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Abstract

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Plants in arctic and alpine environments are mainly limited by abiotic factors such as temperature. Therefore, climate warming is expected to strongly affect plant performance in tundra areas. At a Swiss Alpine location, we investigated *Polygonum viviparum*, a ubiquitous forb of tundra vegetation, under experimentally increased temperature for three years. It was postulated that the reproduction-related characters of *P. viviparum* react to temperature increase according to the previously reported changes along elevational and latitudinal gradients: taller flowering stems with more and larger reproductive organs and a shift from vegetative, i.e. bulbils, to sexual reproductive organs. In addition, vegetative growth was measured as width of the largest leaf. Open top chambers (OTCs) passively elevated mean air temperature by c. 1 °C. While there was a considerable daytime effect of OTCs on air temperature, the mean effect over the entire growing season was reduced due to nighttime cooling inside the chambers. We observed significant treatment effects on some of the measured reproductive variables: plants inside OTCs developed longer flowering stems and increased mean bulbil mass compared with control plants growing at ambient temperature. However, we detected no significant effect of increased temperature on leaf width as the response variable for above-ground vegetative growth. A low number of bulbils in plants under increased temperature in the second year of observation yielded a significantly negative effect of temperature and the interaction temperature × year on this variable. This is interpreted as a carry-over effect due to the developmental preformation of inflorescences, which may blur short-term responses to experimental manipulation. Furthermore, possible allocation to below-ground organs and biotic interactions, such as above-ground competition or reduced photosynthetically active tissue due to

increased herbivore activity inside OTCs, are proposed as explanations for the observed response patterns.

Key words: Alpine, ITEX, *Polygonum viviparum*, reproduction, temperature increase, vegetative growth.

Introduction

Low temperatures and short growing seasons are considered to be among the most prominent limitations for the performance of arctic and alpine plants. Temperature affects biotic processes throughout the growing season. As a consequence, tundra soils characteristically show low nutrient levels because of low microbial decomposition rates (Körner 1989, Bowman et al. 1993, Nadelhoffer et al. 1997). Furthermore, if winter sets in early, the entire reproductive effort of a year may be destroyed (Molau 1993b). According to global change scenarios, climate warming will be pronounced in regions of high elevations and latitudes (Maxwell 1992, Chapin and Körner 1995, Guisan et al. 1995). Increased temperature may both accelerate biotic processes and prolong the growing season in arctic and alpine tundra areas due to the earlier snow melt in spring and the later snow fall in autumn. Because of the generally low temperatures in these regions, even a small increase in temperature may already induce marked responses of plants and microbes.

Several studies on tundra plant responses to temperature increase, using various experimental approaches, have been carried out which indicate that a temperature increase affects plant performance in an individualistic way (Henry and Molau 1997, Arft et al. 1999). Most of these investigations were carried out in the Arctic, whereas only few studies report on such experiments at temperate alpine sites (e.g., Stenström et al. 1997, Suzuki and Kudo 1997, Welker et al. 1997). These studies demonstrate that most tundra plants, whose performance lies below optimum under the current environmental conditions, indeed respond to experimental changes in their environment. Furthermore, it was shown that effects were more pronounced in the high Arctic than at sites of more southerly latitudes (Stenström et al. 1997, Arft et al. 1999).

Polygonum viviparum, a widespread perennial geophyte of tundra areas, mainly reproduces vegetatively with bulbils grown in the lower part of the inflorescences (Peterson 1981). Even though individuals of *P. viviparum* grow smaller with increasing elevation or latitude, the allocation pattern with regard to reproductive, structural, and storage organs remains constant along these natural temperature gradients (Bauert 1994). Within the reproductive organs, however, there is a shift towards a higher ratio of bulbils / flowers with increasing elevation or latitude (Bauert 1994). At an Arctic site (Ny Ålesund, Svalbard), reproductive structures were affected by experimentally increased temperature, leading to more and heavier bulbils, whereas both vegetative growth and reproduction parameters in *P. viviparum* positively responded to experimental nutrient input (Wookey et al. 1994). These authors concluded that the development of reproductive and vegetative structures in *P. viviparum* might show differential sensitivity to a changing environment. Totland and Nyléhn (1998) carried out a temperature manipulation study on *P. viviparum* at a subarctic-alpine site (Finse, Norway). After having grown under an experimentally warmer environment for four years, the harvested plants were heavier and carried heavier bulbils than control plants, but neither bulbil nor flower numbers showed a significant response to temperature increase.

With an experimental increase in temperature during three growing seasons, we examined whether individuals of *P. viviparum* in an Alpine population react according to the changes which are found along elevational and latitudinal gradients (Bauert 1994): (1) Does increased temperature lead to taller flowering stems with more and larger reproductive organs, and (2) is the ratio of investments to sexual vs. vegetative reproduction, i.e. flowers vs. bulbils, higher at increased temperature? Since the measured reproductive variables only showed a subtle positive response to warming during the first experimental season (Gugerli 1996), we hypothesized that enhanced temperature may rather induce a positive effect on the amount of vegetative, photosynthetically active tissues, possibly coupled with a shift in allocation from reproduction to vegetative growth. In the following two seasons, we therefore measured leaf size to investigate (3) whether plants produce larger leaves at increased temperature.

