

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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2 **addition on fruit production in an alpine heath and meadow community**

3

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21

22 **Abstract**

23 Global change is causing changes in temperature, precipitation, and nutrient availability. Alpine and
24 polar regions are predicted to be among the most vulnerable for these changes. We applied a seven-
25 year factorial experiment with warming and nutrient addition in two alpine vegetation communities. We
26 analyzed relationship between fruit production and monthly mean, max and min temperatures during
27 the fall of the pre-fruiting year, fruiting summer, whole fruit production period, and effects of summer
28 and winter precipitation on fruit production. Nutrient addition and combined nutrient addition and
29 warming increased total fruit production, and fruit production of graminoids in the later years in the
30 Heath and Meadow and had a positive effect on forbs in the Meadow. In contrast fruit production of
31 evergreen shrubs were negative affected by all treatments in the Meadow and Heath, while fruit
32 production of deciduous shrubs was negatively affected in the Meadow. Minimum and mean
33 temperatures were more important than max temperatures, and max temperatures of the fall before
34 flowering was more important than max temperature during the flowering year. Winter precipitation
35 had significant effect on total fruit production, fruit production of deciduous shrubs and forbs in the
36 Heath, and on evergreen shrubs and forbs in the Meadow. Increased nutrient availability increased fruit
37 production over time in contrasting high alpine plant communities, while experimental warming had no,
38 or negative effect. Additionally, the results indicate that warmer summers may have limited impact on
39 fruit production of high alpine plants. Instead, max temperatures during the fall before the fruiting year,
40 and minimum temperatures may be more important.

41

42 Keywords: Arctic; climate change; cold spells; plant reproduction; fruit production; ITEX; Tundra

43

44 **1. Introduction**

45 Alpine and polar regions are foreseen to be highly vulnerable to climate change with increased climatic
46 variability and climatic events in the future which may affect plant reproductive success. Reproductive
47 success of plants in cold regions can be affected by several environmental factors. Similar to the
48 advancement of flowering of plants in temperate regions in response to climate change (Berg et al.
49 2019; Renner et al. 2021), timing of flowering of plants in high alpine and polar regions are also affected
50 by the temperature/climate (Miller-Rushing and Inouye 2009; Panchen and Gorelick 2015; Legault and
51 Cusa 2015; Hall et al. 2018), flower production (Inouye et al. 2003; Kudo and Hirao 2006; Liu et al. 2012),
52 seeds and seedlings (Bernareggi et al. 2015; Briceño et al. 2015), and fruit production (Alatalo et al.
53 2021). The responses can be affected by growing degree days (GDD), thawing degree days (TDD), min
54 and max temperatures (White 1979; Inouye et al. 2003; Hollister et al. 2005; Kudo and Hirao 2006;
55 Legault and Cusa 2015). Temperature can also affect bud formation both during the actual flowering
56 year (many forbs and graminoids) and in the “previous fall” for plants that initiate their flower buds the
57 year before actual flowering (many deciduous and evergreen shrubs) (Molau et al. 2005; Alatalo et al.
58 2021). With minimum temperature often being more important than max temperatures (Bergman et al.
59 1996; Alatalo et al. 2021), as buds and flowers can be vulnerable to frost, and pollinators are less active
60 during cold periods (Bergman et al. 1996; Inouye 2008; Wheeler et al. 2016). In addition, changes in
61 plant phenology due to warmer springs may cause disruption of plant-pollinator interactions (Høye et al.
62 2013; Kudo and Ida 2013; Kudo 2014). Both increased winter and summer precipitation have been
63 shown to have negative effect reproductive success of plants (Phoenix et al. 2001; Bjorkman et al. 2015;
64 Lawson and Rands 2019; Alatalo et al. 2021). The effect of the different climate parameters on plant
65 reproduction can also vary among plant functional groups and the timing when it occurs (Molau 1993;
66 Alatalo et al. 2021). In addition, reproductive success of flowering plants in cold regions can be limited
67 by relatively few pollinators and highly variable weather conditions (Alatalo and Molau 2001; Lundemo

68 and Totland 2007; Peng et al. 2014; Straka and Starzomski 2015). Flies which are important as
69 pollinators in cold areas (Bergman et al. 1996), have been shown to decrease in abundance and richness
70 with accompanying warming during the last decades in Greenland (Loboda et al. 2018). Vegetation in
71 high alpine and polar regions are also often nutrient limited (Chapin et al. 1986; Shaver and Kummerow
72 1992), and this can also affect plant reproduction (Wookey et al. 1995; Moulton and Gough 2011;
73 Alatalo and Little 2014). Therefore, anthropogenic nutrient depositions and increased mineralization
74 due to climate change will likely also affect plant communities (Neftel et al. 1985; Cleve et al. 1990;
75 Grandy et al. 2008; Clark et al. 2013).

