



# Impact of ambient temperature, precipitation and seven years of experimental warming and nutrient addition on fruit production in an alpine heath and meadow community



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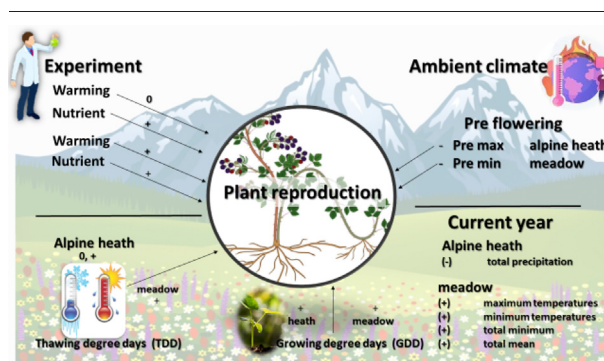
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## HIGHLIGHTS

- We studied the potential impact of global change on alpine fruit production.
- The effect of ambient climate parameters varied among plant communities.
- GDD was positively correlated with fruit production in both communities.
- Increased nutrient availability increased fruit production over time.
- Experimental warming had no, or adverse effect on fruit production.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Alpine and polar regions are predicted to be among the most vulnerable to changes in temperature, precipitation, and nutrient availability. We carried out a seven-year factorial experiment with warming and nutrient addition in two alpine vegetation communities. We analyzed the relationship between fruit production and monthly mean, maximum, and minimum temperatures during the fall of the pre-fruiting year, the fruiting summer, and the whole fruit production period, and measured the effects of precipitation and growing and thawing degree days (GDD & TDD) on fruit production. Nutrient addition (heath:  $27.88 \pm 3.19$  fold change at the end of the experiment; meadow:  $18.02 \pm 4.07$ ) and combined nutrient addition and warming (heath:  $20.63 \pm 29.34$  fold change at the end of the experiment; meadow:  $18.21 \pm 16.28$ ) increased total fruit production and fruit production of graminoids. Fruit production of evergreen and deciduous shrubs fluctuated among the treatments and years in both the heath and meadow. Pre-maximum temperatures had a negative effect on fruit production in both communities, while current year maximum temperatures had a positive impact on fruit production in the meadow. Pre-minimum, pre-mean, current mean, total minimum, and total mean temperatures were all positively correlated with fruit production in the meadow. The current year and total precipitation had a negative effect on the fruit production of deciduous shrubs in the heath. GDD had a positive effect on fruit production in both communities, while TDD only impacted fruit production in the meadow. Increased nutrient

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availability increased fruit production over time in the high alpine plant communities, while experimental warming had either no effect or a negative effect. Deciduous shrubs were the most sensitive to climate parameters in both communities, and the meadow was more sensitive than the heath. The difference in importance of TDD for fruit production may be due to differences in snow cover in the two communities.

## 1. Introduction

Alpine and polar regions are seen to be highly vulnerable to climate change, with increased climatic variability and climatic events expected in the future, which may affect plant reproductive success (Alatalo et al., 2021). The reproductive success of plants in cold regions can be affected by several environmental factors. Similar to the advancement of the flowering of plants in temperate regions in response to climate change (Berg et al., 2019; Renner et al., 2021), in high alpine and polar regions temperature/climate also affects the timing of the flowering of plants (Miller-Rushing and Inouye, 2009; Panchen and Gorelick, 2015; Legault and Cusa, 2015; Hall et al., 2018), flower production (Inouye et al., 2003; Kudo and Hirao, 2006; Liu et al., 2012), seeds and seedlings (Bernareggi et al., 2015; Briceño et al., 2015), and fruit production (Alatalo et al., 2021). The responses can be affected by growing degree days (GDD), thawing degree days (TDD), and minimum and maximum temperatures (White, 1979; Inouye et al., 2003; Hollister et al., 2005; Kudo and Hirao, 2006; Legault and Cusa, 2015). Temperature can also affect bud formation both during the actual flowering year (many forbs and graminoids) and in the “previous fall” for plants that initiate their flower buds the year before actual flowering (many deciduous and evergreen shrubs) (Molau et al., 2005; Alatalo et al., 2021). With minimum temperature often being more important than maximum temperatures (Bergman et al., 1996; Alatalo et al., 2021) as buds and flowers can be vulnerable to frost (Inouye, 2008; Wheeler et al., 2016). Increased winter and summer precipitation have been shown to have a negative effect on reproductive success in plants (Phoenix et al., 2001; Bjorkman et al., 2015; Lawson and Rands, 2019; Alatalo et al., 2021). The impact of the different climate parameters on plant reproduction can also vary among plant functional groups and the timings when reproduction occurs (Molau, 1993; Alatalo et al., 2021). Vegetation in the high alpine and polar regions is also often a nutrient limited field (Chapin et al., 1996; Shaver and Kummerow, 1992), which can also affect plant reproduction (Wookey et al., 1995; Moulton and Gough, 2011; Alatalo and Little, 2014). Therefore, anthropogenic nutrient deposits and increased mineralization due to climate change will likely also affect plant communities (Nefel et al., 1985; Cleve et al., 1990; Grandy et al., 2008; Clark et al., 2013).

Experimental studies focusing on different aspects of global change impacting plant reproduction in alpine and polar regions have found contrasting effects from experimental warming (Liu et al., 2012; Alatalo and Little, 2014; Cui et al., 2017; Alatalo et al., 2021). Studies have focused on phenology (Wookey et al., 1993; Alatalo and Totland, 1997; Totland and Alatalo, 2002; Aerts et al., 2004; Mallik et al., 2011), flower production (Semenchuk et al., 2013), seed production (Wookey et al., 1993; Alatalo and Totland, 1997; Cui et al., 2017; Zhang et al., 2019), and fruit production (Wookey et al., 1993; Alatalo and Little, 2014; Alatalo et al., 2021). Studies on the effect of experimental nutrient addition have focused on seed/fruit production (Wookey et al., 1993, 1995; Gough et al., 2015; Lavrenov et al., 2017), phenology (Wookey et al., 1995; Zhang et al., 2014; Xi et al., 2015), reproductive allocation/effort (Wookey et al., 1995; Moulton and Gough, 2011; Petraglia et al., 2013; Zhang et al., 2014), and seed germination/seedling mortality (Milbau et al., 2017).

This study is part of a set of different climate change experiments at the Latnjajaure field station. We have previously reported the impact of warming and nutrient addition on the growth, abundance, diversity, and richness of plants (Alatalo et al., 2014, 2015). In the current study, we focus on the impact of seven years of warming and nutrient addition, as well as ambient climate parameters (maximum, minimum, and average temperatures, winter and summer precipitation), on reproductive success (in terms of fruit set) in two contrasting alpine plant communities, a

nutrient and species-poor heath (Alatalo et al., 2015, 2017), and a meadow with relatively higher species richness and nutrient content (Alatalo et al., 2014, 2017). As heatwaves during summers are expected to become more frequent (Dosio et al., 2018), maximum temperature was chosen as a point of interest. Furthermore, flower buds are initiated either during the previous year or the flowering year. Thus, the response to climate parameters in the previous (for many evergreen and deciduous shrubs) or present year (for many forbs and graminoids) will differ between broad functional plant groups (Molau et al., 2005). Therefore the flowering of forbs and graminoids is more likely to be affected by the climate in the current year, while the climate in the previous fall will likely affect the flowering of evergreen and deciduous shrubs (Alatalo et al., 2021).

We hypothesize that 1) warming and nutrient addition will have a positive impact on total fruit production for all plant functional groups (graminoids, forbs, deciduous and evergreen shrubs); 2) nutrient addition will have a positive impact on total fruit production for all plant functional groups (graminoids, forbs, deciduous and evergreen shrubs); 3) ambient temperature during the fall of the previous year and the current year will be positively correlated with the fruit production of deciduous and evergreen shrubs; 4) ambient temperature during the current year will be positively correlated with fruit production of graminoids and forbs; 5) minimum temperatures will be more important than maximum temperatures for fruit set; 6) both winter and summer precipitation will be negatively correlated with fruit production.

## 2. Methods

### 2.1. Study area

Latnjajaure field station is located above the tree line at a 1000 m elevation in the valley of Latnjavagge (68°21'N, 18°29'E), near Abisko, northern Sweden. The climate is classified as sub-arctic, with cool summers and relatively mild winters; the valley is snow-covered for most of the year. The mean annual temperature ranged between  $-2.89\text{C}$  (1995) and  $-1.56\text{C}$  (2000), with the winter minimum ranging between  $-21.7\text{C}$  (1997) and  $-28.8\text{C}$  (1999). The mean annual precipitation ranged between 607 mm (1996) and 877 mm (2000). July is usually the warmest month, with mean temperatures ranging between  $5.93\text{C}$  (1995) and  $9.92\text{C}$  (1997). Physical conditions in the valley soils vary from dry to wet and from acidic to base-rich, with an associated variation in plant communities (Molau and Alatalo, 1998; Lindblad et al., 2006; Björk et al., 2007; Alatalo et al., 2014, 2017). The meadow community has a well-developed vegetation cover, dominated by *Carex vaginata*, *Carex bigelowii*, *Festuca ovina*, *Salix reticulata*, *Salix polaris*, *Cassiope tetragona*, *Bistorta vivipara*, and *Thalictrum alpinum* (Molau and Alatalo, 1998; Alatalo et al., 2014). The more sparsely vegetated heath community on an acid moraine ridge is dominated by *Betula nana*, *Salix herbacea*, and *Calamagrostis lapponica* (Molau and Alatalo, 1998; Alatalo et al., 2015). Phytosociological classification groups the heath and meadow broadly into LOI-03B Phyllodoce-Vaccinium myrtilli Nordhagen 1943 and KOB-01A Kobresio-Dryadion Nordhagen 1943 (Walker et al., 2018).

