

Scientific paper

Tundra plant responses to experimental and natural temperature changes

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Abstract: The present five-year study of tundra plant responses to temperature variation is the first longer-term study emanating from the International Tundra Experiment (ITEX). Fieldwork was carried out at the Latnjajaure Field Station in a subarctic-alpine environment in northern Swedish Lapland during 1993–97. Five species were studied: *Cassiope tetragona*, *Dryas octopetala*, *Eriophorum vaginatum*, *Polygonum viviparum* (four years only), and *Ranunculus nivalis*. Experimental warming was established by using standardized open-top chambers (OTCs) according to the ITEX protocol. Assessed response variables include phenology, growth, and reproduction. All species responded positively to experimental warming by an accelerated flowering phenology and by increased propagule weight. In vegetative growth all species except the evergreen *C. tetragona* increased significantly in the warming treatment. After three years some long-term effects have built up, particularly in reproductive effort, e.g., an increase in ovule number per flower. Summer climate was very variable during the study period, and the target species responded much stronger to the warming treatment in the coldest than in the warmest years. The importance of long-term studies in tundra ecosystems is highlighted.

1. Introduction

Arctic and alpine plants are known to be particularly sensitive to climate change and atmospheric nutrient deposition, both being components of Global Change (e.g., Chapin *et al.*, 1995; Callaghan *et al.*, 1996; Henry and Molau, 1997; Molau and Alatalo, 1998; Alatalo and Molau, 2000). Among the climatic variables, ground surface temperature is the most powerful determinant of tundra plant responses in the Low Arctic, whereas precipitation increases in importance in the High Arctic (Wookey *et al.*, 1993; Henry and Molau, 1997; Molau, 1997a). After snowmelt, the temperature at the ground surface is determined by a combination of variables, e.g., albedo, global solar radiation, air mass temperature, soil moisture, and permafrost.

Thanks to its susceptibility to Climate Change and relative simplicity of the ecosystem, the tundra may serve as an “early warning system” and is the optimal study system for experimental simulation of climatic variables in accordance with the prognoses for the next century (Callaghan *et al.*, 1996). Surface temperature manipulations, simulating one major component of Climate Change in arctic and alpine tundra, have been the main method in

the International Tundra Experiment (ITEX) initiated in 1990 (Henry and Molau, 1997). The aim of the research program is to study the responses of tundra plants to temperature enhancement. A set of circumpolar species was selected as study organisms (Molau and Mølgaard, 1996; Murray, 1997), representing all the major life forms in the tundra. For each species, selected response variables for growth and reproduction were provided in the ITEX Manual (Molau, 1993a; Molau and Mølgaard, 1996). At present, ITEX comprises research parties operating at thirty different field stations in thirteen countries. The first collection of results was recently published as a separate issue of *Global Change Biology* (vol. 3, 1997, Suppl. 1; see Henry and Molau, 1997, for review). This gathering of sixteen, mostly multisite, species-oriented studies covered short-term responses to experimental warming, *i.e.*, two or three growing seasons. This effort was followed up by a meta-analysis of the results from the ITEX stations during a workshop at the NCEAS computing facility in Santa Barbara, CA (Arft *et al.*, 1999).

In the present study, I present extended data sets for five of the "ITEX species" (*sensu* Murray, 1997) from one of the keystone sites in ITEX, the Latnjajaure Field Station in northern Swedish Lapland (subarctic-alpine). Five-year records on phenology, growth, and reproduction are provided for *Cassiope tetragona*, *Dryas octopetala*, *Eriophorum vaginatum*, and *Ranunculus nivalis*, and a four-year data set for *Polygonum viviparum*. In addition there is a nine-year record on flowering frequency in *E. vaginatum* (1992–2000). The aim of the study is to present more long-term data sets, which are rare in ecological field experiments in arctic and alpine environments, and to compare the results with the short-term results previously reported from ITEX (Henry and Molau, 1997; Arft *et al.*, 1999). The following questions are addressed: (1) How do the short-term (1–3 yr) results hold in the longer term?, (2) Are there other responses becoming visible only in the longer term records?, (3) Which climatic variables are the determinants of plant responses in the unmanipulated plots?, and (4) Can generalizations be made for responses of entire life forms or functional types of vascular tundra plants?

2. Materials and methods

2.1. Field site and plant communities

The fieldwork was conducted in northernmost Sweden at the Latnjajaure Field Station (LFS) in the valley of Latnjavagge, 68°21'N, 18°29'E, at 1000 m elevation. LFS belongs to the Abisko Scientific Research Station, run by the Royal Swedish Academy of Sciences. My research group from the Göteborg University has been operating at LFS since 1990. In 1990 and 1991, meteorological data were recorded only throughout the growing seasons, but from early spring 1992 a year-round automatic climate station has provided a continuous data set.

The valley is covered by snow for most of the year, and the climate is characterized by cool summers and relatively mild, snow-rich winters (annual minimum ranging from –27.3 to –21.7°C), with a mean annual temperature of –2.0 to –2.7°C (data from 1993–97). Annual precipitation ranges from 605 mm (1996) to 990 mm (1993); the mean for 1990–97 was 808 mm. July is the warmest month with a mean temperature ranging from +5.4°C (1992) to +9.9°C (1997).

The vegetation in the valley comprises a wide range of communities of various species

richness. The soils of these ecosystems vary from dry to wet and from siliceous and acidic (pH=4) to calcareous and circumneutral (pH=6; Björk, 2000). Even though the geographical situation is subarctic-alpine (or “arcto-alpine”), the vegetation of the area is representative of the latitudinal Low Arctic, with *Cassiope tetragona*, *Dryas octopetala*, and *Carex bigelowii* among the dominant species (see Molau and Alatalo, 1998).

2.2. Meteorological methods

The LFS is equipped with an automatic climate station in continuous operation since April 1992. The central unit of the system is a Delta-T^{TR} data logger, accommodating data from thirteen different channels, including wind velocity and direction, air temperature, global radiation, and soil temperatures at various depths. The temperature sensors, recording hourly means, maxima, and minima are installed in a standard Stevenson Screen, in shelter at 2 m above ground. The data logger records data for all channels every minute and stores data as hourly means, maxima, and minima. In the summer season, a manual weather station is in operation according to the SMHI (Sveriges Meteorologiska och Hydrologiska Institut) standards, read daily at 0700 and 1900 hours Normal Time.

2.3. The plant species

Cassiope tetragona (Ericaceae) is a circum-arctic perennial dwarf-shrub in which the leaves remain photosynthetic for about five years. They are not shed after senescence, but remain on the shoot, allowing for retrospective growth analysis back at least 25 years in time (Callaghan *et al.*, 1989; Havström *et al.*, 1993). Vegetative reproduction occurs by layering (radiating ramets rooting while still attached to the maternal plant), except in dry heaths where individuals remain dense and well delimited. In all ITEX at Latnjajaure, four plants per plot were used (see below) in the studies. In the case of *C. tetragona*, the identified individual “plants” are dense tufts (10–40 cm diam.) of stems belonging to the same ramet, but within a plot all four “plants” may belong to the same genet, even though physiological integration was broken long ago. A population genetic study employing the RAPD method indicates that there are often 2–3 genotypes within each plot (Molau, unpubl. data), and morphological markers (*e.g.*, pedicel coloration) show the same spatial scale of variation. The plot means used in this study are thus likely to represent more than one genotype in most cases. Pollination mediated by bumblebees is infrequent, and the species seems to rely upon selfing for its reproductive success (Molau, 1993b). The dry capsules contain 3–400 tiny seeds each. At snowmelt in the early summer they are all dehisced, their seeds dispersed, but the actual process has remained enigmatic until recently. Fruit maturation is extremely late in this species, and a massive seed release in the month of September was recorded for the first time in 1997 (Molau, unpubl. data). In all other years, capsule dehiscence was not observed albeit awaited; snow accumulation started too early at least in 1993 and 1994. In most years, therefore, seed release takes place under the winter snow pack and dispersal is then very local, *i.e.*, within a meter or less. Dispersal away from the site of seed formation is thus a rare event.