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

87 This study is part of a set of different climate change experiment at the Latnjajaure field
88 station. We have previously reported the impact of warming and nutrient addition on growth,
89 abundance, diversity and richness of plants (Alatalo et al. 2014, 2015). In the current study we focus on
90 the impact of seven years of warming and nutrient addition, and ambient climate parameters, on the
91 reproductive success (in terms of fruit set) in two contrasting alpine plant communities, a nutrient and

92 species poor heath (Alatalo et al. 2015, 2017), and a meadow with relatively higher species richness and
93 nutrient content (Alatalo et al. 2014, 2017). We hypothesize 1) that both warming and nutrient addition
94 will have a positive impact on fruit set of total and all plant functional groups (graminoids, forbs,
95 deciduous and evergreen shrubs). 2) Ambient temperature during the fall of the previous year and the
96 current year will be positively correlated with fruit production of deciduous and evergreen shrubs. 3).
97 Ambient temperature during the current year will be positively correlated with fruit production of
98 graminoids and forbs. 4). Minimum temperatures will be more important than max temperatures for
99 fruit set. 5) Both winter and summer precipitation will be negatively correlated with fruit production.

100

101 **2. Methods**

102 **2.1. Study area**

103 Latnjajaure field station is located above treeline at 1000 m elevation in the valley of Latnjavagge
104 (68°21'N, 18°29'E), near Abisko, northern Sweden. The climate is classified as sub-arctic, with cool
105 summers and relatively mild winters, the valley is snow covered for most of the year. Mean annual
106 temperature ranged between -2.89C (1995) and -1.56C (2000), with winter minimum ranging between -
107 21.7C (1997) and -28.8C (1999). Mean annual precipitation ranged between 607mm (1996) – 877mm
108 (2000). July is normally the warmed month, with mean temperatures ranging between 5.93C (1995) and
109 9.92C (1997). Physical conditions in the valley soils vary from dry to wet, and from acidic to base-rich,
110 with an associated variation in plant communities (Molau and Alatalo 1998; Lindblad et al. 2006; Björk et
111 al. 2007; Alatalo et al. 2014, 2017). The meadow community has a well-developed vegetation cover,
112 dominated by *Carex vaginata*, *Carex bigelowii*, *Festuca ovina*, *Salix reticulata*, *Salix polaris*, *Cassiope*
113 *tetragona*, *Bistorta vivipara* and *Thalictrum alpinum* (Molau and Alatalo 1998; Alatalo et al. 2014). The
114 more sparsely vegetated heath community is dominated by *Betula nana*, *Salix herbacea* and
115 *Calamagrostis lapponica* (Molau and Alatalo 1998; Alatalo et al. 2015).

116

117 **2.2. Experimental design and measurements**

118 We randomly assigned 20 1 m² plots in the heath and meadow to treatments, control (C, 8 plots),
119 nutrient addition (N, 4 plots), warming (W, 4 plots) by Open Top Chambers (OTCs), and combined
120 warming and nutrient addition (WN, 4 plots) (Molau and Alatalo 1998). The OTCs increased the
121 temperature by 1.5 to 3C compared to control plots experiencing ambient temperature (Molau and
122 Alatalo 1998). Nutrient addition was applied by dissolving 5 g of nitrogen (as NH₄NO₃) and 5g of
123 phosphorus (P₂O₅) in 10 l of meltwater which was then applied for each plot (1 m²) (Molau and Alatalo
124 1998). The OTCs were left on the plots for the whole period of the study.

125 To assess reproductive success, we counted fruit production of all plant species in the plots at
126 the end of each vegetation season (late August, 1994-2000). Fruit production, or infructescences (as in
127 graminoids), is a good proxy for reproductive success as it is correlated with seed production (Alatalo
128 and Molau 2001). In addition to total fruit production, we grouped fruit production into functional
129 groups (evergreen shrubs, graminoids, deciduous shrubs, forbs) (Chapin et al. 1996).

130

131 **2.3. Statistical analysis**

132 To check the significant differences among treatments, years, vegetation and their interactions in fruit
133 production for the four plant functional groups (graminoids, forbs, deciduous and evergreen shrubs) and
134 total fruit production (all plant functional groups combined), General linear model for factorial
135 experiment was used. Analysis of variance of fruit production was performed, the additive model for
136 analysis of variance was:

$$137 X_{ij} = \mu + Y + T + V + (Y \times T) + (Y \times V) + (T \times V) + (Y \times T \times V) + \epsilon_{ij}$$

138 where X_{ij} is the fruit production. μ is the grand mean of all recorded observations. Y is the single factor
139 effect of year on fruit production. T is the single factor effect of treatment on fruit production. V is the

140 single factor effect of vegetation on fruit production. While $(Y \times T)$, $(Y \times V)$, and $(T \times V)$ are the first order
141 interactions between two factors. The second order interaction is represented as $(Y \times T \times V)$. ϵ_{ij} represents
142 the experimental error. The formulated equation explains the sources of variation that can be observed
143 in the fruit production when conducting statistical analysis. Bonferroni Pairwise Comparisons test was
144 used to compare between each two means. The statistics software package Minitab (Minitab 17, 2010,
145 Computer software, State College, PA: Minitab) was used to obtain ANOVA tables and means
146 comparisons.