### 2.2. Experimental design and measurements

We randomly assigned 20  $1\text{ m}^2$  plots in the heath and meadow to treatments: control (C, eight plots), nutrient addition (N, four plots), warming by Open Top Chambers (OTCs) (W, four plots), and combined warming and nutrient addition (WN, four plots) (Molau and Alatalo, 1998). The plots within each plant community (meadow and heath) were located within an area of  $50 \times 50\text{ m}$ , and the two plant communities were separated by

roughly 400 m in distance. The temperature loggers installed in the control and OTC plots revealed that OTCs increased the temperature by 1.5 to 3°C compared to the control plots experiencing ambient temperature (Molau and Alatalo, 1998). Nutrient addition was applied by dissolving 5 g of nitrogen (as  $\text{NH}_4\text{NO}_3$ ) and 5 g of phosphorus ( $\text{P}_2\text{O}_5$ ) in 10 L of meltwater, this was then applied to each plot (1 m<sup>2</sup>) (Molau and Alatalo, 1998). The OTCs were left on the plots for the whole period of the study.

To assess reproductive success, we counted the fruit production of all plant species in the plots at the end of each vegetation season (late August 1994–2000). Fruit production, or infructescence (as in graminoids), is a good proxy for reproductive success as it is correlated with seed production (Alatalo and Molau, 2001). In addition to total fruit production, we grouped fruit production into functional groups (evergreen shrubs, graminoids, deciduous shrubs, forbs) (Chapin et al., 1996). While species level was not used in our analyses, species were determined using the local flora of Scandinavian mountains (Nilsson, 1991).

### 2.3. Statistical analysis

We drew boxplots showing fold changes in fruit production of total fruits and fruits of functional groups in different treatments among the years. The boxplots were drawn using the ggplot2 R package (Wickham, 2009). To check the significant differences among treatments, years, vegetation and their interactions in fruit production for the four plant functional groups (graminoids, forbs, deciduous and evergreen shrubs) and total fruit production (all plant functional groups combined), a permutational repeated measure analysis of variance of fruit production was performed. The formulated analysis contains the sources of variation that can be observed in fruit production when conducting a statistical analysis. A permutational repeated measure ANOVA was conducted using the permuco R-package (Frossard and Renaud, 2021). Mann-Whitney tests were used to compare fruit production between treatments and control plots in each year. We calculated the effect size ( $r$ ) for the Mann-Whitney test as has been suggested by Fritz et al. (2012). As suggested by these authors, we considered  $r > 0.5$  a large effect,  $0.3 < r < 0.5$  a medium effect, and  $0.1 < r < 0.3$  a small effect. We drew a line plot showing the changes in effect sizes in different treatments across the years. This plot was drawn using the ggplot2 R-package. The other analyses were performed in R ver. 4.0.2 (R Core Team, 2020).

To analyze the relationship between fruit production and ambient climate parameters, we used the cor.test function in R. Precipitation, Maximum temperature, minimum temperature, mean temperature, thawing degree days (TDD), and growing degree days (GDD) were considered for the ambient climate. The fruiting process in vegetation is governed by the climatic conditions prior to the fruiting period (the fall of the year before the fruit is produced), the current period (the year the fruit is produced), and the climate regime during the whole fruiting period (Molau et al., 2005; Alatalo et al., 2021). Therefore, the period has been divided into three categories: pre (prior to the fruiting period, i.e., August, September, and October of the year before fruit production); current (current fruiting period, i.e., May, June, July, and August), and total (whole period of fruiting, i.e., August, September, October, May, June and July). The means of all four climatic parameters were considered for the three periods. Except for TDD and GDD, the correlation was estimated between all climatic parameters for the three periods with fruit production of the four plant functional groups (graminoids, forbs, deciduous and evergreen shrubs) and total fruit production (all plant functional groups combined). We only used the fruit production in control plots for this analysis.

## 3. Results

### 3.1. The effects of experimental warming and nutrient addition on total fruit production

There was a significant impact by year and treatment, and a significant interaction between year and treatment, and between year and vegetation,

on total fruit production (Table 1). With total fruit production varying significantly among years and treatments (Table S1). In general, nutrient addition and the combination of warming and nutrient addition increased total fruit production in the later years of the experiment (From 1996 to 2000) in both communities (Fig. 1). Similarly, total fruit production in control plots in both the heath and meadow varied over time, peaking in 1997–1999. In contrast, experimental warming alone tended to increase total fruit production in the heath (in the three first years of the experiment) but not affect the fruit production of meadow communities (Fig. 1).

The results of the Mann-Whitney test showed that there was a significant difference between the total fruit production of N and control plots in the later years of the experiment (i.e., 1999 and 2000 for the heath, and 2000 for the meadow), with a gradual increase in the effect size ( $r$ ) reaching the largest effect in the final year (Fig. 2). Warming treatment showed a large effect size in total fruit production in 1998 and 1999 for the heath and 1998 for the meadow. We observed a small effect size of combined warming and nutrient addition (WN) in the heath. However, we detected a significant and large effect size for WN for the meadow in 1996. During the other years, the effect sizes of WN treatment were the same for both heath and meadow vegetation.

### 3.2. The effects of experimental warming and nutrient addition on fruit production by plant functional groups

#### 3.2.1. Fruit production of graminoids

Fruit production of graminoids was significantly affected by year and treatment (Table 1). Also, there was a significant interaction between year and treatment (Table 1, Table S2). Nutrient addition and the combination of nutrient addition and warming dramatically increased fruit production of graminoids in both the heath and meadow communities. The positive effect of these two treatments increased over time in both communities (Fig. 1). On the other hand, for both the control and warming treatment, graminoid fruit production remained unaffected during the experiment. The increase of fruit production in the heath was mainly driven by a large increase of *Calamagrostis lapponica* (Wahlenb.) Hartm.

Nutrient addition in the heath showed a significant difference from control plots, with a large effect size in 1996 and 1998–2000. In the meadow, other than in 1997, there was a significant difference between fruit production of N and control plots that showed a large effect size (Fig. 2). In the heath, warming treatment showed an increased effect size for graminoid fruit production over the years. In 1998, a significant difference with a large effect size was observed between fruit production of W and the control treatments. In the meadow, W treatment had no significant effects on fruit production of graminoids (Fig. 2). In the heath, WN treatment and N treatment had a similar pattern of effect size and significant differences over the years. WN treatment significantly increased fruit production of meadow graminoids in 1998 and 1999.

#### 3.2.2. Fruit production of forbs

There was a significant effect of year and vegetation on fruit production of forbs (Table 1, Table S3). Forb fruit production varied over the years in the control plots in the heath and meadow, and it showed an increasing trend in meadow vegetation until 1998. Nutrient addition dramatically increased the fruit production of forbs in the heath in 1997; this would then return to a similar rate as 1995 by the end of the experiment. The other treatments had no effects on forb fruit production in the heath. Nutrient addition and the combination of nutrient addition and warming tended to have a positive effect on forbs in the meadow from year three (1996) onwards (Fig. 1). Warming had no effect on the fruit production of forbs in the meadow. The results of the Mann-Whitney showed that there was no significant difference between control and treatments in the heath as long as forb fruit production is considered. In the meadow, N treatment led to a significant increase with a large effect size on forb fruit production in 1999.

**Table 1**

Permutation-based repeated measure analysis of variance results showing the impacts of year (1994, 1995, 1996, 1997, 1998, 1999, 2000) and treatment on total fruit production and on the fruit production of graminoids, forbs, evergreen shrubs, and deciduous shrubs in an alpine meadow and heath community at Latnjajaure in subarctic Sweden. Experimental treatments: warming with open-top chambers (OTC), nutrient addition, and a combined warming and nutrient addition. *Dfn* = numerator degrees of freedom, *dfd* = denominator degree of freedom, *F* = F-statistics, *P* value = significance level; **bold** indicates significance at  $P \leq 0.05$ .