Dryas octopetala (Rosaceae) is a trailing, semi-evergreen (ranging from wintergreen to truly evergreen) dwarf-shrub, the individual leaves of which remain photosynthetic for 1–2 years at our site. As in the former species, vegetative spread by layering is the dominant mode of dispersal within the local communities. Small flies pollinate the white flowers with

yellow anthers. Reproductive effort in terms of flower number produced per clone varies greatly among years (reflecting last year's climate), and so does reproductive success in terms of seed set (reflecting the present year's climate). The plumed seeds are wind-dispersed. Seed germinability is linearly correlated with seed mass (Welker *et al.*, 1997).

Eriophorum vaginatum (Cyperaceae), the arctic cottongrass, is a wintergreen sedge with monocarpic tillers. Individual leaves remain green for a little more than one year (Mark *et al.*, 1985; Shaver and Laundre, 1997; Wallberg, 1997; this study). Unlike most other species of the genus, *E. vaginatum* is a phalanx strategist, forming dense tussocks that may reach considerable age. Thanks to its superficial root system, it thrives on very shallow soils on top of an anaerobic layer as in boreal peat bogs or (in the tundra) in areas with permafrost and a shallow active layer. The circumpolar tussock tundra community dominated by *E. vaginatum*, covers more than 900000 km² in the Low Arctic (Bliss and Matveyeva, 1992). At Latnjajaure there is about 2 ha of this plant community, but despite the restricted patch size it is highly typical, developed in a flat area of local permafrost at the outlet of the lake. Flowering in *E. vaginatum* varies greatly among years and events of masting are highly synchronized over large regions within the Arctic (Shaver *et al.*, 1986; Molau and Shaver, 1997). Flowering takes place soon after snowmelt; the prefloration time is only 3–15 d at Latnjajaure. The blackish flowering spikes are born close to the ground surface and efficiently intercept incoming radiation, thereby being relatively independent of the ambient air temperature (Molau and Rosander, 1995). Subsequent elongation of the culm prior to seed dispersal reflects the level of ovule fertilization (reproductive success); culms of unfertilized inflorescences will not elongate at all, and the degree of culm elongation is therefore a good measure of fertilization rate (Molau and Shaver, 1997). The plumed seeds are efficiently wind dispersed; seed weight is linearly correlated with germinability (Molau and Shaver, 1997).

Polygonum viviparum (Polygonaceae) is a perennial herb with a short ascending rhizome, lacking horizontal rhizomes. This species is abundant in the dry, mesic, and moist meadows at Latnjajaure, but occurs, although more sparsely, in acidic heaths as well. Vegetative dispersal is nevertheless abundant in this species, brought about by asexually produced bulbils replacing most (sometimes all) of the flowers. Flowers occur only in the top section of the spike, but are usually not functional in terms of sexual reproduction. Despite high genetic variability within populations at Latnjajaure, only female flowers have been found (Bauert, 1996; Molau, pers. obs.). This is the normal condition in *P. viviparum*, but sexually reproducing populations with hermaphrodite flowers are known from the Central European Alps (Bauert, 1993). Seed production has never been recorded at Latnjajaure. A very long preformation lag phase (four years), from initiation to final development and maturation, of leaves and inflorescences was recently reported by Diggle (1997) from the Colorado Alpine.

Ranunculus nivalis (Ranunculaceae), the snow buttercup, is another perennial herb with small, spatially well-defined individuals. They have a short ascending rhizome and lack vegetative dispersal by horizontal rhizomes. *Ranunculus nivalis* is known as one of the species having the shortest prefloration time in the tundra; often the time lag from snowmelt to flowering is only a few days (Molau, 1997b). The yellow flowers are pollinated by small flies, and even if the species has some potential for self-pollination (Molau, 1993b) it is mainly outbreeding. The nutlets are green and photosynthetic during the process of

maturation (Molau, 1997b). *Ranunculus nivalis* is a characteristic plant in moist and wet alpine meadows with a good snow protection, and it is also found in nutrient-rich, less extreme snowbeds.

Several other species have been studied at Latnjajaure by other members of the research group, viz., *Carex bigelowii* (Stenström and Jónsdóttir, 1997), *Salix herbacea* (Jones *et al.*, 1997), *Saxifraga oppositifolia* (Stenström *et al.*, 1997), and *Silene acaulis* (Alatalo and Totland, 1997).

2.4. Measurements

Passive heating in the ITEX setup at Latnjajaure was achieved by using standard open-top chambers (OTCs; Fig. 1; Molau, 1993a; Molau and Mølgaard, 1996; Marion *et al.*, 1997). The hexagonal OTCs have a basal diameter of 1 m and are made of 3 mm thick polycarbonate plastic. They were installed at snowmelt in late May 1993 and have been permanently out in the field since then. The OTCs increase the ground surface temperature by 1.5–3°C, depending on vegetation cover and soil moisture (see Marion *et al.*, 1997, for review). For all species in this study, I have used 5 OTCs paired with 5 1-m² control plots, one for each OTC. In each plot (OTC or control) 4 individual plants were marked and monitored. The plant closest to the center of each quarter of a plot was chosen. For all subsequent comparisons and tests, only plot means of these four tagged plants were used. The design of the experiments and analyses follows Johnstone *et al.* (1996).

The variables measured can be grouped as qualitative and quantitative. Qualitative variables include mainly phenological measures, *e.g.*, time of snowmelt, prefloration time, postfloration time (days from flowering to seed dispersal), and time of leaf senescence or abscission. Quantitative variables encompass growth variables (*e.g.*, leaf size and shoot height) as well as reproductive ones, in terms of reproductive effort (RE; *e.g.*, flower number, ovule number) and reproductive success (RS; *e.g.*, seed number, seed weight). For each of the study species, the actual response variables were identified in the ITEX Manual (Molau and Edlund, 1996). Phenological data were recorded daily during the fieldwork in 1993–97. Growth responses were normally assessed by using some measure of leaf size. In

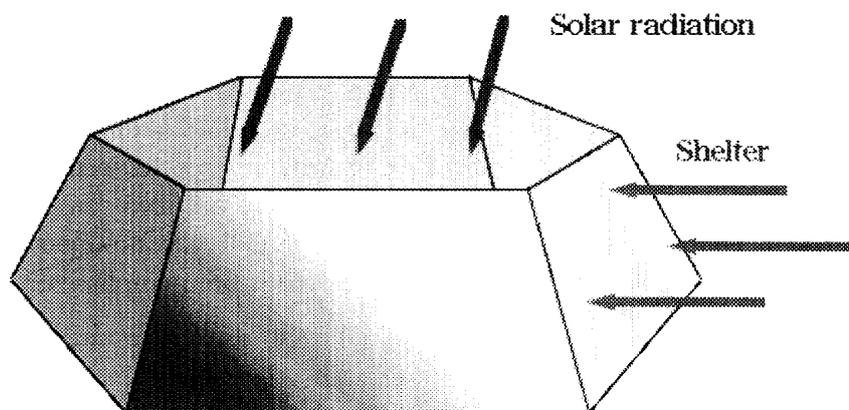


Fig. 1. A standard ITEX hexagonal open-top chamber (OTC). In the Latnjajaure set of OTCs, all panels are 60 cm wide at base and 40 cm high; the inclination of the walls is 73°.

C. tetragona, however, annual shoot increments were measured. Main shoots of each of the tagged “plants” were harvested in August 1997, and later analyzed under a stereo lens. This measuring method is more accurate than the non-destructive field measures reported in Molau (1997b); consequently, there are some discrepancies in the figures between the two studies, even though the interannual variation shows similar trends.

Quantitative variables were scored once a year at appropriate times. Seeds or bulbils were harvested at the time of maturation and stored in paper bags at room temperature; they were later weighed individually in the autumn of the year of harvest on a microgram Mettler AT80 balance at the Botanical Institute, Göteborg University. If available, 20 seeds or bulbils per ramet were weighed. In total over 1993–97, 2418 *D. octopetala*, 3058 *Eriophorum vaginatum*, and 3141 *R. nivalis* nutlets were individually weighed, as well as 2419 *P. viviparum* bulbils.

