The influence of experimental warming on flowering phenology of Moss Campion, *Silene acaulis*

Experimentel hiting ávirkar blóming hjá leggstuttari túvublómu (Silene acaulis)

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Úrtak

Í níggju ár kannaðu vit, á hvønn hátt experimentel hiting ávirkar tey ymisku stigini í blómingini hjá leggstuttari túvublómu, *Silene acaulis* í Føroyum. Hitin varð experimentelt øktur við smáum sekshyrntum vakstrarhúsum, ið eru gjørd úr polycarbonate. Tey eru opin í erva og tí navnið „Open top Champers" (OTC). Kanningarnar vórðu gjørdar í fjallaøki í 600 m hædd, har blómustigini hjá leggstuttari túvublómu regluliga vórðu mátað í vakstrartíðini frá mai til juli mánað í tíggju OTC og tíggju kontrollum. Kanningarnar, ið vit skriva um í hesi grein, eru frá 2001 og hvørt ár frá 2007-2010. Vit skrivaðu upp tíðarskeiðið, tá fyrsti blómuknubbin var sjónligur, tíðarskeiðið tá fyrsta blóman var útsprungin, tá fyrsta og seinasta krúnublað følnaði. Kanningarnar eru ein partur av altjóða samstarvinum „International Tundra Experiment" ITEX, ið er eitt samstarv millum fleiri støð serliga á norðraru hálvu, har kanningar verða gjørdar. Kanningarnar hava til endamáls at granska árinið av veðurlagsbroytingum á plantuvøkstur. Úrslitini frá hesari kanning vísa greiðar munir millum OTC og kontrollarnar. Sum heild komu øll stigini í blómingini umleið eina viku fyrr í OTC enn í kontrollunum. Longdin á øllum blómingartíðarskeiðinum var ikki ymisk í OTC og kontrollunum. Okkara OTC øktu bara hitan umleið 1°C um summarið og broyttu neyvan vetrarhitan. Hetta og ymisk onnur viðurskifti gera, at úrslitini ikki siga okkum alla søguna um broytingarnar í føroyskum plantuvøkstri, sum fara at koma av globalu upphitingini.

Abstract

Over a period of nine years we studied the influence of experimental warming on the flowering phenology of Moss Campion, *Silene acaulis* in the Faroes. The temperature was experimentally elevated with hexagonal greenhouses called open top chambers (OTC´s) made by polycarbonate. The experi-

ment was conducted in an alpine area at 600 m a.s.l. where the flowering stage of *Silene acaulis* was measured regularly during the growing season from May to July in ten OTC´s and ten control plots. In this paper, we present observations from 2001 and every year from 2007 to 2010. We measured four events in the flowering stage: first visible bud (FB), first flowering date (FO), first petal drop (FPD) and last petal drop (LPD). This experiment is a part of „The International Tundra Experiment" (ITEX) that is a collaborative, multisite experiment using a common temperature manipulation to examine the influence of climate change on vegetation. The results from our experiment showed statistically significant changes between the OTC´s and the control plots for all four events. Typically, the events occurred about one week earlier in the OTC´s. The length of the flowering period from FB to LPD was not significally different in the OTC´s from the control plots. The warming induced by the OTC´s in our experiment was only about 1°C in the summer and less than that in the winter. This and other confounding effects such as sheltering imply that care should be taken when using our results to predict phenological in the Faroes changes induced by global warming.

Introduction

Several studies have shown earlier timing of flowering recently and this has been linked to climate change (Sherry *et al*., 2007; Miller-Rushing and Primack, 2008). Other studies show that species are responding individually to changes in climate (Fitter *et al*., 1995; Henry and Molau, 1997; Fitter and Fitter, 2002). Early flowering plants, annuals as well as insect pollinating species, showed the greatest sensitivity (Fitter and Fitter, 2002).

As the growing season in the alpine areas is very short, prompt timing of the flowering is necessary. The initiation of flowering requires long days with high temperatures that follow a period with short days for initiation of flowering primordial (Crawford, 2008). In arctic and alpine plant populations, the flowering phenology appears to be particularly critical as it affects the breeding system as well as the reproduction success. Short and cool summers limit the production of viable seeds (Bell and Bliss, 1980; Phillipp *et al.*, 1990).