| Source of variation | <i>dfn/dfd</i> | Total    |               | Graminoids |               | Forbs    |               | Evergreen shrubs |               | Deciduous shrubs |               |
|---------------------|----------------|----------|---------------|------------|---------------|----------|---------------|------------------|---------------|------------------|---------------|
|                     |                | <i>F</i> | <i>P</i>      | <i>F</i>   | <i>P</i>      | <i>F</i> | <i>P</i>      | <i>F</i>         | <i>P</i>      | <i>F</i>         | <i>P</i>      |
| Year                | 6/192          | 23.442   | <b>0.0002</b> | 19.7711    | <b>0.0002</b> | 3.375    | <b>0.012</b>  | 4.301            | <b>0.0028</b> | 2.2122           | 0.0658        |
| Treatment           | 3/32           | 4.193    | <b>0.0112</b> | 15.3696    | <b>0.0002</b> | 1.9978   | 0.1454        | 2.7479           | 0.0856        | 0.2104           | 0.8746        |
| Veg                 | 1/32           | 2.828    | 0.0938        | 0.0474     | 0.8292        | 12.3893  | <b>0.0018</b> | 1.0065           | 0.3054        | 9.1339           | <b>0.0056</b> |
| Y × T               | 18/192         | 5.174    | <b>0.0002</b> | 6.0652     | <b>0.0002</b> | 0.9787   | 0.475         | 1.6878           | 0.0764        | 1.3707           | 0.1826        |
| Y × V               | 6/192          | 3.316    | <b>0.0028</b> | 0.2632     | 0.951         | 2.3526   | 0.0538        | 3.2011           | <b>0.0174</b> | 0.7155           | 0.5968        |
| T × V               | 3/32           | 1.165    | 0.3514        | 1.3939     | 0.2714        | 1.8275   | 0.171         | 0.168            | 0.8404        | 0.2104           | 0.8746        |
| Y × T × V           | 18/192         | 1.177    | 0.2776        | 1.0288     | 0.4234        | 0.7808   | 0.6682        | 0.6956           | 0.7492        | 1.1335           | 0.332         |

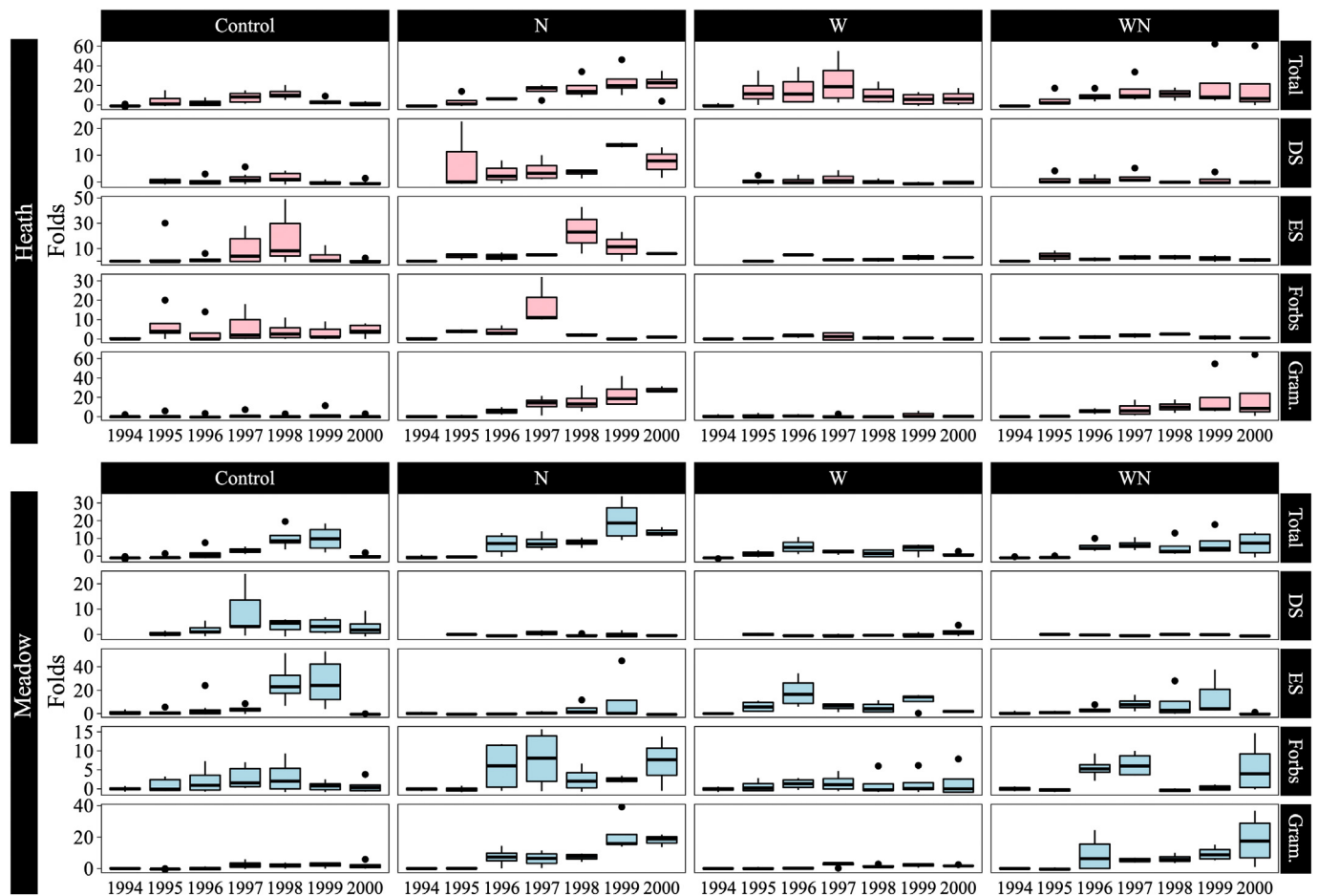
**3.2.3. Fruit production of evergreen shrubs**

There was a significant effect of year on fruit production of evergreen shrubs (Table 1, Table S4). There were significant interactions between year and vegetation for evergreen shrubs (Table 1). Specifically, fruit production was the highest in the control plots experiencing ambient conditions, with warming, nutrient addition, and the combined warming and nutrient addition treatments all having no effect or a weak negative effect on fruit production in both the meadow and heath (Fig. 1). There was no significant difference between the control and treatments of heath in terms of evergreen shrub fruit production. In the meadow, N treatment with a large effect size significantly reduced fruit production of evergreen

shrubs in 1998. Warming also decreased fruit production of evergreen shrubs in the meadow, reaching the largest effect sizes in 1998 and at the end of the experiment (Fig. 2).

**3.2.4. Fruit production of deciduous shrubs**

There was a significant effect of vegetation on the fruit production of deciduous shrubs (Table 1). In the heath, while the impact of treatments varied greatly among years, fruit production of deciduous shrubs tended to be highest in the control and N plots (Fig. 1, Table S5). In contrast, in the meadow, fruit production of deciduous shrubs tended to be highest in the control plots (Fig. 1, Table S5). In the heath, N and NW treatment



**Fig. 1.** Response in terms of fold changes of total fruit production (fruit production by all species), and the fruit production of deciduous and evergreen shrubs, forbs and graminoids across treatments in 1994–2000, in an alpine heath and meadow community at Latnjajaure in subarctic Sweden. Treatments: control, warming with open-top chambers (W), nutrient addition (N), and combined warming and nutrient addition (WN). *N* = 8 plots for control, 4 plots for W, N and WN. DS = Deciduous Shrubs, ES = Evergreen Shrubs, Gram. = Graminoids.

