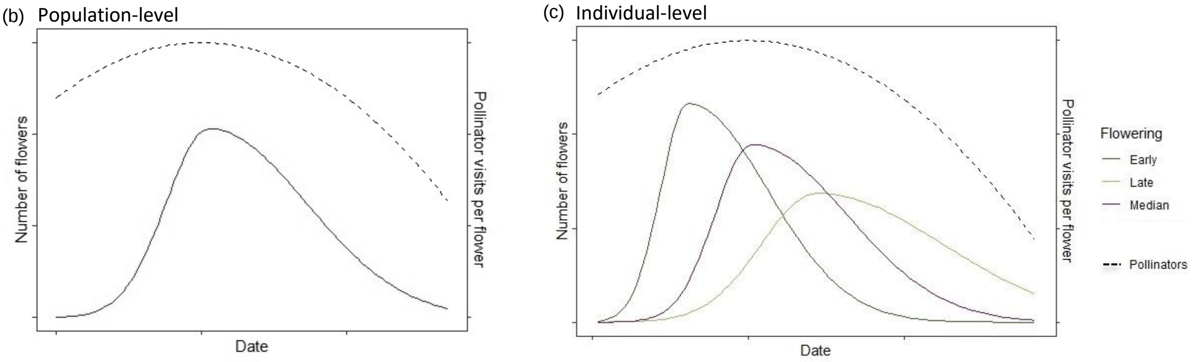
5.2.3 Population bloom time ♀🌱🌱🌱

Silene acaulis is a pioneer species adapted to plant communities in early successional stages and fairly low interspecific competition (Holway & Ward, 1965; Jones & Richards, 1962). Within populations, early flowers were expected to face less interspecific pollinator competition and have more time to complete fruit production (Hypothesis H3). This study supports this hypothesis and found higher fruit set probabilities in early flowers within the season than in late flowers (Figure 15a). Other studies have found more pollinator visits on early flowers than on late flowers in the season, though this might be shifting with climate change and plant-pollinator mismatch (Elzinga et al., 2007; Ison et al., 2018; Kharouba et al., 2018; Reid et al., 2014; Wheeler et al., 2015). Fewer flowering species early in the season could result in higher pollinator fidelity and more efficient pollination among early flowers (Gallagher & Campbell, 2020; Mosquin, 1971). Finally, floral herbivores, which were observed in the Low-Arctic site, often prefer peak or late-season (Ågren & Ågren, 2019; Elzinga et al., 2007). This study indicates an advantage of early flowers within *S. acaulis* populations, which might experience less pollinator competition and floral herbivory than late flowers.

In the Low-Arctic site, a non-linear relationship between population bloom time and the logit of the fruit set was found. The first female flowers in the Low-Arctic site had slightly lower fruit set probabilities than a few days later (Figure 15). The hermaphrodites included in this study flowered on average earlier than females. This could imply that lower temperatures or pollinator abundance in the onset of the growing season, and not asynchrony with pollen donors, was the cause of the slightly lower fruit set among the earliest flowers within the season. Later in the season, there was a much more rapid decline in fruit set probabilities in the Low-Arctic site than in the High-Arctic site. In the Low-Arctic site, a variety of other flowering species surrounded the study plants (Table 2). Several of these surrounding species have larger flowers than *S. acaulis* and might be more attractive to pollinators (Bergman et al., 1996). Females in the Low-Arctic site produced about half as many fruits per flower as females in the High-Arctic site, indicating higher levels of interspecific pollinator competition at the Low-Arctic site. These findings support the view of *S. acaulis* thriving in sites with low interspecific competition, though also maintaining viable populations in more competitive sites by early flowering (Canelles et al., 2018; Delph & Carroll, 2001; Svoen et al., 2019).



(a) Variations in flowering time of *Silene acaulis*



(b) Population-level

(c) Individual-level

Figure 15 Flowering phenology in the early-flowering cushion plant S. acaulis based on the results of this study. The upper panel (a) show an illustration portraying plants flowering early, median and late in the season. The lower panels show flowering at the (b) population level and (c) individual level. The fruit set among females in the Low-Arctic site, where there was no frost event, was used as a proxy for pollinator visits per flower (dotted line). Both at the individual level and within the whole population, most flowers bloomed early. Flowers blooming early and within peak floral display had higher female fruit set probability in this study, thus are portrayed with the highest pollinator visits per flower.

5.3 Site-specific fruit set patterns

5.3.1 High-Arctic site: Frost exposure ♀❄

Flowers on *S. acaulis* are vulnerable to frost and early flowers are more at risk of frost events than late flowers. If a frost event occurred, frost exposed flowers were not expected to show the same impact of within-plant flowering on fruit production as flowers not exposed to frost (Hypothesis H4). A frost event did occur in the High-Arctic site and approximately half of the flowers among the study plants were exposed to frost. Compared to flowers without frost exposure, frost exposed flowers produced 5.3% less fruit per flower than flowers not exposed to frost. However, total fruits per flower proportions were not lower in plants with more flowers exposed to frost. Other studies of Caryophyllaceae have shown resources to be allocated within inflorescence after manual removal of flowers (Guitián & Navarro, 1996; Medrano et al., 2000; Torices & Mendez, 2010). Possibly, resources were allocated within inflorescences after frost exposure. However, an experimental study will be needed for a more complete understanding of resource allocation within *S. acaulis* after frost exposure.

Frost exposed flowers in the High-Arctic site did not show the same fruit set patterns as flowers not exposed to frost. In contrast to flowers not exposed to frost, flowers outside peak floral display within individuals, and late flowers among all frost exposed flowers had slightly higher fruit set probabilities. These relationships were weak and only based on a small range of bloom times. However, differences in fruit set probabilities could indicate varying degrees of frost damage across cushions. Despite the frost event, 24.5% of frost exposed flowers produced fruit. This could signify that frost exposure varied between flowers and that degree of frost damage impacted the fruit set. Other studies have noted that the style, stigma, and flowers stalk are most at risk of frost (Hacker et al., 2011; Junttila & Robberecht, 1993; Larcher et al., 2010; Neuner et al., 2013). However, Hacker et al. (2011) showed that the internal heat gradient in *S. acaulis* interrupts ice formation internally and each reproductive shoot must therefore be exposed to an autonomous ice nucleation event to freeze. This study adds to evidence that not all reproductive shoots in *S. acaulis* are necessarily damaged by frost and that the internal heat gradient in the cushion might protect some flowers from frost damage.