147 To analyse the relationship between fruit production and ambient climate parameters we used
148 Pearson correlation coefficient in MS-Excel (Microsoft). Precipitation, maximum temperature, minimum
149 temperature and mean temperature were considered for ambient climate. The fruiting process in
150 vegetation govern by the climatic conditions prior to the fruiting period (the fall before the year when
151 the fruit is produced), current period (the year the fruit is produced) along with the climate regime
152 during the period of whole fruiting process. Therefore, the period has been divided into three categories
153 as pre (prior fruiting period i.e. August, September and October of the year before fruit production);
154 current (current fruiting period i.e. May, June, July and August) and total (whole period of fruiting i.e.
155 August, September, October, May, June and July). Means of all four climatic parameters were
156 considered for the three periods. Association (correlation) was estimated between all climatic
157 parameters for all the three periods with fruit production of the four plant functional groups
158 (graminoids, forbs, deciduous and evergreen shrubs) and total fruit production (all plant functional
159 groups combined). The significance of the correlation was adjudged at 5% level of significance by
160 standard protocol i.e. t-test.

161

162 **3. Results**

163 **3.1. Effect of experimental warming and nutrient addition on total fruit production**

164 There was a significant impact by year, treatment, and vegetation community, and a significant
165 interaction between year and treatment, and between year and vegetation, on total fruit production
166 (Table 1, Figure 1). With total fruit production varying significantly among years, treatments, and
167 vegetation communities (Appendix S1, see the Supplementary Data with this article). In general,
168 nutrient addition and the combined warming and nutrient addition increased total fruit production in
169 the later years of the experiment (year six and seven) in both communities (Fig. 1), and total fruit
170 production being higher in the Meadow compared to the Heath (Fig. 1, Appendix S1). Similarly, total
171 fruit production in control plots in both the Heath and Meadow varied over time, peaking in years 4-6 of
172 the experiment. In contrast, experimental warming alone tended to decrease total fruit production in
173 both communities (Fig. 1).

174

175 **3.2. Effect of experimental warming and nutrient addition on fruit production by plant functional** 176 **groups**

177

178 **3.2.1. Fruit production of graminoids**

179 Fruit production of graminoids was significantly affected by year and treatment (Table 1). There were
180 significant interactions between year and treatment, and treatment and vegetation, for graminoids
181 (Table 1, Appendix S2, see the Supplementary Data with this article). Nutrient addition and combined
182 nutrient addition and warming dramatically increased fruit production of graminoids in both the heath
183 and meadow community. With the positive effect of nutrient addition and the combined warming and
184 nutrient addition increasing over time in both communities (Fig. 2). The increase of fruit production in
185 the Heath was mainly driven by a large increase of *Callamagrostis lapponica*.

186

187 **3.2.2. Fruit production of forbs**

188 There was significant effect of year, treatment, and vegetation on fruit production of forbs (Table 1).
189 There was a significant interaction between year and vegetation, and treatment and vegetation, for
190 forbs (Table 1, with the fruit production varying considerably both between years, treatments, and
191 vegetation (Fig. 2, Appendix S3, see the Supplementary Data with this article). Nutrient addition and
192 combined nutrient addition and warming tending to have a positive effect on forbs in the Meadow from
193 year three onwards (but not in the Heath) (Fig. 2). Warming had no effect on fruit production of forbs in
194 either plant community (Fig. 2).

195

196 **3.2.3. Fruit production of evergreen shrubs**

197 There was significant effect of year, treatment, and vegetation on fruit production of evergreen shrubs
198 (Table 1). There were significant interactions between year and treatment, and year and vegetation for
199 evergreen shrubs (Table 1), with fruit production varying considerably between years, treatments, and
200 vegetation communities (Fig. 3, Appendix S4, see the Supplementary Data with this article). Specifically,
201 fruit production was highest in the control plots experiencing ambient conditions, with warming,
202 nutrient addition, and the combined warming and nutrient addition treatments all having a negative
203 effect on fruit production in both the Meadow and Heath (Fig 3).

204

205 **3.2.4. Fruit production of deciduous shrubs**

206 There was significant effect of year, treatment, vegetation, and a significant interaction between year
207 and vegetation on the fruit production of deciduous shrubs (Table 1). In the Heath, while the impact of
208 treatments varied greatly among years, fruit production of deciduous shrubs tended to be highest in
209 control and warming plots, (Fig. 3, Appendix S5, see the Supplementary Data with this article). In
210 contrast, in the Meadow, fruit production of deciduous shrubs tended to be highest in the control plots

211 and in the plots receiving nutrient addition alone (Fig. 3, Appendix S5, see the Supplementary Data with
212 this article).