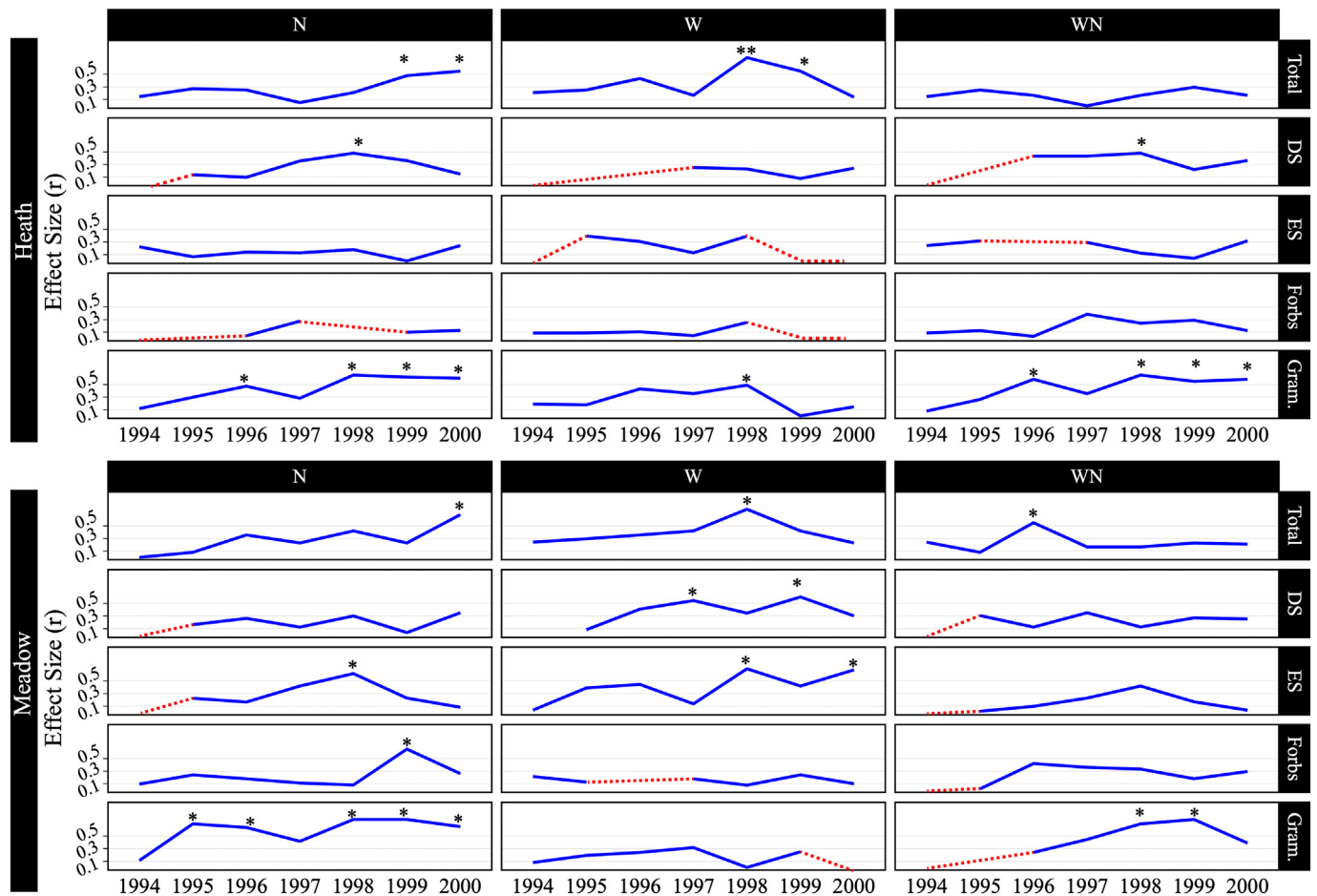


Fig. 2. Variation of the effect size of a Mann-Whitney test comparing total fruit production and the fruit production of deciduous and evergreen shrubs, forbs and graminoids between control and treatment plots in 1994–2000, in an alpine heath and meadow community at Latnjajaure in subarctic Sweden. Treatments: control, warming with open-top chambers (W), nutrient addition (N), and combined warming and nutrient addition (WN). N = 8 plots for control, 4 plots for W, N and WN. DS = Deciduous Shrubs, ES = Evergreen Shrubs, Gram. = Graminoids. \* shows the significant difference between the fruit production of control and treatment plots (\* p-value < 0.05; \*\* p-value < 0.01; \*\*\* p-value < 0.001). The red-dashed line was used when the effect size value could not be calculated.

significantly affected fruit production of deciduous shrubs in 1998. In the meadow, warming treatment led to a significant decrease in fruit production in 1996 and 1998 (Fig. 2).

### 3.3. The effects of ambient climate parameters on fruit production

#### 3.3.1. The heath

The fruit production process in the heath was affected by different climatic parameters. The total fruit production was positively affected by GDD and negatively affected by the pre-maximum temperature. Evergreen shrubs in the heath were only affected by pre-maximum temperature, which had a negative impact. The fruit production of deciduous shrubs in the heath was positively correlated with GDD, while the current and total precipitation, pre-minimum, and maximum temperatures had a negative correlation with fruit production. We could not detect any significant correlation between fruit production of graminoids and forbs with climatic parameters (Table 2 A).

#### 3.3.2. The meadow

The correlation analysis of the relationships between ambient climatic parameters with total fruit production in the meadow showed that pre-maximum temperature negatively affected total fruit production. However, the total-mean temperature positively correlated with total fruit production but pre-maximum temperature was negatively related to fruit production of evergreen shrubs in the meadow. The other climatic variables had no

significant correlation with the fruit production of this functional type. The fruit production of deciduous shrubs in the meadow was positively correlated with TDD, GDD, current maximum temperature, pre-minimum temperature, total-minimum temperature, and mean temperature in its three forms (i.e., pre-, current, and total). TDD, GDD, current, and total mean temperature were positively correlated with the fruit production of forbs. The fruit production of graminoids in the meadow increased at various temperature regimes, such as pre-minimum, total minimum, current mean, and total mean temperature. Also, their fruit production was positively governed by TDD and GDD (Table 2B).

## 4. Discussion

Our results showed that total fruit production was increased in both vegetation types after four years of experimental warming. Nutrient addition treatment and the combination of nutrient addition and warming led to increased fruit production. In both vegetation types, however, after four years, warming treatment impacts on fruit production were neutralized. On the other hand, nutrient addition increased fruit production in both vegetation types. Thus, while the hypothesis that nutrient addition would have a positive effect on plant reproduction was supported, the hypothesis that experimental warming would have a positive effect on plant reproduction was not supported. These findings revealed the importance of the other factor (nutrient availability) for successful fruit production in alpine plants. While spatial nutrient availability has rarely been measured

**Table 2**

Correlation coefficients between fruit production and ambient climate parameters in an alpine heath and Meadow, at Latnjajaure in northern Sweden (1994–2000). Precipitation, maximum temperature, minimum temperature and mean temperature. Pre = August, September and October before the fruit production year (i.e., the previous year). Current = May, June and July in the fruit production year (i.e., the current year). Total = the pre and current period (i.e., six months in total). **Bold** indicates a statistical significance at a 5% level.

| Climatic Parameter          | Total            | E. shrubs        | D. shrubs       | Forbs          | Graminoids      |
|-----------------------------|------------------|------------------|-----------------|----------------|-----------------|
| <b>Heath</b>                |                  |                  |                 |                |                 |
| TDD                         | 0.215            | 0.066            | 0.104           | 0.063          | 0.076           |
| GDD                         | <b>0.334*</b>    | 0.179            | <b>0.293*</b>   | 0.066          | 0.089           |
| Pre-Precipitation           | 0.130            | 0.017            | -0.006          | 0.286          | 0.143           |
| Current-Precipitation       | -0.135           | -0.115           | <b>-0.351*</b>  | 0.041          | -0.002          |
| Total-Precipitation         | -0.013           | -0.202           | <b>-0.294*</b>  | 0.140          | 0.103           |
| Pre-Maximum Temperature     | <b>-0.452***</b> | <b>-0.361*</b>   | <b>-0.315*</b>  | 0.125          | -0.003          |
| Current-Maximum Temperature | -0.140           | -0.130           | -0.034          | -0.017         | 0.175           |
| Total-Maximum Temperature   | -0.222           | -0.202           | -0.223          | 0.062          | 0.146           |
| Pre-Minimum Temperature     | -0.150           | -0.242           | <b>-0.311*</b>  | -0.013         | 0.137           |
| Current-Minimum Temperature | 0.201            | 0.101            | 0.131           | 0.159          | -0.090          |
| Total-Minimum Temperature   | 0.123            | -0.068           | -0.040          | 0.115          | 0.110           |
| Pre-Mean Temperature        | -0.178           | -0.222           | -0.263          | -0.046         | 0.000           |
| Current-Mean Temperature    | 0.215            | 0.091            | 0.196           | 0.065          | 0.005           |
| Total-Mean Temperature      | 0.167            | 0.016            | 0.008           | 0.037          | 0.131           |
| <b>Meadow</b>               |                  |                  |                 |                |                 |
| TDD                         | 0.323            | 0.117            | <b>0.740***</b> | <b>0.480*</b>  | <b>0.532**</b>  |
| GDD                         | 0.318            | 0.100            | <b>0.616***</b> | <b>0.550**</b> | <b>0.630***</b> |
| Pre-Precipitation           | -0.042           | -0.097           | -0.067          | -0.068         | 0.196           |
| Current-Precipitation       | 0.019            | 0.091            | 0.032           | -0.382         | -0.236          |
| Total-Precipitation         | 0.151            | 0.176            | 0.125           | -0.290         | -0.027          |
| Pre-Maximum Temperature     | <b>-0.636***</b> | <b>-0.640***</b> | -0.195          | -0.147         | -0.353          |
| Current-Maximum Temperature | 0.111            | 0.052            | <b>0.414*</b>   | 0.346          | 0.049           |
| Total-Maximum Temperature   | -0.011           | -0.042           | 0.352           | 0.090          | -0.100          |
| Pre-Minimum Temperature     | 0.303            | 0.192            | <b>0.377*</b>   | 0.094          | <b>0.456*</b>   |
| Current-Minimum Temperature | -0.165           | -0.314           | 0.320           | 0.198          | 0.178           |
| Total-Minimum Temperature   | 0.271            | 0.067            | <b>0.494**</b>  | 0.372          | <b>0.661***</b> |
| Pre-Mean Temperature        | 0.074            | -0.029           | <b>0.423*</b>   | 0.090          | 0.201           |
| Current-Mean Temperature    | 0.099            | -0.109           | <b>0.590***</b> | <b>0.470*</b>  | <b>0.441*</b>   |
| Total-Mean Temperature      | <b>0.456*</b>    | 0.270            | <b>0.770***</b> | <b>0.445*</b>  | <b>0.566**</b>  |

Numbers in bold indicate a statistical significance at a 5% level.

\* p-value <0.05.

\*\* p-value <0.01.

\*\*\* p-value <0.001.

in alpine climate change studies, the importance of nutrient availability for alpine plant communities on a microscale has been highlighted by a study in the Swizz Alps (Little et al., 2016). Interestingly, they found that nutrients had a negative effect on most traits of the dwarf shrub *Salix herbacea*. They speculated that this may have been caused by increased stress due to higher competition (Little et al., 2016).