Molau (1993) suggested an alternative survival strategy for arctic alpine flowering plants. In his view, the length of the growing season combined with different breeding patterns is critical for reproductive success and cannot be explained by the classical r-and K survival strategies (McArthur and Wilson, 1967). Therefore, Molau divided plant species into two categories: pollen-riskers and seed-riskers. Pollen-riskers are the early flowering species with high risk of ovule abortions due to pollination failure, while the seed-riskers are late flowering species, usually self-pollinating with little or no ovule abortion. However, the seed-riskers are in danger of losing all their seed crops in unfavourable years (Molau, 1993).

Alatalo and Totland, (1997) found that the pollen-risker *Silene acaulis* responded positively to experimental warming both in phenological traits by earlier flowering and in quantitative traits by increased seed production. This finding opposes Molau (1993), who predicted that early flowering species may suffer a disadvantage against late flowering species.

Although the flowering phenology is very important in relation to reproduction success and is vulnerable to changing climate, it is not the only limiting factor for plant survival and reproduction in the arctic alpine area. Changes in community composition that favour some species and not others will also change the competition between species. But the study of flowering phenology is a relatively simple and fast method to track changes in species response as a result of climate change (Menzel and Fabian, 1999; Miller-Rushing and Primack, 2008).

In the present study, we examined the potential effect of climate warming on the flowering phenology of Moss Campion, *Silene acaulis* (L.) Jacq. (Caryophyllaceae) in an alpine area (Sornfelli) in the Faroe Islands. As a common early flowering species in the arctic alpine area of the northern hemisphere, *Silene acaulis* is a suitable species for comparison of responses to climate warming. It is a long-lived early flowering perennial that forms light green mosslike cushions with pink flowers. Four phenological stages were examined, these are: First visual bud of the flower (FB), first flower open (FO), first petal drop (FPD) and last petal drop (LPD).

The *Silene acaulis* population on Sornfelli is trioecious consisting of individuals with female, male and hermaphroditic protandrous flowers (Fig. 1). The insect pollination is only poorly studied in the islands e.g. Hagerup (1951), but the rich representation of dipteran species is the most likely agent.

This experiment is a part of The International Tundra Experiment (ITEX) that is a collaborative, multisite experiment using

a) **b)**

Fig. 1. Silene acaulis a) female flowers b) male flowers.

a common temperature manipulation to examine response in tundra plants at Arctic and Alpine sites (e.g. Molau and Mølgaard, 1996; Henry and Molau, 1997).

The questions that we address in this paper are:

Does experimentally induced temperature enhancement change the flowering phenology of *Silene acaulis*.

Are there any differences between the four different phenological stages examined?

Material and Method

Study site

The study site is on the mountain of Sornfelli (62°04'N, 6°57'W) at 600 m a.s.l. on Streymoy in the central part of the Faroe Islands. The vegetation in the area reaches from open grassland vegetation with sparsely vegetated ground to *Racomitrium* heath vegetation with richly vegetated ground. The plant communities defined from the site are the species-poor *Koenigia islandica*-community, and the species-rich communities *Festuca vivipara-Agrostis capillaris*-community, *Racomitrium*-community and *Racomitrium-Salix herbacea*-community (Fosaa *et al*., 2004).

The climate in the Faroe Islands is highly oceanic with annual mean precipitation of 1500 mm (lowlands) and with measurable precipitation on 75% of the days in the year (Cappelen and Laursen, 1998). The mean annual temperature at the top of the mountain (726 m a.s.l.) is 1.7°C, the mean temperature for the coldest month (February) is -2.0°C and the mean temperature for the warmest month (August) is 6.5°C (Christensen and Mortensen, 2002).

Sampling

In 2001, ten Open Top Chambers (OTC) (Molau and Møhlgaard, 1996; Molau *et al.*, 1997) and ten control plots (Ctrl) were placed inside an enclosure (Fig. 2). The size of these plots are 0.25 m^2. The OTC´s are hexagonal polycarbonate chambers with a height of approximately 0.5 m and a diagonal diameter of less than 1 m. These chambers are commonly used in experiments whose aim is to study the effect of climate change on plant species because they increase the temperature by 1-2°C (Molau and Mølgaard, 1996; Marion *et al*., 1997; Hollister and Webber, 2000). Our OTC's were in the field during the winter during the whole experiment, but from time to time, some of them blew away and were established again in the following spring.

During the growing season, from

2001	2007	2008	2009	2010
Julian day	Julian day	Julian day	Julian day	Julian day
–	143	–	–	–
–	150	146	–	–
157	157	155	153	161
163	164	162	166	168
172	171	172	171	175
183	178	184	178	183
192	183	191	186	192
199	193	197	192	200
211	201	206	201	208
–	208	217	206	214
–	221	226	–	–
–	227	–	–	–
	238			

Table 1. Julian days when the site were monitored

late May to early August, the flowering phenology of *Silene acaulis* was followed. This was done by visiting the site on a regularly basis approximately once a week (Table 1) and measuring the stage of flowering of the selected species. Times of phenological changes were registered as Julian day (number of day in the year). The overall vegetation was measured in 2001, 2005 and 2008 as well as the vegetation cover and height.