213

214 **3.3. Effect of ambient climate parameters on fruit production**

215 **3.3.1. Meadow**

216 The correlation analysis on the relationships between ambient climatic parameters with fruit production
217 in the meadow showed that minimum and mean temperatures were more important than max
218 temperatures. The fruit production of deciduous shrubs in the meadow was negatively correlated with
219 current precipitation, temperature specifically pre-maximum, total maximum, current minimum
220 temperature, however, total minimum and total mean temperature was positively related with seed
221 production in deciduous shrubs. The fruit production of evergreen shrubs in the meadow was having a
222 differential directional relationship with climatic parameters. In this, only pre-max temperature were
223 negatively related with fruit production of evergreen shrubs in the meadow, however, temperature
224 regimes as pre-minimum, current minimum, total minimum, pre-mean, current mean and total mean
225 temperature along with pre-maximum temperature were positively related with fruit production of
226 evergreen shrubs. The fruit production of graminoid in the meadow was increasing with increase in
227 various temperature regimes as pre-minimum, current minimum, total minimum, pre-mean, current
228 mean and total mean temperature, however, it decreased with increase in pre-maximum temperature.
229 All the three regimes of minimum temperature and mean temperature were positively influencing the
230 fruit production of forbs except current minimum temperature. Total functional fruit production in the
231 meadow was positively related with all the three regimes of minimum temperature and mean
232 temperature except current minimum temperature, however pre-maximum temperature was negatively
233 related with total fruit production (Table 2A).

234

235 **3.3.2. Heath**

236 The fruit production process in the heath has a differential regulated by the various climatic parameters.
237 The total fruit production was positively governed by the three regimes of precipitation, minimum
238 temperature and mean temperature except the current precipitation. The pre-maximum temperature
239 governs the negative relationship with total fruit production in the heath. The fruit production of
240 deciduous shrubs in the heath was governed by all the climatic regimes except the current precipitation
241 and total maximum temperature. The climatic parameters role on fruit production of evergreen shrubs
242 in the heath was invariant except the negative role of pre-maximum temperature. Fruit production of
243 graminoid in the heath was positively influenced by all the three regimes of minimum and mean
244 temperature, except the current minimum temperature. Fruit production of forbs in the heath was
245 positively influenced by current and total minimum and mean temperature regimes and negatively
246 related with pre-precipitation (Table 2 B).

247

248 **4. Discussion**

249 Our results showed that fruit production was increased in both vegetation types after seven years of
250 experimental warming. Nutrient addition treatment in the meadow and combined nutrient addition
251 and warming in the heath led to the highest fruit production. Therefore, our proposed hypothesis was
252 partially true. However, after four years, in both vegetation types, warming treatment led to a dramatic
253 decrease in fruit production comparing to the control and the other treatments. On the other hand,
254 nutrient addition increased fruit production in both vegetation types. This finding revealed the
255 importance of the other factor (nutrient availability) for successful fruit production in alpine plants.

256 While we did not monitor the phenological period in the study, changing the phenological
257 period due to warming is one of the critical impacts of climate change (Cleland et al. 2007; Oberbauer et
258 al. 2013; Scranton and Amarasekare 2017). While growing season for plants has increased in the alps

259 (earlier and longer), shorter and delayed growing season has been reported from central Tibet
260 (Oberbauer et al. 2013). Thus, as a result of decreased fruit production period late-flowering species will
261 be more susceptible to warming (Zhu et al. 2016), while prolonged growing season can have a positive
262 effect on reproduction success (Briceño et al. 2015). In addition, plants may exhibit intraspecific
263 variation across their range in their responses to climate and warming (Love and Mazer 2021).

264 Here, we observed that major changes occurred after four years of the experiment. Thus, as
265 Klady et al. (2011) suggested, our finding highlighted the importance of performing long-term studies on
266 the effects of different climate change factors on reproductive success of plants. Comparing the two
267 vegetation types, after four years, we observed more drastic responses of heath community than
268 meadow vegetation. Previous studies on species composition and diversity also suggest that the heath
269 vegetation was more susceptible to warming and nutrient addition than the meadow (Alatalo et al.
270 2014, 2015). The different properties of a vegetation type (e.g., soil factors) modifies its response to
271 climate change impacts (Oberbauer et al. 2013; Alatalo et al. 2015).