While we did not monitor the phenological period in the study, changing the phenological period through warming is one of the critical impacts of climate change (Cleland et al., 2007; Oberbauer et al., 2013; Scranton and Amarasekare, 2017). While the growing season for plants has increased in the alps (earlier and longer), a shorter and delayed growing season has been reported in the central Tibet (Oberbauer et al., 2013). The effects of changes in the growing season may differ between plant species as there may be differences in their plasticity and potential to adapt to changing environmental conditions. For example, plants may respond differently in terms of vegetative traits, or clonal or sexual reproduction (Sedlacek et al., 2015). Over a longer time scale, evolutionary adaptation driven by selection for favorable traits under new environmental conditions is needed for species to survive (Darwin, 1859; Kawecki and Ebert, 2004). However, as many alpine and arctic species are long-lived, they might have problems evolving fast enough to adapt to climate change (Jump and Peñuelas, 2005; Franks et al., 2014). Thus, while the long-living plant species with low dispersal abilities might do poorly, they will continue to occupy the living space on the ground until increased mortality frees space for new individuals from species with better dispersal abilities to colonize. Therefore, high alpine plant community dynamics will be affected both by their generation times and dispersal abilities (Steinbauer et al., 2018).

Changes in the growing season will also likely have contrasting effects on different plant reproductive strategies. As a result of the decreased

fruit production period, late-flowering species will be more susceptible to warming (Zhu et al., 2016), while the prolonged growing season can positively affect reproduction success (Briceño et al., 2015). In addition, plants may exhibit intraspecific variation in their range of responses to climate and warming (Love and Mazer, 2021). Together with a potential home site advantage, this may affect the migratory potential of species (Sedlacek et al., 2015; Steinbauer et al., 2018). At the same time, a widespread increase in plant richness has been reported on mountain summits (Steinbauer et al., 2018). The migratory potential may also differ among species and populations, both due to differences in their dispersal abilities (Midgley et al., 2006), habitat fragmentation (Jump and Peñuelas, 2005), topography (Alatalo and Ferrarini, 2017), and biotic interactions (Grunsven et al., 2007; Rasmann et al., 2014; Sedlacek et al., 2014), which all influence potential future areas with suitable niches (Ferrarini et al., 2019, 2021).

We found that significant changes occurred after four years of the experiment. Thus, as Klady et al. (2011) suggested, our findings highlighted the importance of performing long-term studies on the effects of different climate change factors on the reproductive success of plants. Comparing the two vegetation types, especially in N treatment, we observed more drastic responses in the heath community than from meadow vegetation. Previous studies on species composition and diversity also suggest that heath vegetation was more susceptible to warming and nutrient addition than in the meadow (Alatalo et al., 2014, 2015). Other studies have found contrasting effects of a prolonged growing season, with positive growth responses in arctic shrubs (Hudson et al., 2011; Elmendorf et al., 2012), and no effect on alpine shrubs (Wheeler et al., 2014). The mechanism behind the contrasting responses is unclear; plant functional type, microhabitat, and differences in snowmelt timing have all been suggested as playing a role

(Wipf and Rixen, 2010). The different properties of a vegetation type (e.g., soil factors) modifies its response to climate change impacts (Oberbauer et al., 2013; Alatalo et al., 2015). For example, soil microbial communities may differ between microhabitats and altitudes, affecting the plant responses to climate change (Sedlacek et al., 2014).

Our results revealed vegetation (site) specific responses of different functional types to climate variables. The differential response of functional types to climatic variables and climate change will likely reshape plant community structure in alpine regions (CaraDonna et al., 2014). This supports previous studies that have reported reproductive responses to climate change differing among plant species/functional groups (Klady et al., 2011; Briceño et al., 2015; Carbognani et al., 2016). Graminoids were the only functional group that had a similar response to the treatments in the heath and meadow. We observed an increased fruit production of graminoids in both vegetation types in response to nutrient addition and combined nutrient addition and warming. In contrast, warming alone tended to have no effect. This reflects the responses, in terms of abundance of graminoids, to the specific treatments in both communities (Alatalo et al., 2014, 2015). Seed production increase in graminoids in a warming experiment was also reported in high-arctic Canada (Klady et al., 2011). OTCs used in climate change studies could potentially limit pollen availability (Adamson and Iler, 2021; Alatalo et al., 2021). For example, OTCs decreased visitation rates of pollinators by 92% in a *Delphinium nuttallianum* and by 85% in *Potentilla pulcherrima* in the Rocky Mountains. This caused a significant decline in pollen grains on stigmas in *Delphinium* but not for *Potentilla* (that is autogamous) (Adamson and Iler, 2021). Thus, the current study's increased seed production in graminoids might be due to their ability to self-pollinate (Nygren, 1946). This ability allows some graminoids (such as *C. lapponica*) to overcome the adverse effect of OTCs. There was a contrasting response from the other functional types to the experiment in the meadow and heath vegetation. A similar variation in the responses of different functional types has been reported in tundra vegetation (Oberbauer et al., 2013). Warming in the meadow increased the fruit production of evergreen and deciduous shrubs. However, it had no effects on the fruit production of these two functional groups in the heath (Fig. 2). N and WN treatment in the heath positively affected deciduous shrubs' fruit production. However, only N treatment positively affected evergreen shrubs in the meadow. Forbs' fruit production increased in all plot types in the meadow in our experiment. N treatment in the meadow showed a large positive effect on forbs in 1999. Our findings were in line with studies that have reported the contrasting effects of climate change on fruit production (Klady et al., 2011; Dorji et al., 2013).

Previous studies have shown the importance of TDD and GDD for plant reproduction (Thórhallsdóttir, 1998; Molau et al., 2005; Kawai and Kudo, 2011; Wang et al., 2014; Legault and Cusa, 2015; Arroyo et al., 2021). However, in our current study, TDD had no significant effect on either total fruit production or fruit production of any functional plant groups in the heath. On the other hand, TDD significantly affected the fruit production of deciduous shrubs, forbs, and graminoids in the meadow. The contrasting responses may be due to the difference in snow cover between the plant communities, the heath being situated on an exposed ridge with thinner snow cover. An increased number of days with an air temperature above 0C is, therefore, more likely to have a positive effect in the meadow with more delayed snowmelt compared to the heath, as the snow cover will provide a buffer for plants in the meadow against early cold events (Sturm et al., 2001; Olsson et al., 2003; Kawai and Kudo, 2011). While GDD will differ along elevational gradients, many plant species are thought to have adapted to reproducing at the warmest period of the year; thus populations at higher altitudes require fewer GDD (Wang et al., 2014; Arroyo et al., 2021). Our results from both communities supported this, GDD having a significant effect on flower production.

Except for a negative effect on deciduous shrubs in the heath, precipitation had no correlation with fruit production in this study. The heath is drier than the meadow (Alatalo et al., 2020), and precipitation may therefore have positively affected fruit production in the heath. Heath plants can also be more susceptible to flowering bud freezing due to the light

snow cover on the exposed heath (Oberbauer et al., 2013). Therefore, increased precipitation in the previous year may increase the snow cover and delay the snowmelt, thus decreasing the risk of the freezing of buds and flowers; in contrast, an earlier onset of flowering could negatively affect the reproduction of alpine plants (Iler et al., 2019).

Considering total fruit production in the heath, we observed that fruit production was strongly affected by an increase in the previous year's maximum temperature. This result is in line with the fact that flowering buds in some alpine species were formed in the previous year of fruit production (Oberbauer et al., 2013; Alatalo et al., 2021).

An increase in the maximum temperature of the previous year negatively affected total fruit production in the meadow, but an increase in total mean temperature had positive effects. Both warming and the timing of snowmelt during the spring can affect the phenology of alpine plants. However, the effect can vary among species (Carbognani et al., 2016; Jerome et al., 2021). In addition, an experimental study in the Rocky Mountains showed that while plant phenology of three species (*D. nuttallianum*, *P. pulcherrima*, and *Valeriana edulis*) was impacted by the timing of snow-melt and warming, reproductive success was not (Jerome et al., 2021).

Climatic variables did not govern forb fruit production in the heath. However, in the meadow, TDD and GDD, along with current and total mean temperature, increased the fruit production of forbs. This finding highlighted the nature of forbs in the two communities and the effects of snow cover in winter and delayed flowering in summer on fruit production. We were unable to detect a correlation between the climatic variables and graminoid fruit production in the heath. In contrast, we saw multiple strong correlations between the fruit production of graminoids and climatic variables in the meadow. Along with TDD and GDD, an increase in minimum and mean temperature increased the fruit production of graminoids. An increase in maximum temperature had no adverse effects on fruit production of this functional type. This finding suggests that climate change may favor graminoids (Wehn et al., 2014; Dolezal et al., 2019). As hypothesized, the overall correlation of the current year's ambient temperature with the fruit production of graminoids and forbs was positive.

Other than the negative correlation with the maximum temperature of the previous year, the other climatic variables did not affect the fruit production of evergreen shrubs in the heath or meadow. Deciduous shrubs in the heath showed the highest correlation with climatic factors among the functional groups. While positively correlated with GDD, current and total precipitation and minimum temperature in the previous year negatively correlated with fruit production of this functional type. TDD and GDD strongly affected the fruit production of deciduous shrubs in the meadow. An increase in different temperature factors caused the increased fruit production of deciduous shrubs. Flower buds from evergreen and deciduous shrubs started to form in the previous summer (Molau et al., 2005). Thus, climatic factors related to the increased risk of flowering bud freezing were negatively correlated with the fruit production of shrubs, and those that decreased the risk showed a positive correlation. Therefore, our proposed hypothesis on the effects of climatic variables on the fruit production of shrubs was partially supported. The high maximum temperature of the current year may increase flowering duration. Thus, it positively impacted the fruit-set production of deciduous shrubs in the meadow (Oberbauer et al., 2013; Kudo, 2021).