The phenology was sampled from 2001 in the OTC's and from 2007-2010 also in the grazed control plots outside the enclosure (CtrlO). The events observed were grouped into five different categories which are: First visual bud of the flower (FB), first flower open (FO), first petal drop (FPD), last petal drop (LPD) and the length of the whole event, which is the number of days from FB to LPD (L).

Not all the plots had *Silene acaulis*. Only seven OTC plots and eight Ctrl plots had *Silene acaulis*. Soil temperature was measured with small temperature loggers (TinyTag) that were placed one cm below the soil surface, but there are time gaps and we do not have continuous temperature data for the whole period.

Data analysis and results

The results indicate that all the four events occur earlier in OTC compared to Ctrl by 5-11 days (Table 2) and the differences were all statistically significant at the 5% level when tested with a two-tailed t-test. In order to correct for the inter annual variation in climate over the period of investigation, the data was adjusted by taking the mean number of each of the four events for all Ctrl and subtracting this mean number from Ctrl, and OTC for each plot. This was done for each year separately. After this adjustment, all the differences were significant at the 1% level.

The length of the flowering from FB to LPE did not show a statistically significant difference between Ctrl and OTC. From the sporadic soil temperature measurements, the OTC seems to have been consistently warmer than the Ctrl by 0.7°C in 2006 to 1.3°C in 2008.

From 2001 to 2008, the vegetation cover was found to increase from 67% to 91% in OTC and from 44% to 58% in Ctrl (Fig. 3).

Discussion

The phenological events studied in this

	FB	FO	FPD	LPD	L
Ctrl	168	175	190	202	34
OTC	161	164	184	197	36
Ctrl-OTC	7	11	6	5	-2
p (unadjusted)	$< 10^{-4}$	$< 10^{-5}$	0.002	0.03	0.27
p (adjusted)	$< 10^{-3}$	$< 10^{-8}$	0.0002	0.007	0.27

Table 2. Average day number for the four events from 2001, 2007-2010. FB (First bud visible), FO (First flowering day), FPD (First petal drop), LPD (Last petal drop) and average length of the whole flowering period (L) from the control plots (Ctrl), the OTC and the differences between them. The last two rows show the significance level for the difference using the original (unadjusted) and adjusted values.

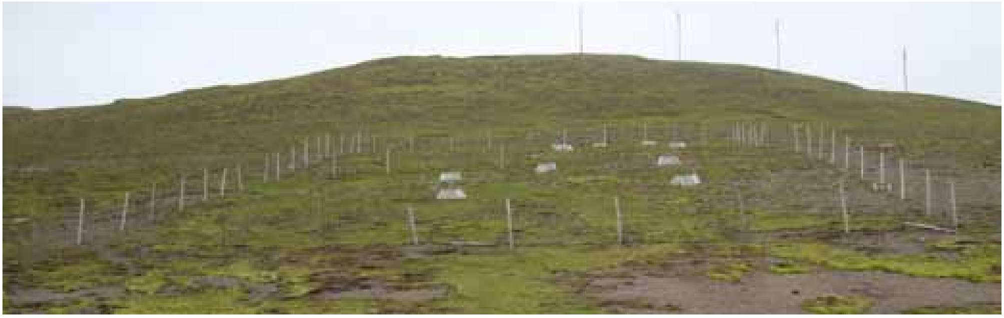


Fig. 2. The study site

experiment started about a week earlier in the warmed plots compared with the control plots, as also is found in many other studies e.g. Alatalo and Totland (1997); Fitter and Fitter (2002). Our soil temperature measurements indicate that the OTC elevated the temperature from 0.7°C in 2006 to 1.3°C in 2008 during the summer period. This is less than experienced by others. Thus, Marion *et al*., (1997) found a temperature difference of 2-3°C, which is closer to the expected Arctic warming during this century (IPCC, 2007).

This illustrats the problem in using experiments like ours to predict consequenses of global warming. Also, the OTC´s work in a passive way; they do not induce temperature differences in the winter, which is hardly realistic in a future global warming scenario. Another drawback with experimental warming in the Faroe Island is that there are very few sunshine hours in the islands and the alpine sites frequently have fog, therefore in some years we only had minor difference in temperature between the OTC plots and controls. In addition, the shelter effect from the Open Top chambers undoubtedly changes the environment inside the OTC´s.