272 Our results revealed vegetation (site-) specific response of different functional types to climate
273 variables. The differential response of functional types to climatic variables and climate change will likely
274 reshape plant community structure in alpine regions (CaraDonna et al. 2014). This support previous
275 studies that have reported reproductive responses to climate change to differ among plant
276 species/functional groups (Klady et al. 2011; Briceño et al. 2015; Carbognani et al. 2016). Graminoids
277 were the only functional group that had a similar response to the treatments at heath and meadow. We
278 observed an increased fruit production of graminoids in both vegetations in response to nutrient
279 addition and combined nutrient addition and warming, while warming alone tended to have a negative
280 effect. This reflects the responses in terms of abundance of graminoids to the specific treatments in
281 both communities (Alatalo et al. 2014, 2015). Seed production increase in graminoids in a warming
282 experiment was also reported from high-arctic Canada (Klady et al. 2011). OTCs that are used in climate

283 change studies could potentially limit pollen availability (Adamson and Iler 2021; Alatalo et al. 2021). For
284 example, OTCs decreased visitation rates of pollinators two species with 92% in a *Delphinium*
285 *nuttallianum* and by 85% in *Potentilla pulcherrima* in Rocky Mountains. This caused a large decline in
286 pollen grains on stigmas in *Delphinium* but not for *Potentilla* (that is autogamous) (Adamson and Iler
287 2021). Thus, the increased seed production in graminoids in the current study might be due to their
288 capability of self-pollination. This ability allows graminoids to overcome the adverse effect of OTCs.
289 There was a contrasting response of the other functional types to the experiment in meadow and heath
290 vegetation. A similar variation in response of different functional types was reported for Tundra
291 vegetation (Oberbauer et al. 2013). Forbs and evergreen shrubs showed a high fruit production in the
292 meadow with a minimum to no increase in the heath. Contrary, deciduous shrubs had an increased fruit
293 production in the heath with no significant increase in the meadow. Our findings were in line with those
294 studies that reported contrasting effects of climate change on fruit production (Klady et al. 2011; Dorji
295 et al. 2013).

296 Except for a weak non-significant negative effect of summer precipitation at the meadow, other
297 precipitation regimes (i.e., summer and winter) were positively correlated with fruit production. The
298 positive correlation was significant in heath for the previous year precipitation and total precipitation.
299 Therefore, our hypothesis that winter and summer precipitation was negatively correlated with fruit
300 production was rejected. The difference between heath and meadow regarding precipitation effects was
301 likely due to the different properties of these two vegetation types. The heath is drier than meadow
302 (Alatalo et al. 2020), and precipitation may therefore have positively affected fruit production there.
303 Heath plants can also be more susceptible to flowering bud freezing due to the lighter snow cover on
304 the exposed heath (Oberbauer et al. 2013). Therefore, increased previous year precipitation can
305 increase the snow cover and delay the snow melt, thus decreasing the risk of freezing of buds and

306 flowers, contrary an earlier onset of flowering could have a negative effect on plant reproduction of
307 alpine plants (Iler et al. 2019).

308 For the heath, climatic variables of the previous year and total (previous and current) had a
309 stronger significant correlation with total fruit production than those of the current year. Considering
310 total fruit production, we observed that fruit production increased with precipitation and minimum
311 temperature increase, contrary increase in maximum temperature had negative impacts on fruit
312 production. This finding implied that the climatic variables of the previous year were more important for
313 fruit production than those of the current year. Also, this result is in line with the fact that flowering
314 buds in some alpine species were formed in the previous year of fruit production (Oberbauer et al. 2013;
315 Alatalo et al. 2021).

316 Total fruit production in the Meadow was more affected by total and previous year temperature
317 than Heath. An increase in maximum temperature negatively affected fruit production, but an increase
318 in mean and minimum temperature had positive effects. Considering these results, our proposed
319 hypothesis on the importance of minimum temperature that maximum temperature was correct. The
320 current year maximum temperature with effects on delaying phenology and affecting pollinator actions
321 had negative impacts on total fruit production (Alatalo et al. 2021). Both warming and timing of snow
322 melt during the spring can affect the phenology of alpine plants, however, the effect can vary among
323 species (Carbognani et al. 2016; Jerome et al. 2021). In addition an experimental study in Rocky
324 Mountains showed that while plant phenology of three species (*D. nuttallianum*, *P. pulcherrima* and
325 *Valeriana edulis*) was impacted by timing of snow-melt and warming, reproductive success was not
326 (Jerome et al. 2021).

327 Forbs in both communities had a similar response to climatic variables. Current year
328 precipitation decreased, and the previous year precipitation increased the fruit production of forbs. This
329 finding highlighted the effects of both snow cover in winter and delayed flowering in summer on fruit

330 productions of forbs. Except for the previous year's precipitation, the other significant climatic variables
331 that affected forbs had stronger effects in the meadow. Depending on the vegetation type and function
332 type (i.e., graminoids or forbs), current temperature showed variable effects on fruit production. As
333 hypothesized, the overall correlation of the current year ambient temperature with fruit production of
334 graminoids and forbs was positive. Fruit production of graminoids in heath and meadow showed a
335 similar response to climatic variables. Except for the current minimum temperature that was significant
336 in Meadow and not significant in Heath. An increase in minimum and mean temperature increased fruit
337 production of graminoids, with an increase in maximum temperature had no adverse effects on fruit
338 production of this functional type. This finding suggest graminoids may be favored by climate change
339 (Wehn et al. 2014; Dolezal et al. 2019).