In addition, the reproductive success of flowering plants in cold regions may be limited by a relatively low number of pollinators and highly variable weather conditions (Alatalo and Molau, 2001; Lundemo and Totland, 2007; Peng et al., 2014; Straka and Starzomski, 2015). Flies which are important as pollinators in cold areas (Bergman et al., 1996) have been shown to have decreased in abundance and richness with accompanying warming over recent decades in Greenland (Loboda et al., 2018). Other studies have shown that pollinators are less active during cold periods (Bergman et al., 1996; Inouye, 2008; Wheeler et al., 2016). In addition, changes in plant phenology due to warmer springs may disrupt plant-pollinator interactions (Høye et al., 2013; Kudo and Ida, 2013; Kudo, 2014).

Ideally, the study would have benefitted from being replicated in other, similar independent alpine ecosystems as the “plots” are not necessarily independent replicates when they are situated within one plant community (Wheeler et al., 2016). Having plant communities along an environmental gradient would have also potentially enabled us to use “space-for-time” substitution in addition to the experimental treatments (Wheeler et al., 2016).

## 5. Conclusions

Our long-term study suggests that, similar to vegetative growth, reproduction in high alpine plant communities may be limited by nutrient availability. Increased atmospheric nutrient deposits caused by human activities may have a large impact over the longer term. Additionally, the results indicate that warmer summers caused by climate change may have a limited impact on the fruit production of high alpine plants. Instead, maximum temperatures during the fall before the fruiting year and minimum temperatures may be more critical. The difference in the importance of TDD for fruit production may be due to differences in snow cover, with TDD being more important in the meadow, which had more delayed snowmelt, compared to the heath on the exposed ridge. However, as the results are based on two plant communities from one high alpine valley, there is a need for studies across a more extensive geographic range to assess the general validity.

## CRediT authorship contribution statement

Conceptualization; JMA, UM. Data curation; JMA. Formal analysis; JMA, JD, RP, TA. Funding acquisition; JMA. Investigation; JMA, AKJ, UM. Methodology; JMA, UM. Resources; JMA. Supervision; JMA, UM. Validation; JMA. Visualization; JMA, MBH. Roles/Writing – original draft; JMA, MBH. Writing – review & editing. JMA, MBH, UM, JD, RP, TA, YB, AKJ,

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## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

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## References

Adamson, C.P., Iler, A., 2021. Open-top warming chambers reduce animal pollination of two subalpine herbs. *J Pollinat Ecol* 29, 231–239.

Aerts, R., Cornelissen, J.H.C., Dorrepaal, E., et al., 2004. Effects of experimentally imposed climate scenarios on flowering phenology and flower production of subarctic bog species. *Glob. Chang. Biol.* 10, 1599–1609.

Alatalo, J.M., Ferrarini, A., 2017. Braking effect of climate and topography on global change-induced upslope forest expansion. *Int. J. Biometeorol.* 61, 541–548.

Alatalo, J.M., Jägerbrand, A.K., Dai, J., et al., 2021. Effects of ambient climate and three warming treatments on fruit production in an alpine, subarctic meadow community. *Am. J. Bot.* 108, 411–422. <https://doi.org/10.1002/ajb2.1631>.

Alatalo, J.M., Jägerbrand, A.K., Erfanian, M.B., et al., 2020. Bryophyte cover and richness decline after 18 years of experimental warming in alpine Sweden. *AoB PLANTS* 12, plaa061. <https://doi.org/10.1093/aobpla/plaa061>.

Alatalo, J.M., Jägerbrand, A.K., Juhanson, J., et al., 2017. Impacts of twenty years of experimental warming on soil carbon, nitrogen, moisture and soil mites across alpine/subarctic tundra communities. *Sci. Rep.* 7, 44489. <https://doi.org/10.1038/srep44489>.

Alatalo, J.M., Little, C.J., 2014. Simulated global change: contrasting short and medium term growth and reproductive responses of a common alpine/Arctic cushion plant to experimental warming and nutrient enhancement. *Springerplus* 3, 157. <https://doi.org/10.1186/2193-1801-3-157>.

Alatalo, J.M., Little, C.J., Jägerbrand, A.K., Molau, U., 2015. Vascular plant abundance and diversity in an alpine heath under observed and simulated global change. *Sci. Rep.* 5, 10197. <https://doi.org/10.1038/srep10197>.

Alatalo, J.M., Little, C.J., Jägerbrand, A.K., Molau, U., 2014. Dominance hierarchies, diversity and species richness of vascular plants in an alpine meadow: contrasting short and medium term responses to simulated global change. *PeerJ* 2, e406. <https://doi.org/10.7717/peerj.406>.

Alatalo, J.M., Molau, U., 2001. Pollen viability and limitation of seed production in a population of the circumpolar cushion plant, *Silene acaulis* (Caryophyllaceae). *Nord. J. Bot.* 21, 365–372. <https://doi.org/10.1111/j.1756-1051.2001.tb00780.x>.

Alatalo, J.M., Totland, Ø., 1997. Response to simulated climatic change in an alpine and subarctic pollen-risk strategist, *Silene acaulis*. *Glob. Chang. Biol.* 3, 74–79. <https://doi.org/10.1111/j.1365-2486.1997.gcb133.x>.

Arroyo, M.T.K., Tamburrino, Í., Pliscoff, P., et al., 2021. Flowering phenology adjustment and flower longevity in a South American alpine species. *Plants* 10, 461. <https://doi.org/10.3390/plants10030461>.

Berg, C.S., Brown, J.L., Weber, J.J., 2019. An examination of climate-driven flowering-time shifts at large spatial scales over 153 years in a common weedy annual. *Am. J. Bot.* 106, 1435–1443. <https://doi.org/10.1002/ajb2.1381>.

Bergman, P., Molau, U., Holmgren, B., 1996. Micrometeorological impacts on insect activity and plant reproductive success in an alpine environment, Swedish Lapland. *Arct. Alp. Res.* 28, 196–202.

Bernareggi, G., Carbognani, M., Petraglia, A., Mondoni, A., 2015. Climate warming could increase seed longevity of alpine snowbed plants. *Alp. Bot.* 125, 69–78.

Björk, R.G., Klemedtsson, L., Molau, U., et al., 2007. Linkages between N turnover and plant community structure in a tundra landscape. *Plant Soil* 294, 247–261. <https://doi.org/10.1007/s11104-007-9250-4>.

Bjorkman, A.D., Elmendorf, S.C., Beamish, A.L., et al., 2015. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Glob. Chang. Biol.* 21, 4651–4661. <https://doi.org/10.1111/gcb.13051>.

Briceño, V.F., Hoyle, G.L., Nicotra, A.B., 2015. Seeds at risk: how will a changing alpine climate affect regeneration from seeds in alpine areas? *Alp. Bot.* 125, 59–68. <https://doi.org/10.1007/s00035-015-0155-1>.

CaraDonna, P.J., Iler, A.M., Inouye, D.W., 2014. Shifts in flowering phenology reshape a sub-alpine plant community. *Proc. Natl. Acad. Sci.* 111, 4916–4921. <https://doi.org/10.1073/pnas.1323073111>.

Carbognani, M., Bernareggi, G., Perucchi, F., et al., 2016. Micro-climatic controls and warming effects on flowering time in alpine snowbeds. *Oecologia* 182, 573–585. <https://doi.org/10.1007/s00442-016-3669-3>.

Chapin, F.I., Bret-Harte, M., Hobbie, S.E., Zhong, H., 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. *J. Veg. Sci.* 7, 347–358.

Clark, C.M., Morefield, P.E., Gilliam, F.S., Pardo, L.H., 2013. Estimated losses of plant biodiversity in the United States from historical N deposition (1985–2010). *Ecology* 94, 1441–1448. <https://doi.org/10.1890/12-2016.1>.

Cleland, E., Chuine, I., Menzel, A., et al., 2007. Shifting plant phenology in response to global change. *Trends Ecol. Evol.* 22, 357–365. <https://doi.org/10.1016/j.tree.2007.04.003>.

Cleve, K.V., Oechel, W.C., Hom, J.L., 1990. Response of black spruce (*Picea mariana*) ecosystems to soil temperature modification in interior Alaska. *Can. J. For. Res.* 20, 1530–1535. <https://doi.org/10.1139/x90-203>.

Cui, S., Meng, F., Suonan, J., et al., 2017. Responses of phenology and seed production of annual *Koenigia islandica* to warming in a desertified alpine meadow. *Agric. For. Meteorol.* 247, 376–384. <https://doi.org/10.1016/j.agrformet.2017.08.034>.

Darwin, C., 1859. *On the Origins of Species by Means of Natural Selection*. John Murray.

Dolezal, J., Dvorsky, M., Kopecky, M., et al., 2019. Functionally distinct assembly of vascular plants colonizing alpine cushions suggests their vulnerability to climate change. *Ann. Bot.* 123, 569–578. <https://doi.org/10.1093/aob/mcy207>.