The statistical analyses were carried out with the StatView 5.0 and SuperANOVA software packages for the Macintosh. Only plot means were employed in the analyses and no transformations were needed to attain normality in the variables analyzed. When ANOVA models have been applied, they are designed according to the “two-way ANOVA without replication” (Sokal and Rohlf, 1981). Treatment (OTC and control) and year are both fixed effects (Sokal and Rohlf, 1981; Johnstone *et al.*, 1996). There is no interaction between time and the individuals as the responses of the individual plants are parallel through time (Sokal and Rohlf, 1981).

3. Results

3.1. Climatic variation among years

The climate during the summers of 1993–97 differed widely (Table 1). In the five-year study period, the 1995 summer was unusually cold and wet. The summer of 1997 was, on the other hand, the warmest on record in the northern Swedish mountains during the century as to mean temperature (SMHI, 1997), and the month of August in 1996 was even further above the record (SMHI, 1996). These two years in conjunction represent a “extreme event”, in this part of Fennoscandia unique during the last century, and perhaps since the onset of the Little Ice Age in Scandinavia some 400 years ago. The impact of these two good summers in conjunction was easily visualized in the vegetation at Latnjajaure: the dwarf birch (*Betula nana*) was sprouting vigorously and increased its biomass by 17% in unmanipulated plots between 1995 and 1997 (Alatalo and Molau, 2000).

The among-year variability in climate is huge, and has a clear impact on seed maturation. In cold summers (*e.g.*, 1992 and 1995) hardly any species in the valley set seed, whereas in the warm summers almost any species produced a full seed complement (Molau and Larsson, 2000). This among-year variability is a normal stress component in the tundra, but the importance of “extreme events” has previously not been emphasized enough (but see Robinson *et al.*, 1998).

3.2. Plant responses

3.2.1. *Cassiope tetragona*

The white arctic heather, *C. tetragona*, showed no response in shoot increments (annual growth increments, AGIs) to the temperature treatment (Fig. 2; Table 2; two-way

Table 1. The climate at Latnjajaure during the summers of 1993-97. Data from the standardized ITEX climate station. TDD= Thawing Degree Days (temperature sum above 0°C).

Time of season Variable	Year				
	1993	1994	1995	1996	1997
<u>May</u>					
Mean temperature (°C)	-0.06	-2.19	-1.69	-2.19	-1.56
Maximum temperature (°C)	+11.0	+9.5	+9.6	+8.4	+7.1
Minimum temperature (°C)	-7.4	-12.6	-14.3	-14.9	-8.8
TDD	52.4	16.2	40.9	23.3	20.7
Precipitation (mm)	80.0	32.1	40.1	14.3	30.1
Global radiation (MJ/m ²)	612	669	661	698	632
<u>June</u>					
Mean temperature (°C)	+1.60	+2.73	+4.36	+3.21	+5.26
Maximum temperature (°C)	+12.0	+12.6	+13.2	+11.3	+17.0
Minimum temperature (°C)	-5.5	-3.8	-0.9	-3.0	-5.7
TDD	65.3	79.2	131.1	98.4	165.4
Precipitation (mm)	60.1	30.1	44.7	91.2	6.2
Global radiation (MJ/m ²)	572	557	534	519	663
<u>July</u>					
Mean temperature (°C)	+8.46	+7.61	+5.93	+7.37	+9.92
Maximum temperature (°C)	+18.1	+20.3	+18.3	+15.2	+20.5
Minimum temperature (°C)	+2.0	-1.6	-1.6	-0.3	+0.7
TDD	262.4	236.1	184.5	228.3	307.5
Precipitation (mm)	63.6	56.7	81.4	42.8	38.7
Global radiation (MJ/m ²)	510	506	460	477	612
<u>August</u>					
Mean temperature (°C)	+6.57	+7.56	+5.28	+9.91	+8.88
Maximum temperature (°C)	+14.4	+21.1	+17.4	+19.1	+19.7
Minimum temperature (°C)	-0.6	-3.2	-1.5	+0.9	+0.4
TDD	203.6	236.3	163.9	307.1	275.2
Precipitation (mm)	63.3	38.9	142.0	66.7	54.2
Global radiation (MJ/m ²)	277	372	310	376	345
<u>Summer (June-August)</u>					
Mean temperature (°C)	+5.54	+5.97	+5.19	+6.83	+8.02
Maximum temperature (°C)	+18.1	+21.1	+18.3	+19.1	+20.5
TDD sum	531.3	551.6	479.5	633.8	748.1
Total precipitation (mm)	187.0	125.7	268.1	200.7	99.1
Global radiation sum (MJ/m ²)	1359	1435	1304	1372	1620

ANOVA, $F_{1,44}=0.006$, $p=0.99$). On the other hand, it showed significant among-year variation in shoot increments ($F_{4,44}=21.77$, $p<0.0001$), regardless of treatment, which must be induced by interannual variation in some environmental variable(s) other than temperature itself (*cf.* Molau, 1997b; Kudo *et al.*, 1999). There were no significant correlations with the preceding summer's climate as to the responses in shoot increment and reproduction in the control plots.

The number of flowers per monitored plant varied greatly among years in the control

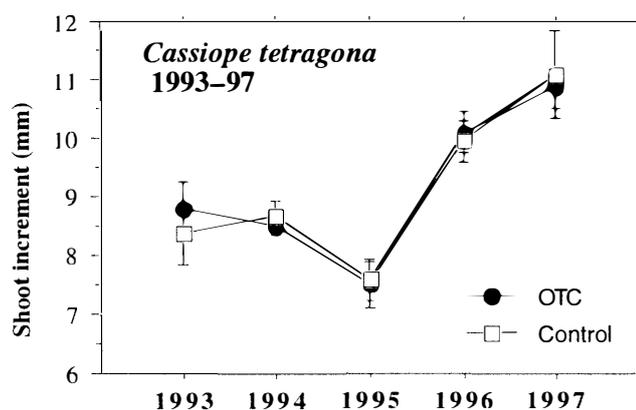


Fig. 2. Variation in the average length (\pm SE) of annual shoot increments of *Cassiope tetragona* in OTCs and controls at Latnjajaure in 1993-97.

Table 2. Summary table. Means of response variables for the study plant species at Latnjajaure 1993-97 (1994-97 for *P. viviparum*). Data are given as mean \pm SE. The number of years of observation equals 5 in all species except *P. viviparum* (4 years). Data sources are annual means across all five plots within each of the two treatments (control and experimental warming). RS, reproductive success, is calculated as bulbil number for *P. viviparum*, fruit:flower ratio for *C. tetragona*, and seed:ovule ratio in the other species. The vegetative growth variables are species-specific (see text). The year of implementation (1993) is omitted from the thaw dates (i.e., data from 4 years are provided for all species with regard to this variable). Day numbers: 1 June = 152, 1 July = 182, 1 August = 213.

Species	Treatment	Thaw date (day no.)	Prefloration time (d)	Reproductive success	Propagule weight (mg)	Vegetative growth
<i>Cassiope tetragona</i>	control	154.4 \pm 5.7	32.6 \pm 1.5	0.44 \pm 0.06	3.83 \pm 0.79	9.12 \pm 0.32
	OTC	151.0 \pm 4.6	28.4 \pm 1.4	0.48 \pm 0.03	5.59 \pm 0.68	9.14 \pm 0.29
<i>Dryas octopetala</i>	control	142.7 \pm 4.2	50.0 \pm 2.8	0.28 \pm 0.07	0.34 \pm 0.04	17.1 \pm 0.3
	OTC	139.5 \pm 3.5	37.5 \pm 1.3	0.32 \pm 0.06	0.41 \pm 0.04	20.9 \pm 0.4
<i>Eriophorum vaginatum</i>	control	154.9 \pm 3.5	9.8 \pm 0.6	0.13 \pm 0.02	0.54 \pm 0.03	158 \pm 11
	OTC	153.3 \pm 4.4	6.4 \pm 0.5	0.10 \pm 0.02	0.86 \pm 0.02	200 \pm 29
<i>Polygonum viviparum</i>	control	142.7 \pm 4.2	56.7 \pm 2.1	20.8 \pm 1.9	1.12 \pm 0.05	423 \pm 13
	OTC	139.5 \pm 3.5	54.2 \pm 2.2	24.4 \pm 2.1	1.24 \pm 0.06	554 \pm 24
<i>Ranunculus nivalis</i>	control	154.9 \pm 2.0	14.1 \pm 1.3	0.28 \pm 0.03	0.41 \pm 0.02	16.9 \pm 0.5
	OTC	151.0 \pm 2.5	13.5 \pm 1.4	0.22 \pm 0.03	0.50 \pm 0.02	22.0 \pm 0.5

plots, from an average of 3.6 in 1996 to 54.1 in 1994; this variation corresponds well in magnitude to that reported from Ellesmere Island in the Canadian High Arctic by Johnstone and Henry (1997). In the Ellesmere data set there was a significant positive correlation between flower number per shoot and July TDD the year prior to flowering (Pearson product-moment correlation, $r=0.891$, $p<0.01$; Johnstone and Henry, 1997); this r -value is only slightly higher than in my data set from Latnjajaure ($r=0.809$, adjusted $r^2=0.540$, $p=0.0972$, $n=5$ control plot means).