340 Except for the negative correlation of the maximum temperature of the previous year, the other
341 climatic variables had no effects on fruit production of evergreen shrubs in heath. Contrary, fruit
342 production of this functional type in the meadow was governed by climatic variables. The response of
343 evergreen shrubs to climatic variables in the meadow were similar to the response of forbs in this
344 community. Deciduous shrubs in heath showed the highest correlation to the climatic factors. Total,
345 minimum temperature, and precipitation increase led to more fruit production in this functional type.
346 Precipitations had a negative impact on deciduous shrubs in the meadow but a positive impact on
347 deciduous shrubs of heath. The maximum temperature of the previous year reduced fruit production of
348 deciduous shrubs. Flower buds of evergreen and deciduous shrubs initiate in the previous summer
349 (Molau et al. 2005). Thus, climatic factors related to the increased risk of flowering bud freezing were
350 negatively correlated with fruit production of shrubs, and those that decreased the risk showed a
351 positive correlation. Therefore, our proposed hypothesis on the effects of the climatic variables on the
352 fruit production of shrubs was partially supported. The high maximum temperature of the current year

353 may increase the risk of early flowering and change biotic interactions. Thus, it negatively impacted the
354 fruit-set production of shrubs (Oberbauer et al. 2013; Kudo 2021).

355

356 **5. Conclusions**

357 Our results suggest that nutrient availability is a more crucial factor limiting reproduction in high alpine
358 plant communities. Increased atmospheric nutrient deposits due to human activities may therefore have
359 a large impact over a longer term. Additionally, the results indicate that warmer summers due to climate
360 change may have a limited impact on fruit production of high alpine plants. Instead, max temperatures
361 during the fall before the fruiting year, and minimum temperatures may be more important.

362

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370

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577 **Table 1.** “Type III Tests of Fixed Effects” from linear mixed models analysis, based on REML testing on
 578 the effects of year (1995, 1996, 1997, 1998, 1999, 2000, 2001) and treatment on total fruit production
 579 and on fruit production by graminoids, forbs, evergreen shrubs, and deciduous shrubs, in an alpine
 580 meadow and heath community at Latnjajaure, subarctic Sweden. Experimental treatments: warming
 581 with open-top chambers (OTC), nutrient addition, and a combined warming and nutrient addition. *Df* =
 582 degrees of freedom, *F* = F-statistics, *P* value = significance level; **bold** indicates significance at $P \leq 0.05$.

Source of variation	<i>df</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	16.80	0.000	13.69	0.000	7.01	0.000	7.45	0.000	5.26	0.000
Treat	3	9.19	0.000	34.15	0.000	8.55	0.000	6.46	0.000	2.86	0.038
Veg	1	5.61	0.019	0.09	0.770	77.77	0.000	32.96	0.000	52.84	0.000
Y x T	18	3.51	0.000	4.05	0.000	1.58	0.066	2.56	0.001	1.05	0.401
Y x V	6	2.49	0.024	0.19	0.980	4.9	0.000	4.94	0.000	2.89	0.010
T x V	3	2.22	0.086	3.30	0.021	7.67	0.000	0.59	0.622	1.78	0.152
Y x T x V	18	0.80	0.694	0.78	0.718	1.37	0.147	1.14	0.311	0.77	0.738
Error	224										

583

584

585 **Table 2.** Correlation coefficients between fruit production and ambient climate parameters in an alpine
586 heath and Meadow, at Latnjajaure northern Sweden (1995-2001). Precipitation, maximum temperature,
587 minimum temperature and mean temperature. Pre = August, September and October before the fruit
588 production year (i.e. the previous year). Current = May, June and July in the fruit production year (i.e.
589 the current year). Total = the pre and current period (i.e. six months in total). **Bold** indicate statistically
590 significance at 5% level.

Heath Climatic Parameter	Deciduous shrubs	Evergreen shrubs	Graminoids	Forbs	Total
Pre-Precipitation	0.33	0.06	-0.08	0.18	0.21
Current-Precipitation	0.12	0.06	0.03	-0.13	0.07
Total-Precipitation	0.25	0.11	0.03	-0.04	0.18
Pre-Max Temperature	-0.17	-0.28	-0.16	0.02	-0.28
Current-Max Temperature	-0.24	-0.11	0.03	-0.02	-0.16
Total-Max Temperature	-0.11	-0.09	0.02	-0.05	-0.10
Pre-Min Temperature	0.25	0.02	0.25	0.09	0.28
Current-Min Temperature	0.37	0.08	0.07	0.24	0.31
Total-Min Temperature	0.49	0.11	0.25	0.28	0.49
Pre-Mean Temperature	0.17	-0.01	0.22	0.06	0.19
Current-Mean Temperature	0.29	0.07	0.18	0.26	0.33
Total-Mean Temperature	0.37	0.15	0.30	0.17	0.43