Dorji, T., Totland, Ø., Moe, S.R., et al., 2013. Plant functional traits mediate reproductive phenology and success in response to experimental warming and snow addition in Tibet. *Glob. Chang. Biol.* 19, 459–472. <https://doi.org/10.1111/gcb.12059>.

Dosio, A., Mentaschi, L., Fischer, E.M., Wyser, K., 2018. Extreme heat waves under 1.5 C and 2 C global warming. *Environ. Res. Lett.* 13 (054006).

Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., et al., 2012. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat. Clim. Chang.* 2, 453–457. <https://doi.org/10.1038/nclimate1465>.

Ferrarini, A., Bai, Y., Dai, J., Alatalo, J.M., 2021. A new method for broad-scale modeling and projection of plant assemblages under climatic, biotic, and environmental cofiltering. *Conserv. Biol.* <https://doi.org/10.1111/cobi.13797>.

Ferrarini, A., Dai, J., Bai, Y., Alatalo, J.M., 2019. Redefining the climate niche of plant species: a novel approach for realistic predictions of species distribution under climate change. *Sci. Total Environ.* 671, 1086–1093.

Franks, S.J., Weber, J.J., Aitken, S.N., 2014. Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evol. Appl.* 7, 123–139. <https://doi.org/10.1111/eva.12112>.

Fritz, C.O., Morris, P.E., Richler, J.J., 2012. Effect size estimates: current use, calculations, and interpretation. *J. Exp. Psychol. Gen.* 141, 2–18. <https://doi.org/10.1037/a0024338>.



- Frossard, J., Renaud, O., 2021. Permutation tests for regression, ANOVA, and comparison of signals: the permuco package. *J. Stat. Softw.* 99. <https://doi.org/10.18637/jss.v099.i15>.
- Gough, L., Bass, H., McLaren, J.R., 2015. Effects of increased soil nutrients on seed rain: a role for seed dispersal in the greening of the Arctic? *Arct. Antarct. Alp. Res.* 47, 27–34. <https://doi.org/10.1657/AAAR0014-055>.
- Grandy, A.S., Sinsabaugh, R.L., Neff, J.C., et al., 2008. Nitrogen deposition effects on soil organic matter chemistry are linked to variation in enzymes, ecosystems and size fractions. *Biogeochemistry* 91, 37–49. <https://doi.org/10.1007/s10533-008-9257-9>.
- Grunsven, R.H.A.V., Van Der Putten, W.H., Bzemer, T.M., et al., 2007. Reduced plant-soil feedback of plant species expanding their range as compared to natives. *J. Ecol.* 95, 1050–1057.
- Hall, E.S., Piedrahita, L.R., Kendzierski, G., et al., 2018. Climate and synchrony with conspecifics determine the effects of flowering phenology on reproductive success in *Silene acaulis*. *Arct. Antarct. Alp. Res.* 50, e1548866.
- Hollister, R.D., Webber, P.J., Bay, C., 2005. Plant response to temperature in northern Alaska: implications for predicting vegetation change. *Ecology* 86, 1562–1570.
- Høyte, T.T., Post, E., Schmidt, N.M., et al., 2013. Shorter flowering seasons and declining abundance of flower visitors in a warmer Arctic. *Nat. Clim. Chang.* 3, 759.
- Hudson, J.M.G., Henry, G.H.R., Cornwell, W.K., 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. *Glob. Chang. Biol.* 17, 1013–1021. <https://doi.org/10.1111/j.1365-2486.2010.02294.x>.
- Iler, A.M., Compagnoni, A., Inouye, D.W., et al., 2019. Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *J. Ecol.* 107, 1931–1943. <https://doi.org/10.1111/1365-2745.13146>.
- Inouye, D., 2008. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 89, 353–362.
- Inouye, D., Saavedra, F., Lee-Yang, W., 2003. Environmental influence on the phenology and abundance of flowering by *Androsace septentrionalis* (Primulaceae). *Am. J. Bot.* 90, 905–910.
- Jerome, D.K., Petry, W.K., Mooney, K.A., Iler, A.M., 2021. Snow melt timing acts independently and in conjunction with temperature accumulation to drive subalpine plant phenology. *Glob. Change Biol.* 27, 5054–5069. <https://doi.org/10.1111/gcb.15803>.
- Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.* 8, 1010–1020. <https://doi.org/10.1111/j.1461-0248.2005.00796.x>.
- Kawai, Y., Kudo, G., 2011. Local differentiation of flowering phenology in an alpine-snowbed herb *Gentiana nipponica*. *Botany* 89, 361–367. <https://doi.org/10.1139/b11-024>.
- Kawecki, T.J., Ebert, D., 2004. Conceptual issues in local adaptation. *Ecol. Lett.* 7, 1225–1241. <https://doi.org/10.1111/j.1461-0248.2004.00684.x>.
- Klady, R.A., Henry, G.H.R., Lemay, V., 2011. Changes in high arctic tundra plant reproduction in response to long-term experimental warming. *Glob. Chang. Biol.* 17, 1611–1624. <https://doi.org/10.1111/j.1365-2486.2010.02319.x>.
- Kudo, G., 2021. Habitat-specific effects of flowering advance on fruit-set success of alpine plants: a long-term record of flowering phenology and fruit-set success of *Rhododendron aureum*. *Alp. Bot.* 131, 53–62. <https://doi.org/10.1007/s00035-021-00248-9>.
- Kudo, G., 2014. Vulnerability of phenological synchrony between plants and pollinators in an alpine ecosystem. *Ecol. Res.* 29, 571–581. <https://doi.org/10.1007/s11284-013-1108-z>.
- Kudo, G., Hirao, A.S., 2006. Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global-change impacts. *Popul. Ecol.* 48, 49–58. <https://doi.org/10.1007/s10144-005-0242-z>.
- Kudo, G., Ida, T.Y., 2013. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* 94, 2311–2320. <https://doi.org/10.1890/12-2003.1>.
- Lavrenov, N.G., Zauzanova, L.D., Onipchenko, V.G., 2017. Seed reproduction traits of alpine plants depend on soil enrichment. *Russ. J. Ecol.* 48, 545–550.
- Lawson, D.A., Rands, S.A., 2019. The effects of rainfall on plant–pollinator interactions. *Arthropod-Plant Interact* 13, 561–569. <https://doi.org/10.1007/s11829-019-09686-z>.
- Legault, G., Cusa, M., 2015. Temperature and delayed snowmelt jointly affect the vegetative and reproductive phenologies of four sub-Arctic plants. *Polar Biol.* 1–11. <https://doi.org/10.1007/s00300-015-1736-6>.
- Lindblad, K.E.M., Nyberg, R., Molau, U., 2006. Generalization of heterogeneous alpine vegetation in air photo-based image classification, Latnjajaure catchment, northern Sweden. *Pirineos* 161, 74–79. <https://doi.org/10.3989/pirineos.2006.v161.1>.
- Little, C.J., Wheeler, J.A., Sedlacek, J., et al., 2016. Small-scale drivers: the importance of nutrient availability and snowmelt timing on performance of the alpine shrub *Salix herbacea*. *Oecologia* 180, 1015–1024. <https://doi.org/10.1007/s00442-015-3394-3>.
- Liu, Y., Mu, J., Niklas, K.J., et al., 2012. Global warming reduces plant reproductive output for temperate multi-inflorance species on the tibetan plateau. *New Phytol.* 195, 427–436. <https://doi.org/10.1111/j.1469-8137.2012.04178.x>.
- Loboda, S., Savage, J., Buddle, C.M., et al., 2018. Declining diversity and abundance of high Arctic fly assemblages over two decades of rapid climate warming. *Ecography* 41, 265–277. <https://doi.org/10.1111/ecog.02747>.
- Love, N.L.R., Mazer, S.J., 2021. Region-specific phenological sensitivities and rates of climate warming generate divergent temporal shifts in flowering date across a species' range. *Am. J. Bot.* 108, 1873–1888. <https://doi.org/10.1002/ajb2.1748>.
- Lundemo, S., Totland, Ø., 2007. Within-population spatial variation in pollinator visitation rates, pollen limitation on seed set, and flower longevity in an alpine species. *Acta Oecol.* 32, 262–268. <https://doi.org/10.1016/j.actao.2007.05.007>.
- Mallik, A.U., Wdowiak, J.V., Cooper, E.J., 2011. Growth and reproductive responses of *Cassiope tetragona*, a circumpolar evergreen shrub, to experimentally delayed snowmelt. *Arct. Antarct. Alp. Res.* 43, 404–409.
- Midgley, G.F., Hughes, G.O., Thuiller, W., Rebelo, A.G., 2006. Migration rate limitations on climate change-induced range shifts in cape proteaceae. *Divers. Distrib.* 12, 555–562. <https://doi.org/10.1111/j.1366-9516.2006.00273.x>.
- Milbau, A., Vandeplas, N., Kockelbergh, F., Nijls, I., 2017. Both seed germination and seedling mortality increase with experimental warming and fertilization in a subarctic tundra. *AoB PLANTS* 9. <https://doi.org/10.1093/aobpla/plx040>.
- Miller-Rushing, A.J., Inouye, D.W., 2009. Variation in the impact of climate change on flowering phenology and abundance: an examination of two pairs of closely related wild-flower species. *Am. J. Bot.* 96, 1821–1829. <https://doi.org/10.3732/ajb.0800411>.
- Molau, U., 1993. Relationships between flowering phenology and life history strategies in tundra plants. *Arct. Alp. Res.* 25, 391–402. <https://doi.org/10.2307/1551922>.
- Molau, U., Alatalo, J.M., 1998. Responses of subarctic-alpine plant communities to simulated environmental change: biodiversity of bryophytes, lichens, and vascular plants. *Ambio* 27, 322–329.
- Molau, U., Nordenhäll, U., Eriksen, B., 2005. Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *Am. J. Bot.* 92, 422–431. <https://doi.org/10.3732/ajb.92.3.422>.
- Moulton, C.A., Gough, L., 2011. Effects of soil nutrient availability on the role of sexual reproduction in an alaskan tundra plant community. *Arct. Antarct. Alp. Res.* 43, 612–620. <https://doi.org/10.1657/1938-4246-43.4.612>.
- Nefel, A., Beer, J., Oeschger, H., et al., 1985. Sulphate and nitrate concentrations in snow from South Greenland 1895–1978. *Nature* 314, 611–613.
- Nilsson, Ö., 1991. *Nordisk Fjällflora*. 3rd edn. Bonniers, Stockholm.
- Nygren, A., 1946. The genesis of some scandinavian species of calamagrostis. *Hereditas* 32, 131–262. <https://doi.org/10.1111/j.1601-5223.1946.tb02778.x>.
- Oberbauer, S.F., Elmendorf, S.C., Troxler, T.G., et al., 2013. Phenological response of tundra traits to background climate variation tested using the international tundra experiment. *Philos. Trans. R. Soc. B Biol. Sci.* 368, 20120481. <https://doi.org/10.1098/rstb.2012.0481>.
- Olsson, P.Q., Sturm, M., Racine, C.H., et al., 2003. Five stages of the Alaskan Arctic cold season with ecosystem implications. *Arct. Antarct. Alp. Res.* 35, 74–81. [https://doi.org/10.1657/1523-0430\(2003\)035\[0074:FSOTAA\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0074:FSOTAA]2.0.CO;2).
- Panchen, Z.A., Gorelick, R., 2015. Flowering and fruiting responses to climate change of two Arctic plant species, purple saxifrage (*Saxifraga oppositifolia*) and mountain avens (*Dryas integrifolia*). *Arct. Sci* 1, 45–58.
- Peng, D.-L., Ou, X.-K., Xu, B., et al., 2014. Plant sexual systems correlated with morphological traits: reflecting reproductive strategies of alpine plants. *J. Syst. Evol.* 52, 368–377.
- Petraglia, A., Carbognani, M., Tomaselli, M., 2013. Effects of nutrient amendments on modular growth, flowering effort and reproduction of snowbed plants. *Plant Ecol. Divers.* 6, 475–486. <https://doi.org/10.1080/17550874.2013.795628>.
- Phoenix, G.K., Gwynn-Jones, D., Callaghan, T.V., et al., 2001. Effects of global change on a sub-Arctic heath: effects of enhanced UV-B radiation and increased summer precipitation. *J. Ecol.* 89, 256–267. <https://doi.org/10.1046/j.1365-2745.2001.00531.x>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Rasmann, S., Pellissier, L., Defosse, E., et al., 2014. Climate-driven change in plant–insect interactions along elevation gradients. *Funct. Ecol.* 28, 46–54. <https://doi.org/10.1111/1365-2435.12135>.
- Renner, S.S., Wesche, M., Zohner, C.M., 2021. Climate data and flowering times for 450 species from 1844 deepen the record of phenological change in southern Germany. *Am. J. Bot.* 108, 711–717. <https://doi.org/10.1002/ajb2.1643>.
- Scranton, K., Amarasekare, P., 2017. Predicting phenological shifts in a changing climate. *Proc. Natl. Acad. Sci.* 114, 13212–13217. <https://doi.org/10.1073/pnas.1711221114>.
- Sedlacek, J., Wheeler, J.A., Cortés, A.J., et al., 2015. The response of the alpine dwarf shrub *Salix herbacea* to altered snowmelt timing: lessons from a multi-site transplant experiment. *PLOS ONE* 10, e0122395. <https://doi.org/10.1371/journal.pone.0122395>.
- Sedlacek, J.F., Bosdorf, O., Cortés, A.J., et al., 2014. What role do plant–soil interactions play in the habitat suitability and potential range expansion of the alpine dwarf shrub *Salix herbacea*? *Basic Appl Ecol* 15, 305–315. <https://doi.org/10.1016/j.baec.2014.05.006>.
- Semenchuk, P.R., Elberling, B., Cooper, E.J., 2013. Snow cover and extreme winter warming events control flower abundance of some, but not all species in high arctic S valbard. *Ecol. Evol.* 3, 2586–2599.
- Shaver, G.R., Kummerow, J., 1992. Phenology, resource allocation, and growth of arctic vascular plants. *Arctic ecosystems in a changing climate* (pp. 193–211). Academic Press.
- Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., et al., 2018. Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature* 556, 231–234. <https://doi.org/10.1038/s41586-018-0005-6>.
- Straka, J.R., Starzowski, B.M., 2015. Fruitful factors: what limits seed production of flowering plants in the alpine? *Oecologia* 178, 249–260. <https://doi.org/10.1007/s00442-014-3169-2>.
- Sturm, M., Holmgren, J., McFadden, J.P., et al., 2001. Snow-shrub interactions in Arctic tundra: a hypothesis with climatic implications. *J. Clim.* 14, 336–344. [https://doi.org/10.1175/1520-0442\(2001\)014<0336:SSIIAT>2.0.CO;2](https://doi.org/10.1175/1520-0442(2001)014<0336:SSIIAT>2.0.CO;2).
- Thórhallsdóttir, T.E., 1998. Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia* 114, 43–49. <https://doi.org/10.1007/s004420050418>.
- Totland, Ø., Alatalo, J., 2002. Effects of temperature and date of snowmelt on growth, reproduction, and flowering phenology in the arctic/alpine herb, *Ranunculus glacialis*. *Oecologia* 133, 168–175. <https://doi.org/10.1007/s00442-002-1028-z>.
- Walker, D.A., Daniëls, F.J.A., Matveyeva, N.V., et al., 2018. Circumpolar Arctic vegetation classification. *Phytocoenologia* 181–201. <https://doi.org/10.1127/phyto/2017/0192>.
- Wang, S., Wang, C., Duan, J., et al., 2014. Timing and duration of phenological sequences of alpine plants along an elevation gradient on the Tibetan Plateau. *Agric. For. Meteorol.* 189, 220–228.
- Wehn, S., Lundemo, S., Holten, J.I., 2014. Alpine vegetation along multiple environmental gradients and possible consequences of climate change. *Alp. Bot.* 124, 155–164. <https://doi.org/10.1007/s00035-014-0136-9>.
- Wheeler, J.A., Cortés, A.J., Sedlacek, J., et al., 2016. The snow and the willows: earlier spring snowmelt reduces performance in the low-lying alpine shrub *Salix herbacea*. *J. Ecol.* 104, 1041–1050.
- Wheeler, J.A., Hoch, G., Cortés, A.J., et al., 2014. Increased spring freezing vulnerability for alpine shrubs under early snowmelt. *Oecologia* 175, 219–229. <https://doi.org/10.1007/s00442-013-2872-8>.