The warming treatment accelerated the prefloration time (thawing-flowering) by 13%, from the grand average of 32.6 d in controls ($n=25$ plot means) to 28.4 d in OTCs ($n=23$). The difference between controls and treatment was highly significant in a two-way

ANOVA ($F_{1,44}=11.80$, $p=0.0014$), although the among-year variation was even larger ($F_{4,44}=20.94$, $p<0.0001$).

Reproductive success is difficult to measure in *Cassiope tetragona*. Capsule dehiscence takes place late in the season, and most years probably under the snow. During our extensive fieldwork at Latnjajaure, I observed massive capsule dehiscence only once, namely on the 12 of September in 1997. The 1997 summer was the warmest on record since our monitoring started in 1990. With no ripe, dehiscing fruits to deal with, the weight of entire, near-maturity fruits from OTCs and control plots were compared in 1995, revealing a near-significant ($p=0.055$) weight increase by the warming treatment (Molau, 1997b).

3.2.2. *Dryas octopetala*

The mountain avens, *D. octopetala*, showed positive responses to temperature amelioration in all variables measured. Like in all other species investigated, phenology was significantly accelerated; in this case plants in OTCs showed a prefloration time on average 12.5 d shorter than in untreated plots (Table 2; Appendix), the difference highly significant in a two-way ANOVA ($F_{1,44}=35.28$, $p<0.0001$). However, also the among-year difference was significant ($F_{4,44}=8.95$, $p<0.0001$), the treatment effect being smallest in the warmest year (1997).

Reproductive effort (number of ovules produced in 1994–97) did not differ significantly between treatments (two-way ANOVA, $F_{1,32}=2.60$, $p=0.117$) or among years ($F_{3,32}=1.87$, $p=0.154$). Reproductive success in terms of fertilization level (seed:ovule ratio) was normally lower in the OTCs than in the controls (Table 2; Appendix), probably due to pollination shortage in the chambers (the species is poorly self-pollinating; Molau, 1993b). The lower pollination level was also manifested in longer flower duration in the OTCs when compared to control plots in a two-way ANOVA ($F_{1,34}=26.09$, $p<0.0001$), with no significant difference among years ($F_{3,34}=2.70$, $p=0.061$). With regard to seed weight, however, *D. octopetala* responded as most tundra plants to temperature enhancement: seeds from plants in OTCs were heavier than in the control plots, at least in cold years; the treatment effect was only near-significant in a two-way ANOVA ($F_{1,39}=3.09$, $p=0.089$) but strongly significant among years ($F_{3,39}=15.88$, $p<0.0001$). In the cold summer of 1995, seeds in OTCs ended up more than three times heavier than in the control plots (Fisher's Protected LSD, $p<0.001$). Seed weight in controls was significantly positively correlated with temperature, especially in terms of TDD (thawing degree days, Pearson product-moment correlation, $r=0.997$, $p<0.0001$). The average seed weight in unmanipulated plants in 1995 (0.12 mg) is below the 0.15 mg level for any germination potential (*cf.* Welker *et al.*, 1997).

With regard to vegetative growth, leaf size increased significantly with enhanced temperature (two-way ANOVA, $F_{1,44}=69.47$, $p<0.0001$), but the effect also differed among the years ($F_{4,44}=3.54$, $p=0.014$); see Fig. 3. In control plots, leaf length showed the highest correlation with TDD of the preceding summer (Pearson product-moment correlation, $r=0.935$, $p=0.016$, $n=5$ years).

3.2.3. *Eriophorum vaginatum*

The arctic cottongrass, *E. vaginatum*, belongs to the vernal flora (Molau, 1993b) and has a very short prefloration time, on average 9.8 d (Table 2). Phenology was significantly

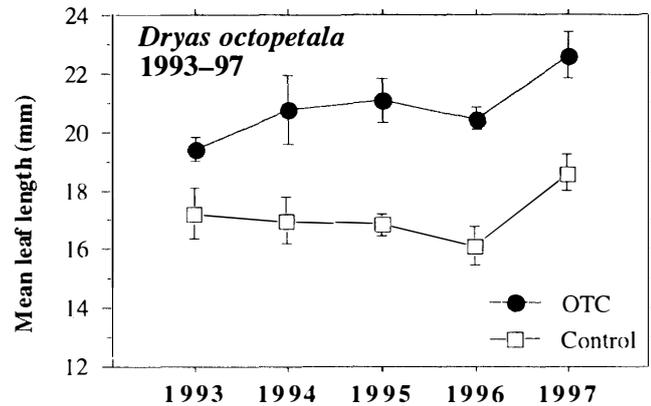


Fig. 3. Variation in the average length (\pm SE) of leaves of *Dryas octopetala* in OTCs and controls at Latnjajaure in 1993–97.

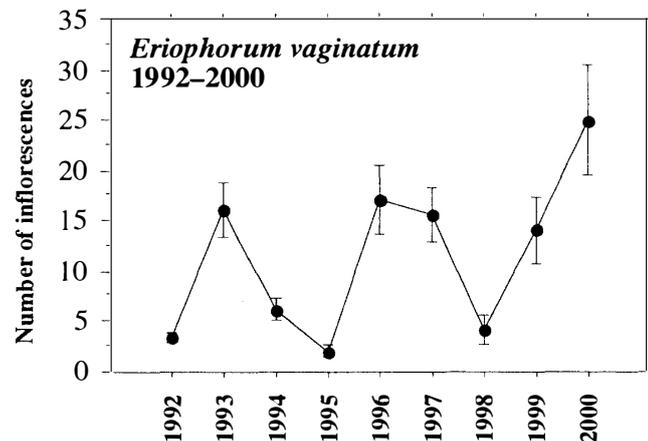


Fig. 4. Mean number (\pm SE) of inflorescences in twenty unmanipulated *Eriophorum vaginatum* tussocks monitored at Latnjajaure in 1992–2000.

accelerated in the enhanced temperature treatment, and the average prefloration time was reduced even more, to 6.4 d, a highly significant difference (two-way ANOVA, $F_{1,44}=25.59$, $p<0.0001$). Also the among-year variation in prefloration was significant ($F_{4,44}=7.76$, $p<0.0001$; see Appendix).

None of the two components of reproductive effort, the number of inflorescences per tussock and the number of ovules per inflorescence, differed significantly between treated and untreated plants. The nine-year monitoring of flowering (inflorescences per tussock) at Latnjajaure 1992–2000 revealed a huge interannual variation (Fig. 4), and all tussocks in the ca. 2 ha stand of *E. vaginatum* tussock tundra at the site seem to be highly synchronized (as they are in the north Alaskan tussock tundra, cf. Molau and Shaver, 1997, and references therein). This synchronous interannual variation was significant also in the tussocks included in the ITEX plots ($F_{4,32}=11.21$, $p<0.0001$). The flowering rate at Latnjajaure seems to be best correlated with TDD the summer three years prior to actual flowering, but the data set still is too small to allow proper testing and modeling. The good flowering years

of 1993, 1996, 1997, 1999, and 2000 correspond with the warmest summers at Latnjajaure during the 90's with a three-year delay, particularly with regard to summer TDD (summer TDD of 1990 was also high: 686.4). The years of minimum flowering in Fig. 4, 1995 and 1998, correspond to cold summers with a three-year delay as well (summer TDD in 1992: 518.8; in 1995: 479.5).