5.3.2 Low-Arctic site: Hermaphrodites ⚥

Silene acaulis is a gynodioecious species with both females and hermaphrodites, though populations with functionally male individuals have been reported (Alatalo & Molau, 2001; Hermanutz & Innes, 1994; Philipp, 2009). Preliminary results in this study found that fruit production greatly varied among hermaphrodites in the Low-Arctic site. Compared to females in the Low-Arctic site, one hermaphrodite had a slightly lower fruit per flower proportion than females, and 11% of flowers produced fruit. Among the three other hermaphrodites, less than 1% of flowers produced fruit and functioned likely mostly as pollen donors. Other studies have also found varying female functions among hermaphrodites in a population, with some hermaphrodites with longer styles and higher fruits per flower proportion than other hermaphrodites (Hermanutz & Innes, 1994; Maurice et al., 1998). These preliminary results add to evidence of varying female function among hermaphrodites in gynodioecious species and that many hermaphrodite flowers in *S. acaulis* are functionally male (Ehrlen, 1991; Stephenson, 1981; Sutherland, 1986, 1987).

Silene acaulis has a dense floral display and hermaphrodites risk geitonogamy, the pollen transport within flowers in a floral display (Harder & Barrett, 1995). This study found that within individuals, hermaphrodite flowers away from peak floral display were more likely to produce fruit than flowers close to peak floral display. Within populations, flowers flowering early or late were more successful than flowers blooming in the middle of the season. Other studies have found that as flower proterandry seldom is synchronized within the plant, the possibility of geitonogamy occurs if pollinators make subsequent visits within a floral display (Galloway et al., 2002; Ishii & Sakai, 2001; Karron & Mitchell, 2012; Snow et al., 1996). During peak floral display, hermaphrodite flowers in pollen donor and pollen recipient stages will overlap and the risk of geitonogamy might be high. If pollinators subsequently visit flowers within a floral display, this could be a pollen transport loss for the plant (Barrett, 2003; Jong et al., 1999). To avoid such a pollen transport loss, hermaphrodite flowers blooming during peak floral display might function mostly as pollen donors and produce less fruit than flowers early or late within the plant. Due to the few hermaphrodite plants included in this study, more research will be needed to study the impact of within-plant floral display on fruit set in hermaphrodite *S. acaulis.* However, these preliminary findings could signify that hermaphrodite flowers function mainly as pollen donors during peak floral display, possibly as a mechanism to avoid geitonogamy.

5.4 Methodological considerations

5.4.1 Time-lapse camera monitoring

Time-lapse monitoring of phenology is becoming widely used as a powerful technique for detailed data collection in demanding field regions (Black et al., 2018; Edwards et al., 2015; Garcia Gonzalez, 2018; Nagai et al., 2016). However, the use of images for data collection also had its drawbacks. Firstly, observer bias might be present in manual image annotation by one observer. Preferably, the same images could be annotated by several observers to gain more insight into possible detection errors. For example, though the flowering data in this study is approximately congruent with other phenology studies on *S. acaulis,* large outliers in floral longevity were observed in the annotation data (Table 6). *Silene acaulis* has many small, overlapping flowers which likely covered the exact withering of flowers in a large floral display to an image observer. Even though the median floral longevity was only slightly longer than in other studies, these outliers show that overlapping flowers might be a challenge in image annotation of flowering plants. Further, only quantitative data on fruit production is possible through images. Though quantitative fruit number has been successfully used as a proxy for fruit production in other studies (Hall et al., 2018; Kempe, 2014; Reid et al., 2014; Svoen et al., 2019), qualitative options of seed number and seed weight inside each fruit capsule would be valuable additions to future studies.

Time-lapse monitoring is an observational method and could be enriched with a complimentary experimental design. A pollinator exclusion and a pollen supplement experiment could be done at each site to investigate pollen limitation differences between hermaphrodites and females. Thus, the self-pollination ability of hermaphrodites could be explored, especially in cushions that appear functionally male. In addition, manual removal of flowers could explore resource allocation within cushions. By manually removing early flowers within plants, one could explore if more resources were diverted within cushions to late flowers. Future studies that combine the observational methods of time-lapse cameras with hands-on experimental approaches could provide a better impression of Arctic flowering phenology and reproductive success.

Finally, the time-lapse images in this study also contained data on arthropod activity around and within *S. acaulis* plants throughout the growing season. Future studies could quantify arthropod abundance with detailed time-lapse photography and through the training of machine learning algorithms. This has already been done for other plant species (Bjerge et al., 2021; Edwards et al., 2015; Garcia Gonzalez, 2018). By identifying different taxonomic groups, one could further classify different functional groups of arthropods and their interactions with flowering plants. Floral herbivores, for example, could impact pollinator visitation by changing flower morphology, volatile production, and nectar production (Elzinga et al., 2007; Lucas-Barbosa, 2016; Ramos & Schiestl, 2019; Rusman et al., 2019). By detailed arthropod quantification by machine learning algorithms, one could further explore the intricate dynamics between a floral herbivore activity, pollinator visitation, and flowering phenology and its impact on fruit production patterns.

5.4.2 Future studies: expanding spatial and temporal scopes

Within each site, study plants were not chosen randomly but were larger and with fewer intrusions and dead areas than plants in the surrounding study populations. Other studies have found that dead areas and intrusive species have a reproductive cost to facilitative plants (Cranston et al., 2012; Schöb et al., 2014). Further, larger *S. acaulis* plants have been shown to produce more flowers, though not all effects are linear (Canelles et al., 2018; Delph & Carroll, 2001; Hermanutz & Innes, 1994). The study plants would therefore likely have more flowers than plants in the study population. The impact of floral displays would likely be weaker in small plants with few flowers than in large plants with abundant flowers. Smaller plants with fewer flowers would also likely have less microclimatic differences and less subsequent variation in bloom time than large dome-shaped cushions. Finally, cushion size is related to age, thus the study plants might be older and with different life-history traits than younger plants in the study populations (DeMarche et al., 2018; Morris & Doak, 1998).

Silene acaulis is a widespread species and can reach over 300 years of age (Jones & Richards, 1962; Morris & Doak, 1998), yet this study only includes data from one year and two sites. Buds of *S. acaulis* are pre-formed the previous year and a multi-year study would have revealed if the fruit set was impacted by conditions in the previous year. Additionally, a multi-year study could explore if the same plants flower early and late each year. By including both female and hermaphrodite plants, one could compare the annual flowering of pollen donors and pollen recipients to reveal assortative mating patterns. If plants flower at the same time each year, this could lead to fine-scale isolation between early and late flowering plants, as shown in studies of other species (Elzinga et al., 2007; Fox, 2003; Weiss-Schneeweiss et al., 2013). Further, such mating patterns might be influenced by the spatial patterns within the population and with other flowering species in the habitat. A future long-term flowering phenology study could reveal how flowering synchrony, both within a population and between different flowering species within a habitat, impacts fruit production.