- White, L.M., 1979. Relationship between meteorological measurements and flowering of index species to flowering of 53 plant species. *Agric. Meteorol.* 20, 189–204. [https://doi.org/10.1016/0002-1571\(79\)90020-7](https://doi.org/10.1016/0002-1571(79)90020-7).
- Wickham, H., 2009. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wipf, S., Rixen, C., 2010. A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. *Polar Res.* 29, 95–109. <https://doi.org/10.1111/j.1751-8369.2010.00153.x>.
- Wookey, P., Parsons, A., Welker, J., 1993. Comparative responses of phenology and reproductive development to simulated environmental change in sub-Arctic and high arctic plants. *Oikos* 67, 490–502.
- Wookey, P., Robinson, C., Parsons, A., 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semi-desert, Svalbard. *Oecologia* 102, 478–489.
- Xi, Y., Zhang, T., Zhang, Y., et al., 2015. Nitrogen addition alters the phenology of a dominant alpine plant in Northern Tibet. *Arct. Antarct. Alp. Res.* 47, 511–518. <https://doi.org/10.1657/AAAR0014-054>.
- Zhang, C., Ma, Z., Zhou, H., Zhao, X., 2019. Long-term warming results in species-specific shifts in seed mass in alpine communities. *PeerJ* 7, e7416. <https://doi.org/10.7717/peerj.7416>.
- Zhang, Z., Niu, K., Liu, X., et al., 2014. Linking flowering and reproductive allocation in response to nitrogen addition in an alpine meadow. *J. Plant Ecol.* 7, 231–239. <https://doi.org/10.1093/jpe/rtt030>.
- Zhu, J., Zhang, Y., Wang, W., 2016. Interactions between warming and soil moisture increase overlap in reproductive phenology among species in an alpine meadow. *Biol. Lett.* 12, 20150749. <https://doi.org/10.1098/rsbl.2015.0749>.