591

Meadow Climatic Parameter	Deciduous shrubs	Evergreen Shrubs	Graminoids	Forbs	Total
Pre-Precipitation	0.04	-0.14	-0.02	0.13	0.00
Current-Precipitation	-0.17	0.06	0.10	-0.04	-0.03
Total-Precipitation	-0.04	0.07	0.13	0.07	0.08
Pre-Max Temperature	-0.51	-0.20	-0.20	-0.15	-0.43
Current-Max Temperature	-0.03	0.17	0.00	0.00	0.04
Total-Max Temperature	-0.20	0.14	0.03	-0.02	-0.03
Pre-Min Temperature	0.15	0.35	0.31	0.44	0.46
Current-Min Temperature	-0.17	0.19	0.19	0.15	0.12
Total-Min Temperature	0.19	0.38	0.37	0.53	0.54
Pre-Mean Temperature	-0.09	0.37	0.29	0.27	0.30
Current-Mean Temperature	0.03	0.37	0.28	0.29	0.35
Total-Mean Temperature	0.20	0.54	0.42	0.43	0.59

592 *Significance of r (minimum value for 0.165 for 5% for 140 sample)*

593 **Figure legends**

594 **Fig. 1.** Response in terms of total fruit production (fruit production by all species) across treatments in
595 1994 -2000, in an alpine heath (top) and meadow community (bottom) at Latnjajaure, subarctic Sweden.
596 Treatments: control (C), warming with open-top chambers (T=temperature), nutrient addition
597 (F=fertilizer), and combined warming and nutrient addition (TF). N = 8 plots for control, 4 plots for T, F
598 and TF.

599

600 **Fig. 2.** Response in terms of fruit production of deciduous and evergreen shrubs, forbs and graminoids
601 across treatments in 1994 -2000, in an alpine heath and meadow community at Latnjajaure, subarctic
602 Sweden. Treatments: control (C), warming with open-top chambers (T=temperature), nutrient addition
603 (F=fertilizer), and combined warming and nutrient addition (TF). N = 8 plots for control, 4 plots for T, F
604 and TF.

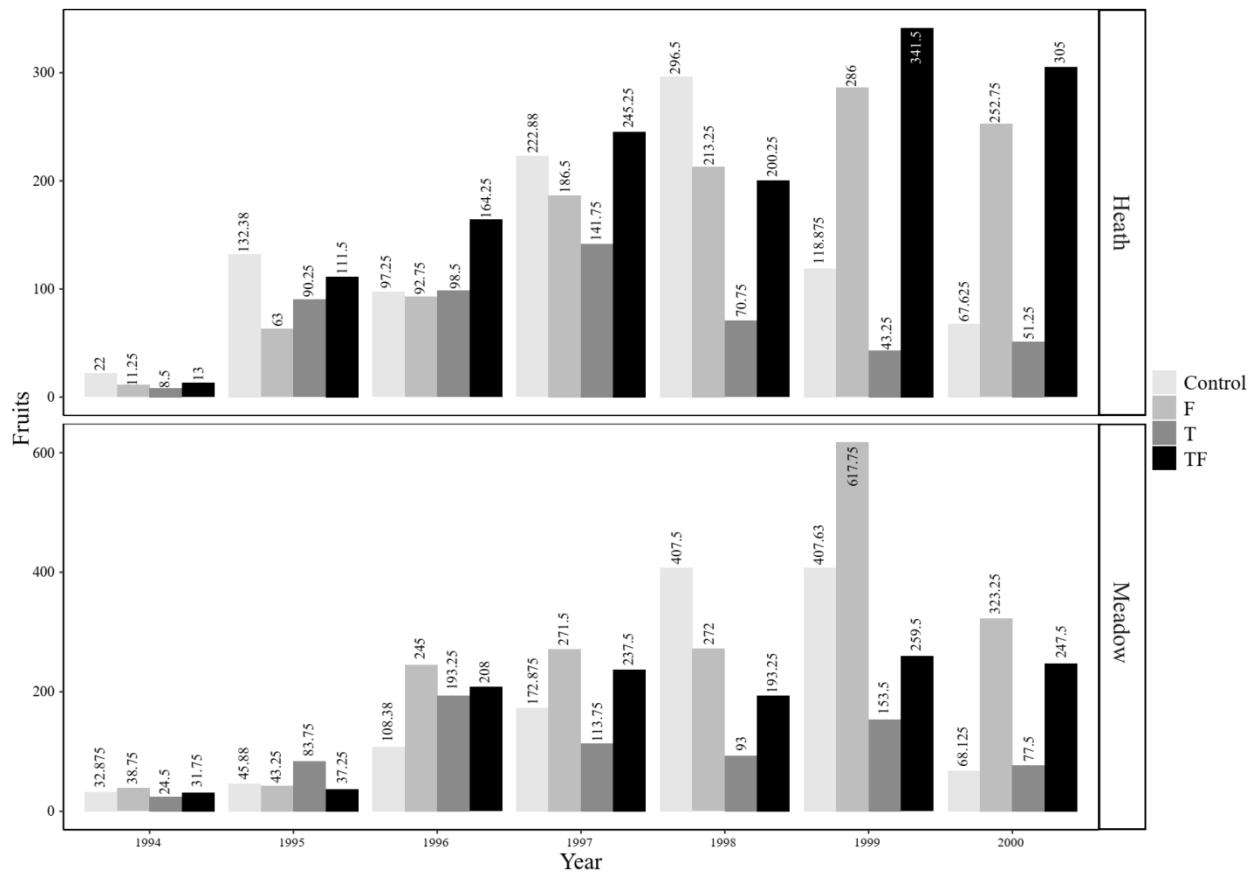
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609 Fig. 1.