In addition, a late thawing induced a postponement of the final development of some tillers, as the number of inflorescences per tussock was negatively correlated with thawing date of the present year (linear regression, $r^2=0.268$, $p<0.0001$, $n=50$). The among-year variation in ovule number per inflorescence (two-way ANOVA, $F_{4,42}=5.74$, $p=0.0009$) was best correlated with the summer TDD one year back in time.

Reproductive success was generally reduced in the OTCs, an obvious chamber effect in this wind-pollinated species, although the level varied greatly among years (Table 2; Appendix). The variation in the percentage of fruiting inflorescences showed a significant dependence on inflorescence density (linear regression, $r^2=0.155$, $p=0.0052$, $n=48$), the main determinant of *E. vaginatum* pollen density in the air. Seed weight (Table 2; Appendix), on the other hand, was significantly higher in the experimentally warmed tussocks (two-way ANOVA, $F_{1,36}=93.83$, $p<0.0001$), and there was also a significant among-year variation ($F_{4,38}=5.31$, $p=0.0017$) where the experimentally induced relative increase in seed weight was largest in the coldest years (see Appendix). Culm elongation was measured only in 1993, but this response variable was then abandoned as it was shown to be linearly correlated to reproductive success in terms of seed:ovule ratio (Molau and Shaver, 1997).

From the monitoring of all individual leaves of one tiller per tussock in 1994–96, the maximum standing crop of green parts of leaves (corresponding to photosynthetic area) per season was calculated (Table 2; Appendix). The average for tussocks in the warming treatment over the years was 26% higher than in control plants, a significant treatment effect (two-way ANOVA, $F_{1,26}=9.92$, $p=0.0041$), whereas the interannual differences were insignificant ($F_{2,26}=0.31$, $p=0.74$). Also the maximum length of the longest leaf per tiller and season was higher in the OTCs (96.2 ± 3.8 mm [mean \pm SE], $n=15$ plot means) than in the controls (83.07 ± 2.3 , $n=15$); here not only the treatment effect was significant ($F_{1,26}=11.20$, $p=0.0025$) but also the variation among years ($F_{2,26}=5.21$, $p=0.0125$). The number of leaves produced per tiller and season did not differ between OTCs and controls ($F_{1,26}=1.08$, $p=0.31$), but the leaves tended to remain green longer in the controls (412 ± 65 d [mean \pm SD], $n=19$) than in the OTCs (400 ± 36 d, $n=19$) although the difference was not significant in a *t*-test (DF=35, $p=0.49$). Leaf elongation rate in early summer was higher in the OTCs than in the controls, but so was also the senescence rate in late August (Fig. 5; cf. Wallberg, 1997).

3.2.4. *Polygonum viviparum*

The alpine bistort, *P. viviparum* (= *Bistorta vivipara*), was studied in the same plots as *D. octopetala* during 1994–97. The four-year monitoring revealed no significant acceleration of phenology in terms of prefloration in the warming treatment compared to controls (two-way ANOVA, $F_{1,35}=1.18$, $p=0.2856$), but this is the most late-flowering species of all five in the study and may respond to other cues as well.

With regard to reproductive effort, the proportion of flowers and asexually produced

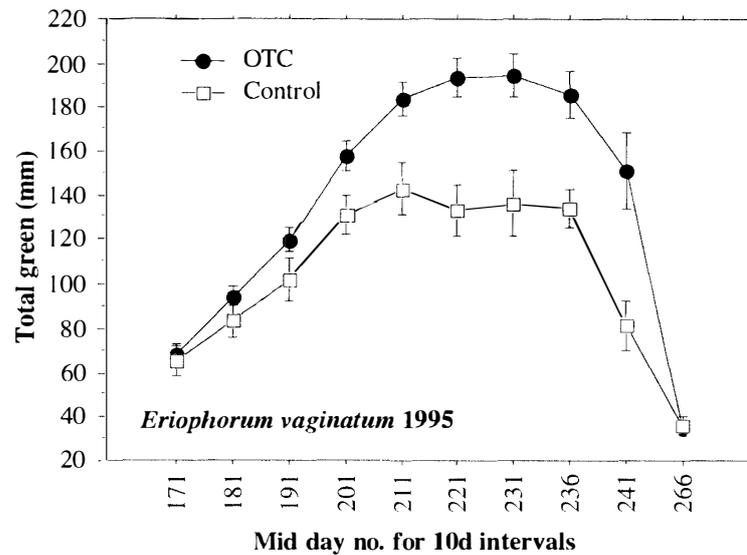


Fig. 5. Mean total length (\pm SD) of green (photosynthetically active) leaf tissue of forty monitored *Eriophorum vaginatum* tillers in OTCs and controls at Latnjajaure in the summer of 1995.

bulbils varied significantly among years ($F_{3,26}=6.53$, $p=0.0013$). The proportion of flowers was highest in the warmest year (1997; 0.209), but otherwise the pattern of variation was not consistent with any climatic variable of the same season. However, flower number in control plots showed a significant correlation to the temperature sum (TDD) of the preceding summer (linear regression, $r^2=0.925$, $p<0.0490$, $n=20$). It should be noted that the genotypes in our area produce unisexual female flowers only; reproduction is brought about only by bulbils (cloning). The number of bulbils per plant varied significantly among years ($F_{3,35}=9.24$, $p<0.0001$); the number also tended to be higher in plants in the OTCs than in controls (Table 2; Appendix), but this difference was not statistically significant ($F_{1,35}=2.66$, $p=0.11$). Bulbil weight was also higher in the OTCs, but as in the case of bulbil number this difference was non-significant ($F_{1,35}=2.71$, $p=0.11$), masked by the stronger interannual variation ($F_{3,35}=3.51$, $p=0.0252$). When the two measures are combined as “bulbil yield”, the total weight of the bulbils produced on an inflorescence, the treatment effect is also significant ($F_{1,35}=7.32$, $p=0.0105$).

The results from Latnjajaure were compared with a recent study of the same species from the central Norwegian ITEX site at Finse (Totland and Nyhlén, 1998; Table 3) over the same four-year period (1994–97). Flower number and bulbil number both showed slightly higher figures in the Finse material, but with overlapping ranges. Bulbil weight, however, differed strongly between the two sites, the Latnja figures being almost twice as high as at Finse. For all three variables, the OTC figures were higher than the corresponding controls at both sites, respectively.

The two measures of vegetative growth, height of the shoot and area of the largest leaf (Table 2; Appendix), both showed a significant increase in the warming experiment, the difference being more pronounced in leaf area (Fig. 6; $F_{1,35}=21.95$, $p<0.0001$) than in shoot height ($F_{1,35}=5.14$, $p=0.0296$). The among-year difference was significant for shoot height ($F_{3,35}=5.20$, $p=0.0043$) but not for leaf area ($F_{3,35}=0.67$, $p=0.57$). Leaf area was measured

Table 3. Comparison of mean values of components of reproductive effort in *Polygonum viviparum* at two ITEX sites: in northern Sweden (Latnjajaure; this study) and central Norway (Finse; Totland and Nyhlén, 1998).