In the northern hemisphere, dome-shaped *S. acaulis* cushions receive more solar energy on south-facing than north-facing sides, creating varied flowering phenology across cushions. However, cushion growth is primarily regulated by soil temperature (Hagen & Spomer, 1989). With rising Arctic temperatures, *S. acaulis* might grow less compact mats instead of dense, dome-shaped cushions to prevent overheating. Less compact mats of *S. acaulis* experience fewer differences in sun angle and microclimate across the plant than dome-shaped cushions. Possibly, this could lead to less varied within-plant flowering variation across plants and might shorten plant flowering time. Long-term observational studies in combination with open-top chamber experiments in several sites could provide valuable insight into how the within-plant flowering phenology of cushion plants might respond to rising Arctic temperatures.

6 Concluding remarks

Silene acaulis is a long-lived plant that will experience many years of flowering in different abiotic and biotic conditions. This study reveals a long flowering period in *S. acaulis* for approximately three weeks, but with a positively skewed peak floral display. In pollinator-dependent females, flowers within this early peak floral display likely produce more fruit than late flowers in most years. In other years, however, the long flowering time could ensure that some late flowers avoid early-season pollinator deficits or frost events. These late flowers might thus function as a bet-hedging strategy for unpredictable events. *Silene acaulis* has a long history with lineages surviving in refugia throughout climatic oscillations and glacial cycles during the Pleistocene. This study yields insight into cushion plant adaptation to climatic change and early-successional habitats, by high tolerance to short-term pollinator mismatch and frost events. A long plant flowering period, combined with early flowering and a peak floral display, seems to ensure at least some flowers will overlap favorable conditions in the short Arctic growing season.

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Appendix 1

I. POPULATION STUDY LOW-ARCTIC SITE

The Low-Arctic population was large and spanned over a myriad of microclimates (-45.37637°E, 61.18054°N) In 2019, six plots of 5x10 meters were established, and distributed equally between open, dry habitat and wet, mossy habitat. Habitats were selected non-randomly and were approximately homogenous for the area required. To ensure flowering data, the presence of at least 30 plants of *S. acaulis* above two centimeter in size was also required. Within each plot, a maximum of 60 plants above two cm were selected, altogether making up 338 plants. In the Low-Arctic site, a random plot was chosen to compare flower size between females and hermaphrodites (N6, Figure 3). Each flowering plant with at least three flowers was measured at one flower east, west, south, north, and the top of each plant in the middle of the flowering timing (13.06.2019). In total, 15 hermaphrodites and 18 females were selected for flower size measurements.

In the Low-Arctic, two dome-shaped cushions were selected (35 cm in diameter, plot NARS-4 and 37 cm in NARS-4). In both cushions, a HOBO MX2301A Temp/RH logger was inserted five cm into the north and south-facing parts of the selected cushions to measure internal temperature. Temperatures were measured from the start of the flowering season and about a month of fruit development, from the 28th of May until the 17th of July 2019, and the average temperature throughout the logger period and the largest deviances between the north and south-facing parts of cushions were calculated.

II. POPULATION STUDY HIGH-ARCTIC SITE

At the High-Arctic site, the population was smaller and within the same habitat (15.33347°E, N 78.21629°N). In 2020, ten transects of ten meters each were established. All plants within 50 cm from either side were included in the population study. In total, 164 plants were included in the population study.

For temperature measurements, one cushion with a size of 41 cm in diameter was selected. On this cushion, HOBO MX2202 Pendant MX Temp/Light loggers were used to measure the surface temperature on the dome-shaped cushions. In general, cushions in the High-Arctic were more dome-shaped than in the High-Arctic, and the same was the case for the selected cushion. Temperatures were measured from the start of the flowering season and about a month of fruit development, from the 8th of June to the 23rd of August 2018 in the High-Arctic site, and the average temperature throughout the logger period and the largest deviances between the north and south-facing parts of cushions were calculated.

III. PRELIMINARY HIGH-ARCTIC STUDY

Since the High-Arctic site was slanted and surrounded by mountains, the nearest open, flat area was chosen for the preliminary microclimate study (15-51510°E, 78.24882°N). Three plots were established ten meters apart at Hotellneset, five kilometers away from the High-Arctic site. In 2018, all *S. acaulis* plants were marked inside, expanding the plots until reaching over 60 plants in total within all three plots. In total 63 plants were selected, where 43 plants flowered (24 female and 26 hermaphrodites). At the end of the season, from 23rd to the 25th of August 2018, a grid system was used to count fruit in each cardinal direction of the plants. To this end, a 1x1 meter metal frame was placed 30 cm over the ground with the plant in the middle and the same end pointing on a north-south axis. The metal frame was split into 100 grids and fruit was counted within each grid. In analysis, the grids were merged into categories. The four grids on top of each cushion were isolated and other grids were divided into north and south-facing parts of the cushion. Within each category, the total amount of fruit set of all females and hermaphrodites was calculated.

Appendix 2

Site	ID	Habitat	n	Us	Female (%)	Invasion (%)	Dead (%)	Size (cm)
Low-Arctic	N1	Open	2	0	50	35±7.1	5±7.1	5±2.8
	N2	Open	1	0	100	15±0	0±0	43±0
	N3	Open	6	0	83	15.8±10.2	4.2±6.6	21.3±8.3
	N4	Open	4	0	75	5±4.1	2.5±5.0	19±10.3
	N5	Closed	5	0	80	8±9.1	0±0	20±17.1
	N6	Closed	3	0	100	21.7±12.6	0±0	20.3±2.5
	NARS-1	Open	60	4	80	5.27±6.11	21.2±16.4	9.03±6.67
	NARS-2	Open	43	5	61	3.22±4.83	30.4±27.4	8.63±5.73
	NARS-3	Open	61	7	65	3.13±5.49	27.0±23.6	8.41±5.17
	NARS-4	Closed	60	24	75	31,6±21.8	12.3±17.0	14.8±9.71
	NARS-5	Closed	60	5	80	48.2±19.8	5.5±12.9	15.3±7.0
	NARS-6	Closed	62	21	71	24.1±32.2	8.7±2.9	6.4±13.5
High-Arctic	B1	Open	5	0	100	6±4.2	3±4.5	13±2.3
	B2	Open	5	0	100	10±11.0	2±4.5	13.3±5.8
	BJOR-1	Open	12	11	100	5±14.5	9.83±19.4	4.15±2.52
	BJOR-2	Open	9	3	83	17.8±13.3	26.7±27.2	15.9±7.93
	BJOR-3	Open	8	6	100	10.6±11.2	0±0	1.88±1.03
	BJOR-4	Open	18	7	73	9.72±18.1	20.3±22.0	3.43±2.74
	BJOR-5	Open	15	3	67	15±18.4	29.3±36.8	5.77±2.47
	BJOR-6	Open	13	7	83	13.8±11.6	30.4±37.5	5.53±2.97
	BJOR-7	Open	25	11	79	8.8±11.3	29.2±36.6	5.81±3.9
	BJOR-8	Open	26	13	39	8.46±13.2	26.5±30.8	4.18±2.95
	BJOR-9	Open	22	12	80	10.2±11.8	18±25.8	3.89±2.24
	BJOR-10	Open	16	3	85	30.6±26.6	30.6±26.6	7.25±4.42
	HOT1	Open	23	10	43	15.8±11.2	22.1±23.3	19.7±4.8
	HOT2	Open	17	0	41	17.1±11.8	23.8±19.3	28.6±12.8
	HOT3	Open	23	4	30	23.6±19.3	35.1±18.7	20.8±6.4