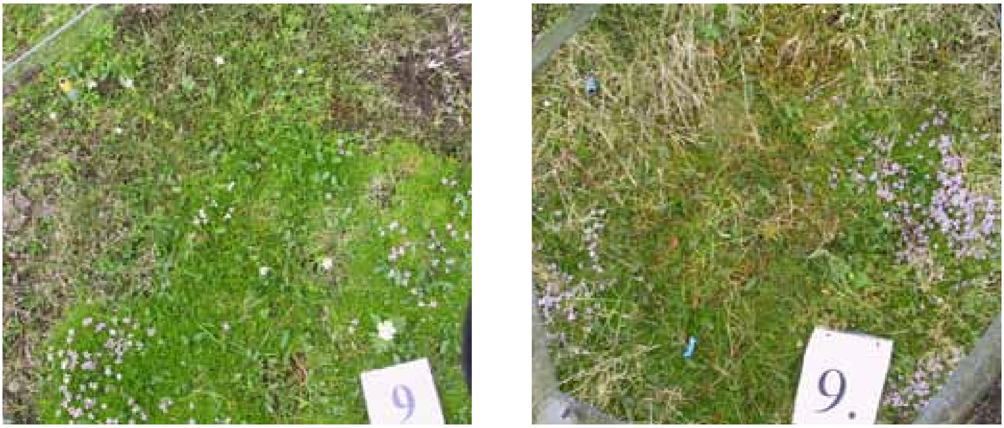
The initiation of flowering in continental areas with steep temperature gradients from very cold winter to warm summer, is linked to snowmelt when the days are getting sunny and lighter. Hollister *et al.* (2005) found in their study that in many cases the snowmelt is a better predictor of plant phenological development than Julian days. In the Faroe Islands, the snow cover is not constant during the winter and spring due to the oceanic climate with relative warm winters, and coold summers. This has the effect that the starting point of flowering is not the snowmelt, but rather the temperature in the months before onset of flowering and also the winter temperature (Miller-Rushing and Primack, 2008).

Accelerating phenologies may also alter patterns of resource allocation within plants with earlier seed and fruit maturation leading to a proportionally greater expenditure on reproductive tissue, possibly at the expense of vegetative growth (Thorhallsdóttir, 1998). Climate warming will not only affect the plants by accelerating their phenology but it will also increase the biomass of the species and could lead to larger seed production. But the larger seed production will not necessarily result in establishment of higher number of mature plants, because survival and establishment of the seedling will depend on the competition and therefore an increase in vegetative growth might instead decrease the number of plants even though the seed production is increased (Henry and Molau, 1997).

As several studies reveal a temperature related shift in species range (Parmesan and Yohne, 2003; Root *et al.,* 2003), it should be expected that species will disappear and new species will invade in the longer term. Earlier studies from the Faroe Islands showed that many alpine species will be affected by a temperature change of 2-3°C (Fosaa *et al*., 2004). This showed that the species are very vulnerable to changing climate and most likely will alter the species composition.

We have not seen any species loss or gain yet in our experiment but, in other studies the diversity of species is found to decline in many warmed plots, due to competition as well as to different temperature tolerance of species. The declining diversity usually happened in the early phase of warming because it takes a longer time for new species to invade an area than for species to disappear. (Chapin *et al*., 1995; Hollister *et al*., 2005). Our experiment shows an increase in vegetation cover and an increase in vegetation height (Fig. 3) especially of taller species like graminoids and some herbs. These plants are growing over *Silene acaulis* and they probably are superior competitors for light and thus photosynthetic activity.

Timing of changes in different taxonomic group is not always synchronous, which can have profound ecological con-



a) b)

Fig. 3. Picture inside the same Open Top Chamber at the beginning of the experiment in a) 2001 and in b) 2009. It is seen that the vegetation cover has increased as well as the size of the Silene acaulis cushion.

sequences (Walther *et al.*, 2002). As the pollination of *Silene acaulis* most likely is by Diptera, a mismatch of timing could lead to less pollination. On the other hand, the period from the FO until the FPD is six days longer in the warmed plots (Table 2) giving the flowers in the warmed plots six days more to finish flower maturation and flower pollination.

In this work, we have only studied the onset and the decline of flowering. In addition, it is necessary to study the pollination biology in order to get a more detailed picture of the effect of climate change on the flowering phenology of *Silene acaulis*. Also, the relationship between the female, male and dioceous species should be examined.

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