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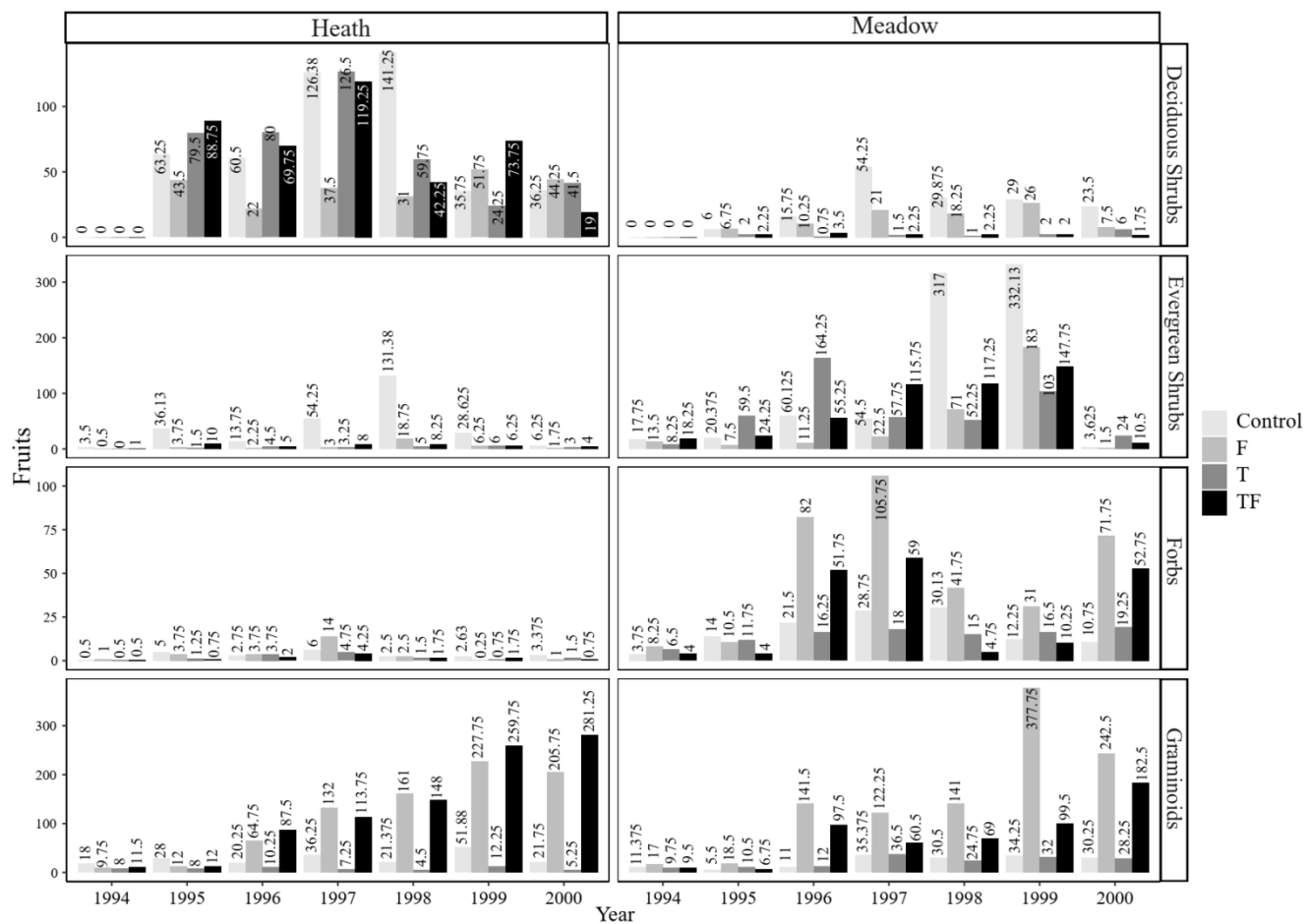
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619 Fig. 2.



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