§ N1-5 = All camera study cushions the Low-Arctic site; NARS = Plot in Low-Arctic Narsarsuaq, Southern Greenland; B1-2 = All camera study cushions in the High-Arctic site; BJOR = Transects in High-Arctic Bjørndalen, Svalbard; HOT = Plots at Hotellneset, a flat area five kilometers away from the High-Arctic site; Open = Well-drained soil, Closed = Wet, moss-covered ground; n = Number of plants; Us = Unknown plant sex or non-flowering plants

§§Invasion, Dead, and Size columns present the mean±SD.

Appendix 3

I. METHODOLOGY TIME-LAPSE ESTABLISHMENT

Time-lapse cameras should monitor *Silene acaulis* plants throughout the whole season, with image intervals of ten seconds (Low-Arctic site in Narsarsuaq) or one minute (High-Arctic site in Bjørndalen). Camera clusters should be named N1-6 in the Low-Arctic site and B1-2 in the High-Arctic site.

II. CAMERA SETTINGS

Each camera should take images every ten seconds throughout the season. Memory cards of 128 GB should be used and external batteries if necessary. One week of images every minute use approximately 50 GB. Therefore, changing memory cards every week throughout the season is recommended. If a solar panel is not installed, batteries will need to be changed approximately once a month.

III. CAMERA SET-UP

Before camera establishment on *Silene acaulis*, a rapid overview of the population should be done before choosing the study plants. Most importantly, the study plants should be of an approximate size as the rest of the populations. Each camera should point to one plant, and the whole plant should be included in each frame. Mark the northern side of the plant with a nail or other marking. Cameras should be placed on a tetrapod, a metal structure with four legs. The camera is placed at a 90-degree angle above each plant. Each camera should be 60 cm above each *Silene* plant. Around each camera there should be an aluminum box to protect from rain, that is screwed into a wooden plate.

IV. MEASUREMENTS ON STUDY PLANTS

For the study plants, the size of each plant should be noted down. This is measured from the north to the south of the plant. Then, a brief note about the surrounding vegetation and any mountains in the immediate surroundings that could block light for the plants should be included. If possible, include a ruler and a compass next to each camera plant in the first photos. This will make it easily find this information when processing the images.

Appendix 4

The annotations should be done in the VGG Image Annotator (VIA 2.0.8.). VIA is an online program that does not require any installation.

I. CREATE ANNOTATIONS

Open the link to VIA 2.0.8. Click on "*Attributes*" in the lower-left corner of the screen circled in red. Write *"state"* as the name and select the dropdown under type and id: "*Bud", "Flower", "Withered", "Immature fruit",* and *"Mature fruit".*

II. DEFINITION OF ANNOTATION STAGES

1. *"Bud"* – Only a pink/white circle is visible.
2. *"Flower"* – As soon as petals can be distinguished.
3. *"Withered"* – No petals visible, they have all curled up/withered.
4. *"Immature fruit"* – A green fruit within a sheath can be distinguished.
5. *"Mature fruit"* –The fruit is brown and clear-cut teeth can be seen.

The first phase is a bud, that turns into a flower. After flowering, all flowers wither and only some will produce fruit. Each fruit has two stages. The first stage is a green fruit within a red/brown sheath. When mature, this fruit will dry out and open to let seeds out. An example of each annotation stage is shown below.

III. UPLOADING IMAGES

To add images, click on "*Add files*" and mark all the images for annotation. The image names will now appear in the box to the left. After importing the images, the first task is to find the first visible bud. Scroll through the images either with the arrows on your keyboard or with the < and > buttons on the black taskbar on the top.

IV. FIRST ANNOTATED IMAGE

Annotation starts when the first bud is visible. Once the starting image is found, zoom in to at least x6. Start with one section and thoroughly check the whole plant for flowers. Each image should be checked twice in this way. To make an annotation, first, select the square from the panel. Make a square covering the bud. Repeat this process for any other buds in the image. The first square will be labeled “1” in the dataset, the second will be labeled “2”, and so on.