Variable	Site	Treatment	Mean \pm SE
Flower number	Latnjajaure	Control	2.75 \pm 0.58
	Latnjajaure	OTC	3.78 \pm 1.03
	Finse	Control	3.15 \pm 1.15
	Finse	OTC	5.28 \pm 2.22
Bulbil number	Latnjajaure	Control	20.8 \pm 1.9
	Latnjajaure	OTC	24.4 \pm 2.1
	Finse	Control	23.0 \pm 2.6
	Finse	OTC	26.3 \pm 3.0
Bulbil weight (mg)	Latnjajaure	Control	1.12 \pm 0.05
	Latnjajaure	OTC	1.24 \pm 0.06
	Finse	Control	0.60 \pm 0.06
	Finse	OTC	0.85 \pm 0.11

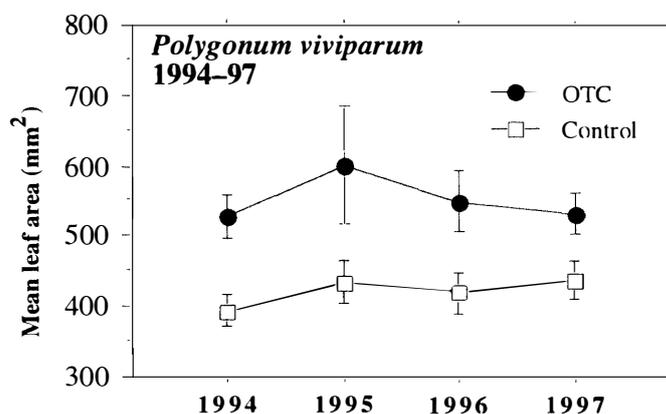


Fig. 6. Variation in leaf area (\pm SE) of *Polygonum viviparum* in OTCs and controls at Latnjajaure in 1994-97.

according to Wookey *et al.* (1993), using an algorithm taking leaf length and width into account.

3.2.5. *Ranunculus nivalis*

The snow buttercup, *R. nivalis*, belongs to the vernal flora of the valley (Molau, 1993b), as manifested by its short prefloration time (on average 14.1 d in control plots; Table 2). The small decrease in prefloration time seen in the warming treatment was far from significant (two-way ANOVA, $F_{1,44}=0.15$, $p=0.70$), whereas there was a significant among-year component to the variation ($F_{4,44}=7.35$, $p<0.0001$). Postfloration time showed the same picture: slightly faster in the OTCs (36.3 ± 1.9 d, mean \pm SE, $n=23$) than in the controls (37.7 ± 2.2 d, $n=23$), with no significant treatment effect ($F_{1,42}=1.46$, $p=0.23$) but a significant among-year component ($F_{4,42}=27.83$, $p<0.0001$).

The best measure of reproductive success in this species, viz. ovule number, increased steadily in the OTCs during the first three years of treatment, after which it leveled out

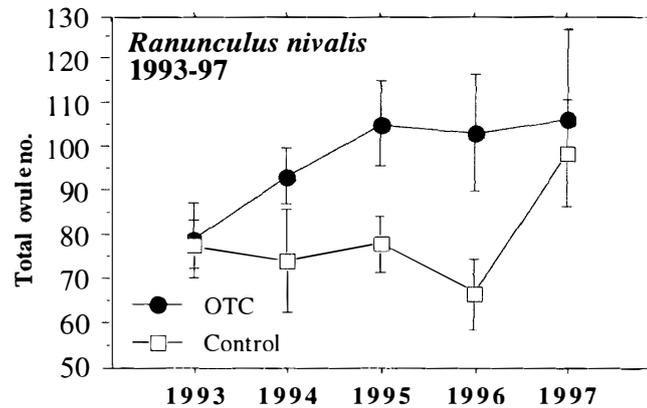


Fig. 7. Variation in the average ovule number (\pm SE) in flowers of *Ranunculus nivalis* in OTCs and controls at Latnjajaure in 1993-97.

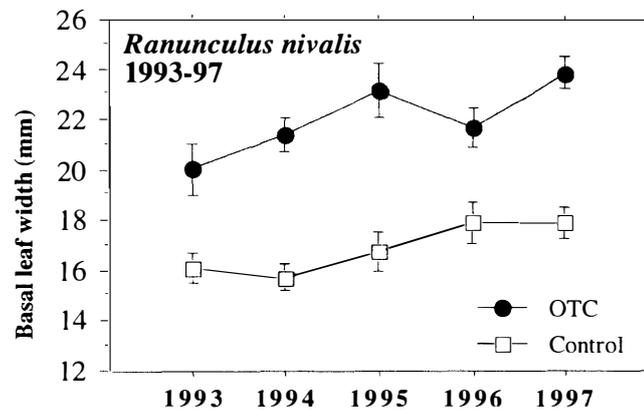


Fig. 8. Variation in the average width (\pm SE) of basal leaves of *Ranunculus nivalis* in OTCs and controls at Latnjajaure in 1993-97.

(Fig. 7). In the control plots the average ovule number varied considerably among years, mainly in response to the climate of the preceding year (linear regression on TDD one year prior to flowering, $r^2=0.947$, $p=0.0024$, $n=25$). After the experiment implementation season of 1993, ovule number remained steadily higher in OTCs than in controls, although there was a marked raise in the controls to almost OTC level following the warm August in 1996 (Fig. 7).

As in the other species in this study, propagule weight increased significantly in the warming treatment (Table 2; Appendix). *Ranunculus nivalis* nutlets were significantly heavier in the OTCs than in the controls (two-way ANOVA, $F_{1,42}=14.11$, $p<0.0001$), and the among-year variance component was highly significant as well ($F_{4,42}=6.09$, $p=0.0006$). Relative reproductive success in terms of seed:ovule ratio did not differ significantly between treatments ($F_{1,42}=2.14$, $p=0.15$) but among years ($F_{4,42}=4.21$, $p=0.0059$).

The most relevant measure of vegetative growth in *R. nivalis*, viz. basal leaf width (see Molau and Edlund, 1996), showed consistently much higher values in the warmed plots than in the controls (Fig. 8; Table 2; Appendix; two-way ANOVA, $F_{1,44}=72.14$, $p<0.0001$).

whereas the among-year component was barely significant ($F_{3,44}=2.73$, $p=0.0405$). The other growth measure recorded during the ITEX process at Latnjajaure, viz. inflorescence height at maturity, showed the same pattern of variation (OTCs 17.4 ± 0.8 cm, controls 12.1 ± 0.7 cm [means \pm SE]; between treatments $F_{1,42}=36.18$, $p < 0.0001$; among years $F_{4,42}=4.37$, $p=0.0048$), but this measure seems to be biased as it covaries with reproductive success: in the control plots, a linear regression showed a significant dependence of shoot height on reproductive success in terms of seed:ovule ratio ($r^2=0.321$, $p=0.0029$, $n=23$; compare *E. vaginatum* above).

A final remark is relevant here: in the wet sedge community where *R. nivalis* has been studied, other species (particularly *Carex lachenalii*, *Calamagrostis stricta*, *Poa arctica*, and *Sphangum warnstorffii*) have responded much more vigorously to the warming treatment. The target species *R. nivalis* is now suffering from competitive exclusion, and is rapidly decreasing in numbers of genets, which are reduced by ca. 50% since the implementation in 1993 (Molau, unpubl. data).

4. Discussion

4.1. Climatic impact variation in time and space

The present study highlights the tundra plants' responsiveness to climatic variability. Even though tundra plants are extremely long-lived and well adapted to environmental fluctuations (Molau, 1993b, and references therein), they do respond vigorously to the among-year variation in climatic variables, particularly temperature (best measured as TDD), growing season length, global radiation, and precipitation. The warming experiment adopted in ITEX is a rather mild perturbation, as the variation in summer temperatures among years exceeds the treatment effect achieved by the OTCs (see Table 1).

However, the climatic cues differ in importance among life forms (functional types), species, and— not least important— even among populations within species according to the position of the study site in that particular species' distributional range in geographic and environmental space (see multisite reports, e.g., Havström *et al.*, 1993; Graglia *et al.*, 1997; Henry and Molau, 1997, and references therein; Arft *et al.*, 1999). Hence, shoot increment in *Cassiope tetragona* responded strongly to interannual temperature variation in the High Arctic and in the high alpine zone in the Subarctic, whereas this response variable was not affected by climate but rather by nutrient availability at a tree-line site near Abisko in northern Sweden (Havström *et al.*, 1993). The Latnjajaure site (subarctic, mid-alpine) lies in between these extremes, probably close to the climatic optimum of *C. tetragona*. In the present five-year study there was no significant increase in shoot increment in the warming treatment, but a significant difference among the years. Precipitation is not limiting here, as it may be in the High Arctic (*cf.* Wookey *et al.*, 1993). Instead, the key factor must be sought among other environmental variables, such as growing season length (earliness of thaw) and radiation. The OTCs alter the precipitation and radiation climate only marginally (Marion *et al.*, 1997). The Ellesmere Island study (Johnstone and Henry, 1997) showed a high correlation between growth and TDD but did not report on radiation climate. However, the number of leaves per annual shoot increment is reported to have a better correlation with temperature (Havström *et al.*, 1993), a quantitative response variable that was not utilized in my study. As pointed out by S. Jonasson (*in litt.*) my data set for

shoot increments in both controls and manipulated plants shows a potential correlation with July mean temperatures, although not significant ($p=0.129$), but this does still not explain the significant lack of differentiation between responses in controls and OTCs. The lack of response to experimental warming is still enigmatic, but parallels that of evergreen *Saxifraga oppositifolia* at the same and other sites (Stenström *et al.*, 1997). Recently, Kudo *et al.* (1999) showed that thawing date and growing season length are important cues for the vegetative performance in *C. tetragona* along a natural snow-cover gradient at Latnjajaure.