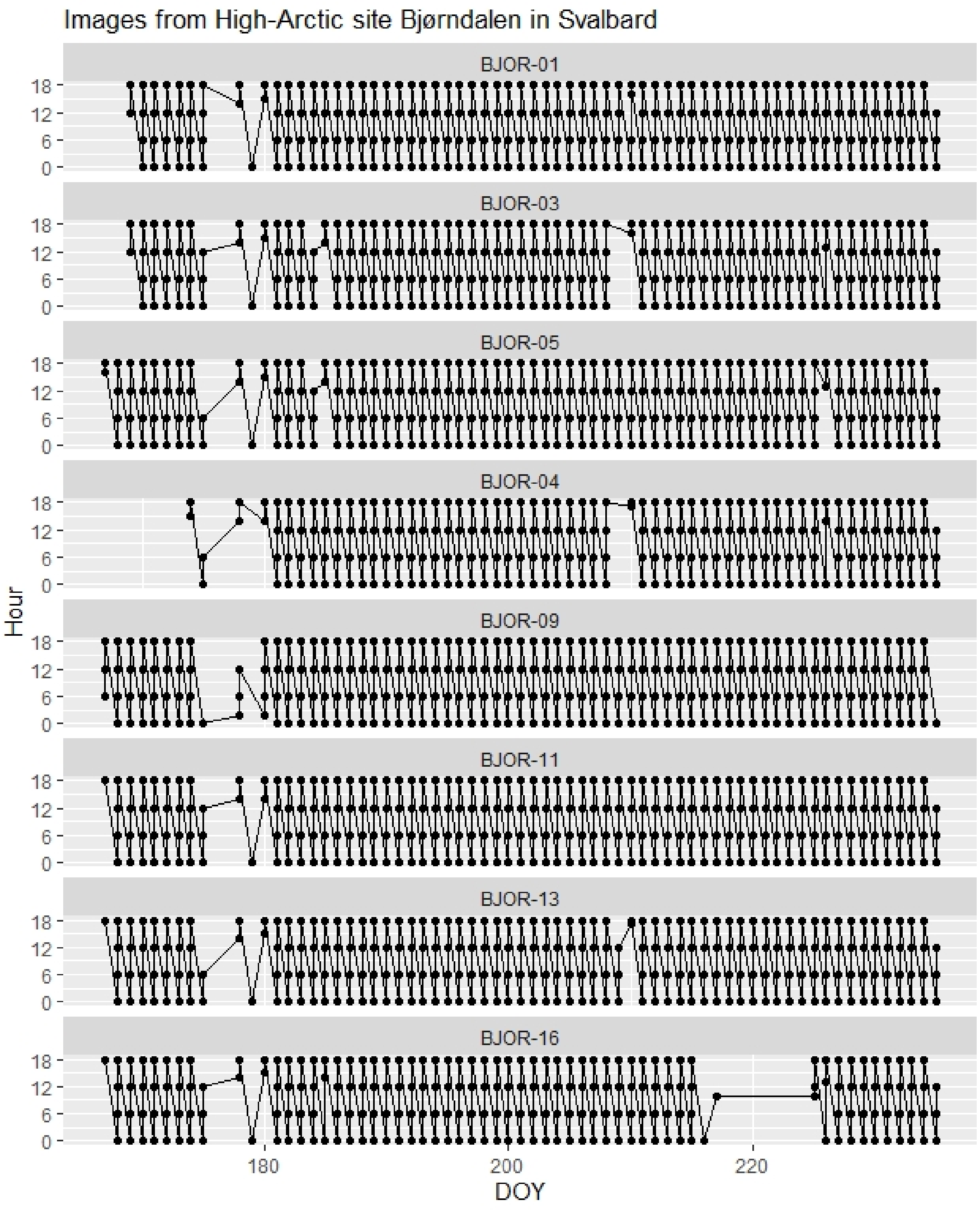
V. COPY ANNOTATIONS

When finished with the first image, annotations are copied to the next image. First, select and copy all the annotations, then paste them to the next image. After pasting, squares are added to any new flowers. This should be done with care to not miss any flowers. If this happens, one cannot go back and mark the flowers in previous images. Pay attention to the numbering of flowers and that numbering is correct throughout the annotation flower.

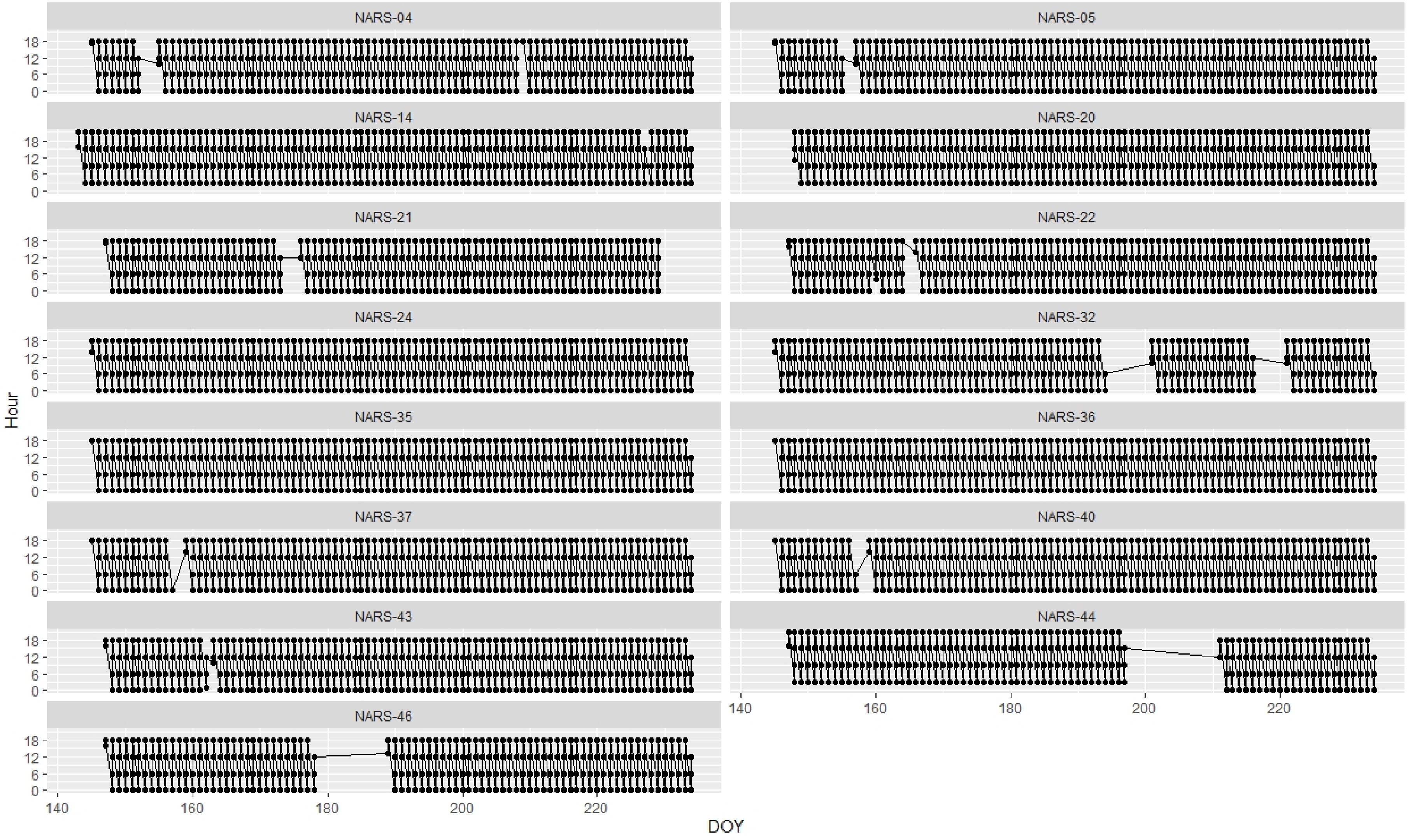
VI. END OF THE ANNOTATION

The annotation ends when all fruits are mature. All annotations at this stage should be either “*Withered”* or “*Mature fruit”.* When finished, save the annotation in both .csv and .json format.

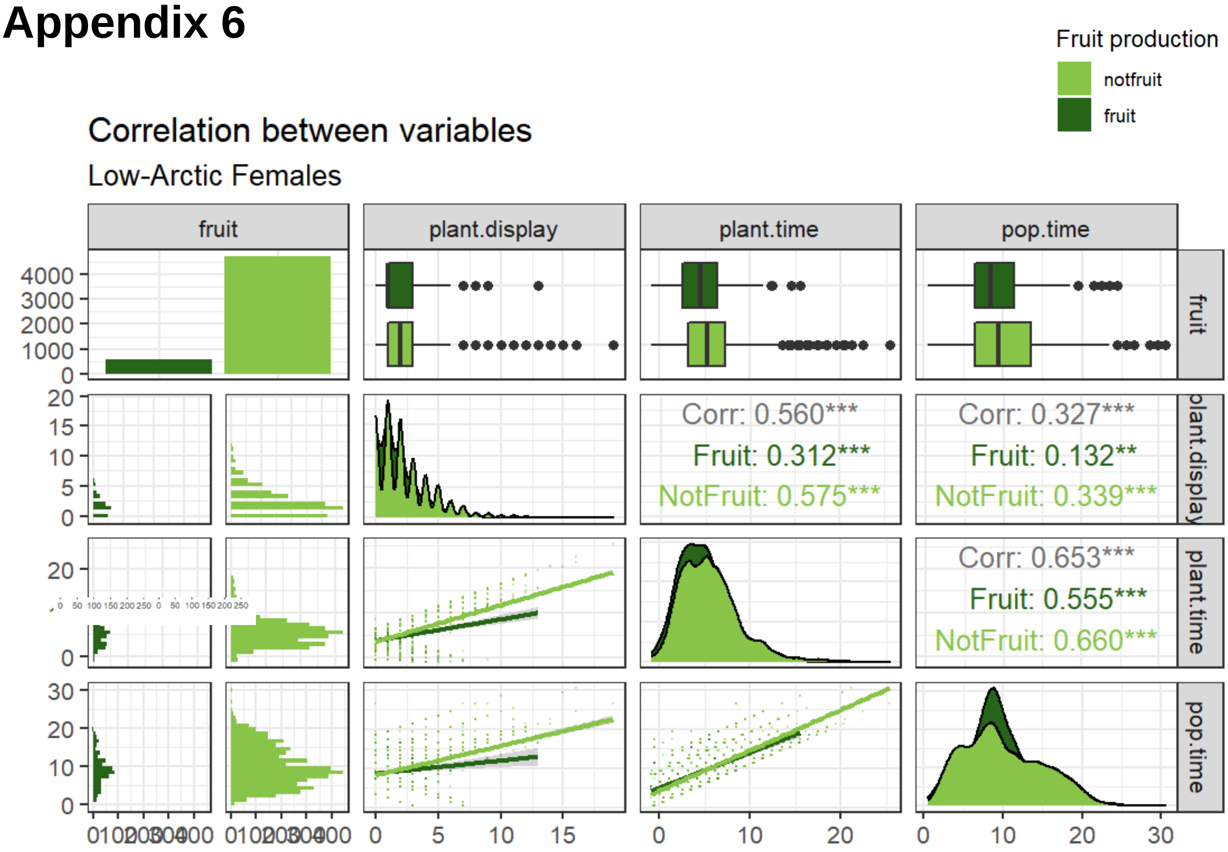
Appendix 5

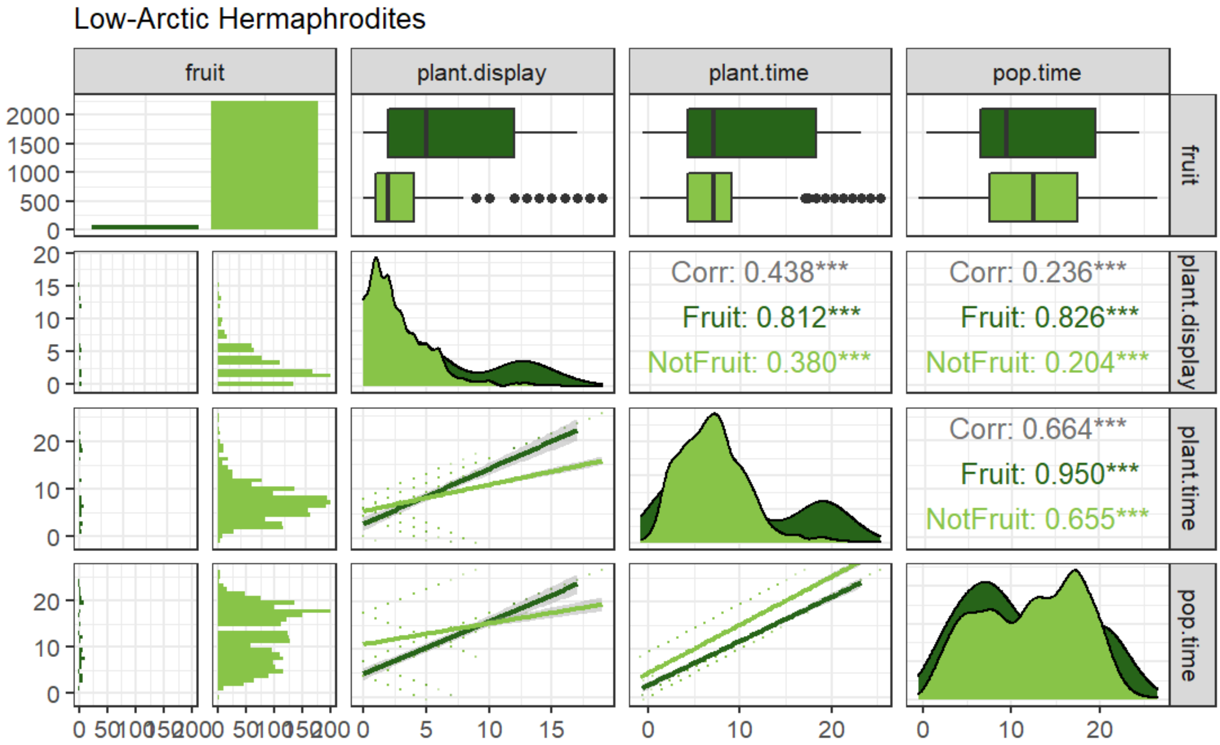

Images from High-Arctic site Bjørndalen in Svalbard
BJOR-01
BJOR-03
BJOR-05
BJOR-04
BJOR-09
BJOR-11
BJOR-13
BJOR-16
Hour
18
12
6
0
180
200
220
DOY