Here, it should be stressed that this is not a generalization that holds true for the entire "functional type" of evergreen dwarf-shrubs; species like *Empetrum hermaphroditum* and *Vaccinium vitis-idaea*, both mainly boreal in their distribution and with their climatic tolerance limit at the Latnjajaure site, respond vigorously to the warming treatment there (Alatalo and Molau, 2000, see also Graglia *et al.*, 1997). Other "arctic specialists" among the evergreen dwarf-shrubs, however, appear to respond in the same manner as *C. tetragona*, e.g., *Saxifraga oppositifolia* (Stenström *et al.*, 1997) and *Diapensia lapponica* (Molau, 1996; Kudo *et al.*, 1999).

4.2. Growth and reproduction

With regard to vegetative growth, the plant's responses are usually conspicuous already during the first season of treatment, even though leaf preformation requires long time in some species, e.g., up to four years in *Polygonum viviparum* (Diggle, 1997). In the latter case, even a five-year study is far too short to generate any reliable analysis of correlation between climate and plant performance in terms of numbers of modules (*i.e.*, leaves) produced, even though their size is usually determined by the climate of the summer of final development.

The picture is even more complex with regard to reproductive structures. Inflorescences are preformed at least one year prior to their final development in most tundra plants (Sørensen, 1941; Molau, 1993b, and references therein), and in some cases the reproductive effort is determined by the summer climate 3–4 years prior to actual flowering (e.g., *Eriophorum vaginatum*, Molau and Shaver, 1997; *Polygonum viviparum*, Diggle, 1997). Here, short-term studies including two or three field seasons will fail to demonstrate any adequate relationships, and even the present longer-term study gives little room for hypothesis testing.

In many, perhaps most, of the tundra vascular plant species, successful reproduction is a more rare event than we have anticipated. My five-year study clearly shows that successful reproduction in tundra plants is rather episodic, as the study period involved everything from very cold summers (1995; hardly any seed set in most plant species in the area) to extremely warm ones (1996, 1997; massive seed output in all species). The importance of extreme climatic events in the tundra has been under-estimated until quite recently. It is becoming increasingly evident that just a few subsequent years of aberrant climate may substantially change plant performance (Callaghan *et al.*, 1996; Robinson *et al.*, 1998; Alatalo and Molau, 2000), thereby influencing species' maintenance in their habitats as well as their overall productivity. Change in stature (from decumbent to ascending) in, e.g., deciduous shrubs such as the dwarf birch (*Betula nana*), may feed back directly to the local climate in terms of reduced albedo, affecting the radiation balance of the area.

Previous studies show that seed weight did not differ significantly between rather

remote ITEX sites in either *Dryas octopetala* (Latnjajaure and Niwot Ridge, Colorado; Welker *et al.*, 1997) or *Eriophorum vaginatum* (Latnjajaure and Toolik Lake, Alaska; Molau and Shaver, 1997). However, bulbil weight in *Polygonum viviparum* was almost twice as high at Latnjajaure than at the Norwegian Finse site, both within the Scandes Mountains. Despite the existing genetical variation within populations of *P. viviparum* demonstrated by Bauert (1993, 1996), most of the variation in characters like propagule weight should be expected to be contributed by differences among populations in a mainly asexually reproducing species (*cf.* Molau and Prentice, 1992, and references therein).

4.3. Response rate

The tundra plant short-term responses to experimental warming (reported in Henry and Molau, 1997, and references therein; Arft *et al.*, 1999) hold true also in the somewhat longer term. In addition, some responses build up through the years, such as the increase in ovule number per flower or inflorescence. Such longer-term responses at the plant level take at least three years to become evident and statistically validated. Responses to warming at the community level require even longer time periods of study (*e.g.*, Chapin *et al.*, 1995; Molau and Alatalo, 1998; Alatalo and Molau, 2000).

Some responses were rather instant, indicative of changes that might take place in a changing climate. In particular, propagule weight increased already the first season of treatment in all study species. From the data set it is evident that a poor summer like that of 1995 does not inflict much seed production, whereas summers like those of 1996 and 1997 may very well be the most important ones in an individual plant's life time when reproductive output is concerned.

4.4. Forecast

The "truly" arctic and alpine evergreen dwarf-shrubs are the most vulnerable to climate warming, whereas graminoids and herbs have the best capability to cope with rapid changes in the environment in the short term. Deciduous shrubs, like the mid-alpine dwarf form of *Betula nana*, seems to be slower starters but winners in the long run if facing temperature increase; these processes are seen in the community level experiments at Latnjajaure after 3–4 years of study (Molau and Alatalo, 1998; Alatalo and Molau, 2000). It should also be underpinned that the plants dealt with in the ITEX program are all "arctic specialists"; species with a mainly boreal distribution and with their upper distributional limits in the Low Arctic or the mid alpine zone, may respond quite differently to the imposed environmental cues (Graglia *et al.*, 1997; Kudo *et al.*, 1999). The observed response spectra in the handful of species studied cannot immediately be applied to entire plant life forms or "functional types", even though some general trends may be identified (see Henry and Molau, 1997; Arft *et al.*, 1999). In the Low Arctic as well as in alpine environments, a shift in balance among the resident plant life forms towards a dominance by deciduous dwarf-shrubs is to be expected in a warmer climate. The immigration of alien species from lower vegetation zones is an even slower process (Callaghan *et al.*, 1996; Molau and Alatalo, 1998).

Short-term growth responses assessed during the first two or three years of an ITEX survey provide a solid starting-point picture of the responses of individual plant species to climate change, even though tuning of the responses in a competitive environment requires

much longer data sets. Reproductive responses require longer-term studies, but in most cases five-year terms seem sufficient. Secondary, indirect responses like those brought about by plant-plant competition, however, need longer study periods and another scale of observation. With the ongoing activities within ITEX and related projects we will hopefully acquire a much better understanding of long-term changes in the tundra within the next decade.

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Appendix

Annual means of plant response variables at Latnjajaure 1993-97 in controls and open-top chambers (OTCs). Values are given as plot means \pm SE; $n=5$ for each year and treatment. Each value is the mean of data from four individual plants in each plot. Thawing dates for 1993 are not analyzed for OTCs (given within brackets) as they were implemented at thawing and consequently had no impact on thawing time that year; they were, however, used for calculating prefloration time as the warming experiment started out as the OTCs were put out.