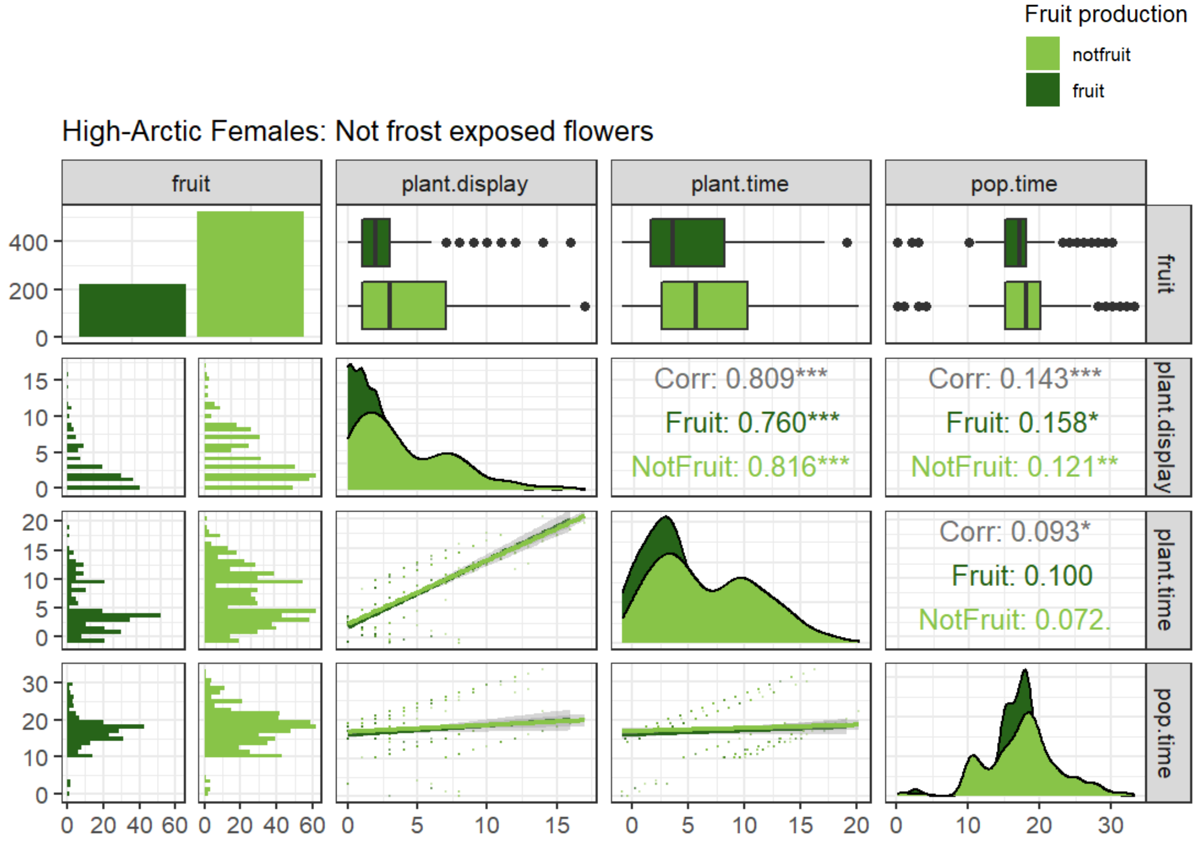
Images from Sub-Arctic/Low-Arctic site Narsarsuaq in Southern Greenland



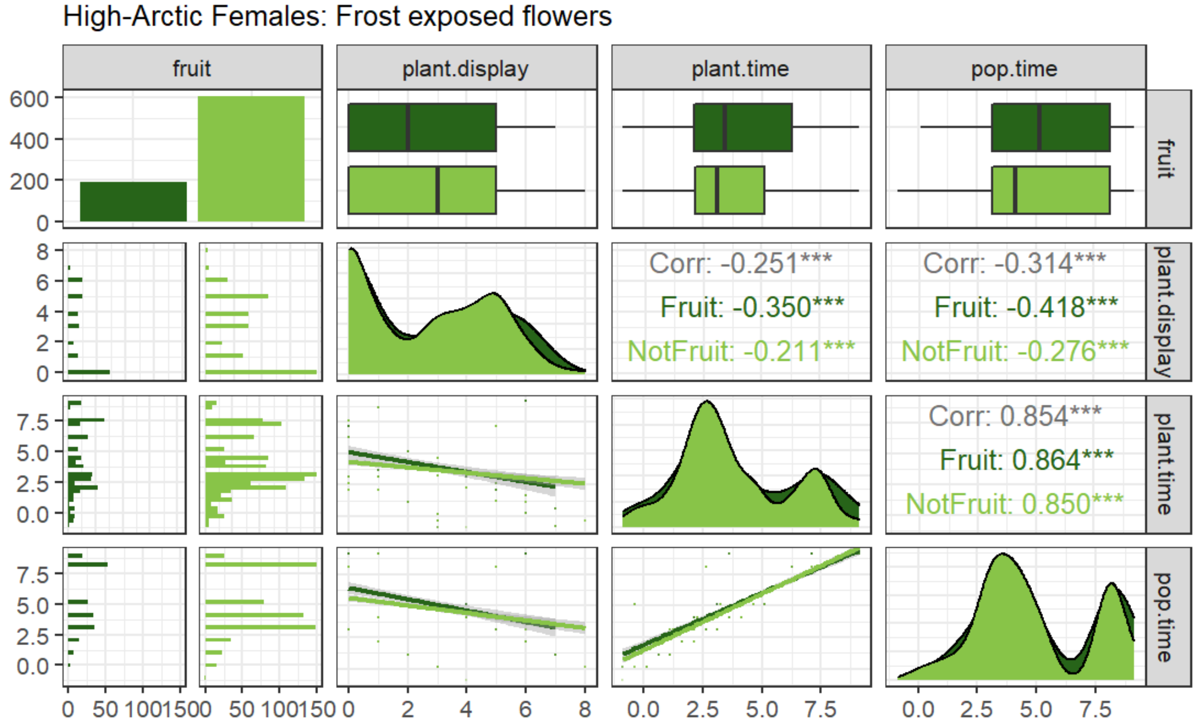
Appendix 6


Fruit production
notfruit
fruit
Correlation between variables
Low-Arctic Females
fruit
plant.display
plant.time
pop.time
Corr: 0.560***
Fruit: 0.312***
NotFruit: 0.575***
Corr: 0.327***
Fruit: 0.132**
NotFruit: 0.339***
Corr: 0.653***
Fruit: 0.555***
NotFruit: 0.660***
4000
3000
2000
1000
0
20
15
10
5
30
0 5 10 15
0 10 20
0 10 20 30


Low-Arctic Hermaphrodites
fruit
plant.display
plant.time
pop.time
Corr: 0.438***
Fruit: 0.812***
NotFruit: 0.380***
Corr: 0.236***
Fruit: 0.826***
NotFruit: 0.204***
Corr: 0.664***
Fruit: 0.950***
NotFruit: 0.655***
2000
1500
1000
500
0
20
15
10
5
0 50 100 150 200
0 5 10 15
0 10 20

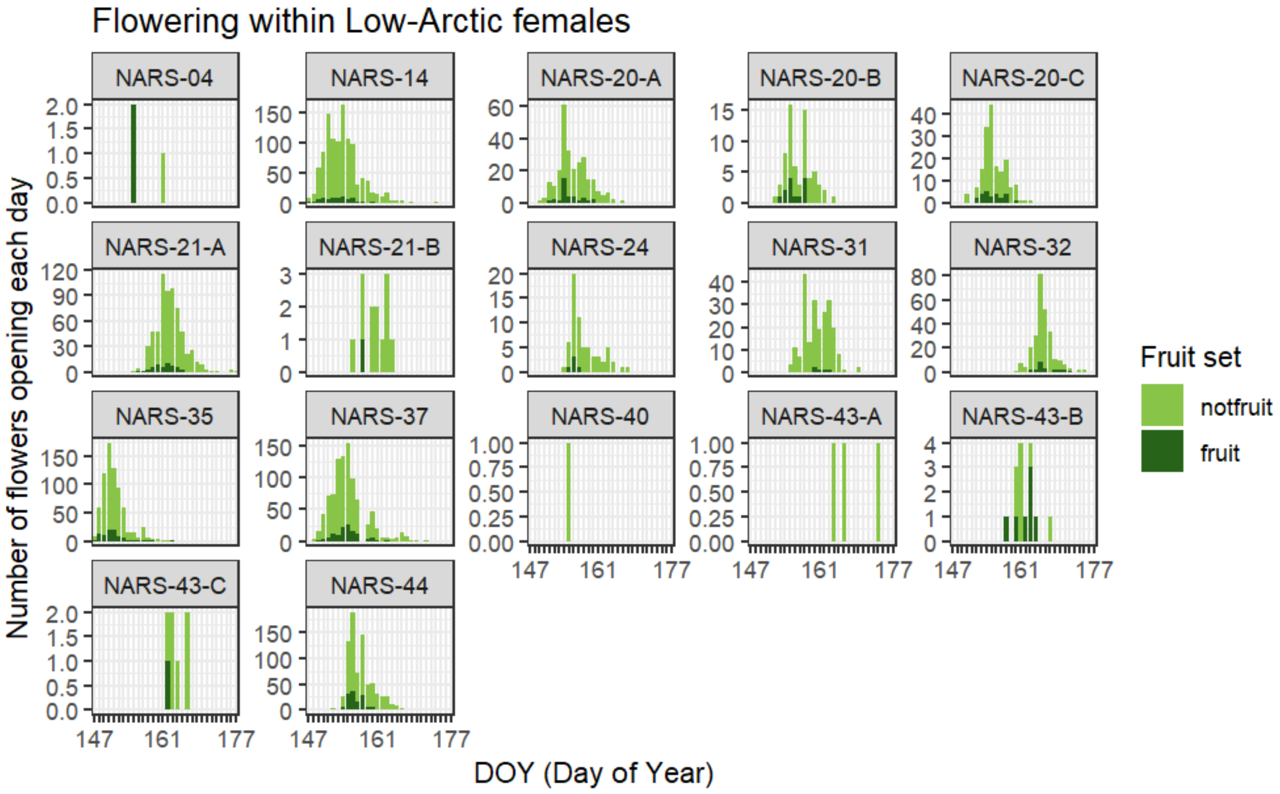


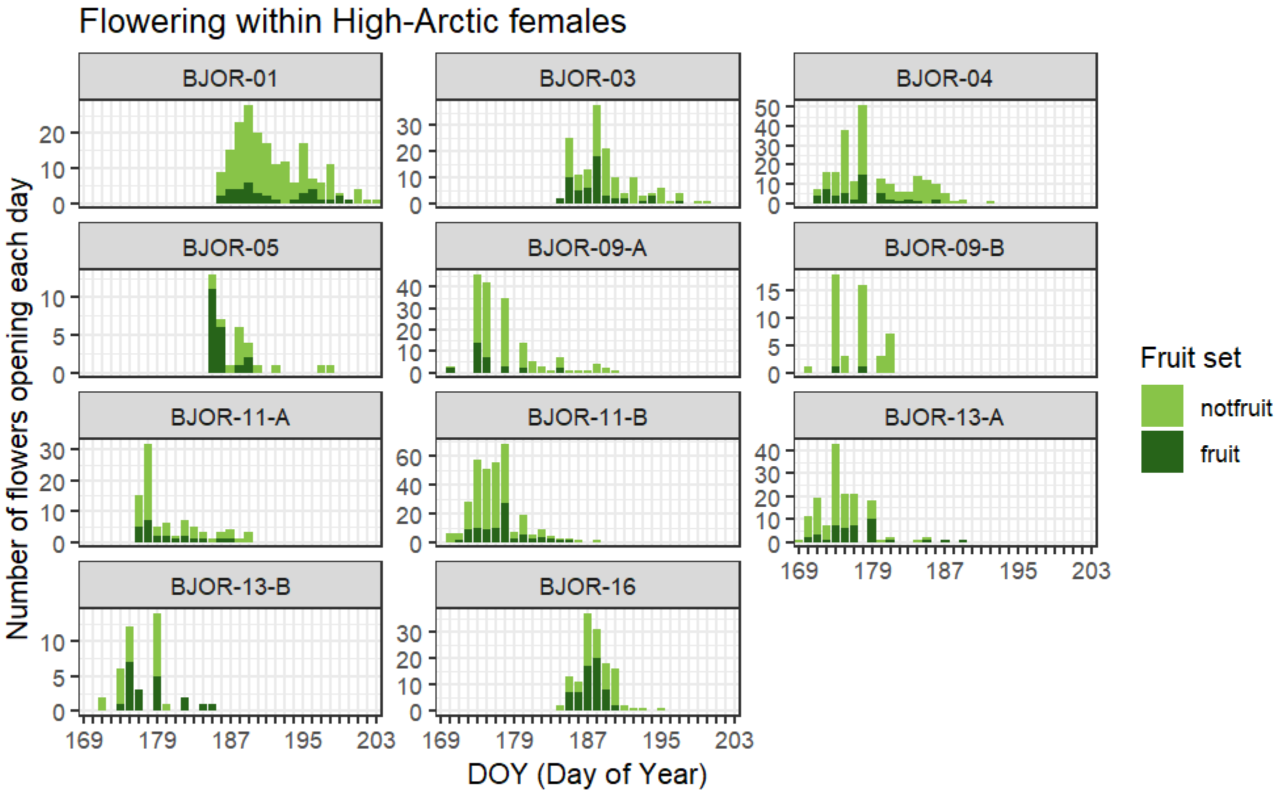
High-Arctic Females: Not frost exposed flowers



High-Arctic Females: Frost exposed flowers

Appendix 7


Flowering within Low-Arctic females
NARS-04
NARS-14
NARS-20-A
NARS-20-B
NARS-20-C
NARS-21-A
NARS-21-B
NARS-24
NARS-31
NARS-32
NARS-35
NARS-37
NARS-40
NARS-43-A
NARS-43-B
NARS-43-C
NARS-44
Number of flowers opening each day
DOY (Day of Year)
147
161
177
Fruit set
notfruit
fruit


Flowering within High-Arctic females
BJOR-01
BJOR-03
BJOR-04
BJOR-05
BJOR-09-A
BJOR-09-B
BJOR-11-A
BJOR-11-B
BJOR-13-A
BJOR-13-B
BJOR-16
Number of flowers opening each day
DOY (Day of Year)
169
179
187
195
203
Fruit set
notfruit
fruit