a. *Cassiope tetragona*

Year	Treatment	Thawing date (day no.)	Prefloration time (d)	Flower duration (d)	Fruit:flower ratio	Fruit weight (mg) ¹	Annual growth increment (mm)
1993	Control	135.6 \pm 1.6	43.0 \pm 1.0	12.7 \pm 1.2	0.63 \pm 0.06		8.37 \pm 0.52
1993	OTC	(135.6 \pm 1.6)	36.6 \pm 2.0	11.2 \pm 1.6	0.53 \pm 0.05		8.78 \pm 0.47
1994	Control	155.1 \pm 5.1	31.4 \pm 1.4	9.5 \pm 0.2	0.54 \pm 0.14		8.66 \pm 0.28
1994	OTC	150.4 \pm 4.9	31.8 \pm 3.4	6.7 \pm 1.9	0.44 \pm 0.06		8.51 \pm 0.16
1995	Control	168.4 \pm 5.4	27.7 \pm 2.7	9.1 \pm 1.8	0.18 \pm 0.09	3.83 \pm 0.79	7.58 \pm 0.36
1995	OTC	163.1 \pm 5.0	25.9 \pm 1.6	12.4 \pm 2.8	0.41 \pm 0.11	5.59 \pm 0.68	7.48 \pm 0.38
1996	Control	153.5 \pm 1.8	34.9 \pm 3.5	13.6 \pm 3.9	0.55 \pm 0.20		9.94 \pm 0.35
1996	OTC	149.6 \pm 1.3	28.4 \pm 0.8	11.2 \pm 1.4	0.58 \pm 0.05		10.10 \pm 0.36
1997	Control	140.7 \pm 0.6	26.8 \pm 1.1	12.6 \pm 0.9	0.33 \pm 0.13		11.07 \pm 0.76
1997	OTC	140.8 \pm 0.8	19.4 \pm 1.1	12.2 \pm 2.1	0.46 \pm 0.07		10.86 \pm 0.36

¹Fruit weight measured only in 1995 (see Molau, 1997b).

b. *Dryas octopetala*

Year	Treatment	Thawing date (day no.)	Prefloration time (d)	Flower duration (d) ¹	Seed:ovule ratio ²	Seed weight (mg)	Leaf length (mm)
1993	Control	137.4 \pm 1.5	47.5 \pm 1.2	9.7 \pm 0.6		0.22 \pm 0.04	17.2 \pm 0.9
1993	OTC	(137.4 \pm 1.5)	42.9 \pm 1.5	10.1 \pm 0.3		0.21 \pm 0.05	19.5 \pm 0.4
1994	Control	133.2 \pm 2.0	65.2 \pm 2.1	8.6 \pm 1.2	0.26 \pm 0.08	0.28 \pm 0.04	17.0 \pm 0.8
1994	OTC	133.2 \pm 2.0	36.8 \pm 1.8	11.4 \pm 0.2	0.22 \pm 0.09	0.36 \pm 0.10	20.8 \pm 1.1
1995	Control	152.5 \pm 1.8	48.1 \pm 2.2	7.8 \pm 0.5	0.11 \pm 0.11	0.12 \pm 0.01	16.8 \pm 0.4
1995	OTC	147.0 \pm 4.2	35.0 \pm 2.7	12.7 \pm 1.1	0.52 \pm 0.17	0.40 \pm 0.09	21.1 \pm 0.8
1996	Control	145.8 \pm 4.0	55.7 \pm 4.3	10.1 \pm 0.4	0.48 \pm 0.20	0.47 \pm 0.02	16.1 \pm 0.6
1996	OTC	144.0 \pm 4.1	40.8 \pm 3.8	13.7 \pm 1.0	0.31 \pm 0.09	0.46 \pm 0.08	20.5 \pm 0.4
1997	Control	139.2 \pm 1.9	33.6 \pm 2.0		0.34 \pm 0.09	0.61 \pm 0.03	18.6 \pm 0.6
1997	OTC	133.8 \pm 2.3	32.3 \pm 1.8		0.22 \pm 0.06	0.61 \pm 0.05	22.6 \pm 0.8

¹Flower duration not recorded in 1997.

²Seed:ovule ratio not calculated in 1993 due to lack of seed set in marked plants.

c. *Eriophorum vaginatum*

Year	Treatment	Thawing date (day no.)	Prefloration time (d)	Postfloration time (d)	Seed : ovule ratio	Seed weight (mg)	Total green length (mm) ¹
1993	Control	142.2±0.7	13.2±1.0	60.1±1.1	0.13±0.02	0.52±0.02	
1993	OTC	(142.2±0.7)	9.5±0.3	54.6±1.2	0.09±0.02	0.80±0.03	
1994	Control	160.2±0.6	9.6±0.9	61.0±3.0	0.05±0.02	0.69±0.07	164.3± 8.7
1994	OTC	159.7±0.3	7.0±0.2	51.9±2.2	0.08±0.02	0.86±0.02	207.3± 12.8
1995	Control	161.0±1.3	9.7±1.9	69.0±2.1	0.08±0.01	0.30±0.03	143.9± 12.9
1995	OTC	160.5±1.1	5.8±1.4	72.5±1.3	0.06±0.02	0.79±0.07	202.2± 14.6
1996	Control	152.1±0.9	9.9±0.5	66.1±1.1	0.09±0.01	0.58±0.03	166.6± 29.4
1996	OTC	151.4±0.6	4.4±0.4	64.0± 2.2	0.20±0.04	0.85±0.03	190.7± 12.6
1997	Control	146.2±2.6	6.6±0.7	40.5±0.9	0.30±0.04	0.54±0.04	
1997	OTC	141.6±1.6	5.2±1.4	35.2±2.9	0.04±0.02	1.03±0.04	

¹Tillers monitored at 5–10 day intervals in the summers of 1994–1996; maximum value of the season used.

d. *Polygonum viviparum*

Year	Treatment	Thawing date (day no.)	Prefloration time (d)	Bulbil no.	Bulbil weight (mg)	Shoot height (cm)	Leaf area (cm ²)
1994	Control	133.2±2.0	62.9±2.6	11.9±1.5	0.99±0.14	9.39±0.64	3.65±0.23
1994	OTC	133.6±1.6	57.6±3.6	13.8±1.6	0.99±0.06	10.64±0.29	5.30±0.31
1995	Control	152.5±1.8	52.6±2.7	23.7±2.9	1.14±0.05	11.80±1.03	4.35±0.30
1995	OTC	147.0±4.2	50.0±1.1	30.7±3.0	1.24±0.11	13.00±0.99	6.01±0.83
1996	Control	145.8±4.0	63.5±6.8	24.4±3.8	1.13±0.05	11.07±0.74	4.21±0.30
1996	OTC	144.0±4.1	53.9±7.5	27.2±3.1	1.44±0.14	11.97±0.59	5.51±0.43
1997	Control	133.8±1.6	51.7±3.3	23.4±3.8	1.23±0.13	11.64±0.35	4.40±0.27
1997	OTC	133.8±2.3	54.3±4.4	25.7±4.4	1.28±0.08	12.49±0.42	5.34±0.29

e. *Ranunculus nivalis*¹

Year	Treatment	Thawing date (day no.)	Prefloration time (d)	Postfloration time (d)	Seed : ovule ratio	Nutlet weight (mg)	Basal leaf width (mm)
1993	Control ²	190.6±5.6	6.4±1.9	24.7±2.5	0.27±0.06	0.32±0.04	16.2±0.3
1993	OTC	(190.6±5.6)	5.5±1.6	22.5±1.5	0.31±0.08	0.41±0.07	20.0±1.0
1994	Control	159.2±1.5	14.0±1.4	35.6±2.0	0.14±0.08	0.39±0.05	15.8±0.8
1994	OTC	154.4±3.6	13.8±3.1	40.4±1.3	0.06±0.02	0.49±0.06	21.5±0.9
1995	Control	155.9±0.6	16.1±2.5	47.1±0.6	0.29±0.06	0.38±0.02	16.8±1.1
1995	OTC	153.8±1.7	16.3±3.4	39.4±3.6	0.27±0.02	0.47±0.03	23.2±0.9
1996	Control	154.8±1.3	20.5±3.1	49.0±5.5	0.23±0.08	0.44±0.04	18.0±1.5
1996	OTC	152.0±1.8	15.7±1.7	46.5±2.1	0.27±0.01	0.58±0.03	21.7±0.9
1997	Control	149.6±2.2	13.6±2.0	33.9±1.0	0.43±0.04	0.51±0.01	17.9±1.0
1997	OTC	143.8±5.3	16.3±3.2	32.6±2.4	0.19±0.04	0.55±0.03	23.9±0.8

¹A few figures for 1993–95 are slightly changed since the report in Molau (1997b); this revision is a result of revisitation of rain-damaged or poorly written field protocols. The deviations are minor and do not affect the analysis results.

²Note unusual late thawing in 1993, due to the abnormal winter snow depth (≥ 3 m at the site in March).