Methods

Species

The perennial, rhizomatous *Polygonum viviparum* L. [= *Bistorta vivipara* (L.) S.F. GRAY] is widespread throughout its arctic-alpine range (Hultén and Fries 1986). It is very common in many different habitat types (Schröter 1926). Flowering stems carry flowers in the upper part and bulbils in the lower part, but individuals may lack either of the two types of reproductive organs. *Polygonum viviparum* mainly regenerates by means of the bulbils (Law et al. 1983). Nevertheless, seeds can occasionally be found both in the Arctic (Söyrinki 1989) and the Alps (Bauert 1994, Gugerli, pers. observation). Though rather infrequent, sexual reproduction leads to considerable genetic variability in arctic and Alpine populations of *P. viviparum* (Bauert 1993, 1996, Diggle et al. 1998). A below-ground corm allows individuals to perennate for at least as long as 26 years (Callaghan and Collins 1981). The summer-green leaves unfold in early summer, usually followed by one single flowering stem per year.

Site

The investigated population of *P. viviparum* was situated in Val Bercla, a north-oriented valley of Southeastern Switzerland (Mulegns, Grisons; 46° 29' N, 9° 35' E; Swiss grid coordinates: 764'800/149'400), on a NNW-facing slope at 2'490 m a.s.l. (cf. Stenström et al. 1997). Bedrock consisted of greenschists, argillacious calcschists, and serpentinite (Dietrich 1969). *Salix retusa* L., *S. herbacea* L., *Silene acaulis* (L.) Jacq., *Saxifraga oppositifolia* L., *S. aizoides* L., *Bartsia alpina* L., *Primula integrifolia* L. em. Gaudin, and *Sesleria caerulea* Kit. dominated the sparse vegetation with a total cover of c. 65 %.

Data collection

We generally followed the standard protocol of the International Tundra Experiment (ITEX; Molau 1993a). ITEX includes the monitoring of vegetative growth, phenology, and reproduction of arctic and alpine plant species under simulated climate change. Hexagonal open top chambers (OTCs) were used to passively increase mean ambient temperature (Marion et al. 1997, Hollister and Webber 2000).

At the time of snow melt in 1994, we selected five pairs of plots. OTCs made of polycarbonate (transparent AXXIS PC; 40 cm high) were randomly assigned to one of the plots per pair, using the other plot per pair as control. Ground surface of the plots

was approximately 1 m². OTCs were removed during winter time so that the date of snow melt was not influenced by the treatment.

Weather and temperature effect: An automatic Squirrel Digital Meter/Logger SQ32 (Grant Instruments) recorded temperature, relative humidity, wind speed, and global radiation 2 m above ground. To quantify the temperature effect of the OTCs, we measured air temperature at 15 cm above ground in two pairs of OTCs and control plots, and soil temperature at 3 cm below ground in one of these plot pairs. Thermistors in the air were protected from direct solar radiation by reflecting foil. Data recording at five-minute intervals lasted from June 7 to September 27 in 1994, from June 18 to September 30 in 1995, and from June 1 to September 30 in 1996. Temperature measurements in experimental and control plots started at the time of snow melt: June 7 (1994), June 30 (1995), and June 1 (1996).

Plant response: We randomly selected four reproducing plants of *P. viviparum* from the central area within each OTC and control plot (total N = 40) in each year. Colors of bulbils, which is a genetically inherited trait (Bauert 1994), differed among plants (Gugerli, pers. observation) and thus guaranteed that the monitored population was not monoclonal. We recorded one vegetative and four reproductive characters of each plant, all of which could be measured non-destructively: leaf width (largest leaf; not recorded in 1994, see Introduction), total length of flowering stem, bulbil number, mean bulbil mass, and flower number per inflorescence. Wookey et al. (1994) showed a strong correlation between leaf width × length and the area of the elliptic leaves in *P. viviparum*. Therefore, we supposed that leaf width could serve as a rough estimator for leaf area. Relative bulbil number was calculated as bulbils/(bulbils + flowers). It is not undisputable where one should draw the line between vegetative growth and vegetative reproduction. But since bulbils are dispersed, we included them in the reproductive organs. We collected bulbils when they were about to fall off the flowering stem, and let them air dry for several weeks. A Mettler H54 AR balance served for determining mean bulbil mass based on eight randomly selected bulbils or, if less were available, all bulbils per plant (accuracy: 0.01 mg). Due to hail, which resulted in the partial loss of bulbils, we determined the bulbil number by counting their bracts and scars on the inflorescences in 1994.

Statistical analysis

We performed mixed-model ANOVAs (according to model 1 in Newman et al. 1997) for each measured character, with blocks (pairs of OTC/control plot) as a random factor, and "temperature" and "year" as fixed factors. Block effects were tested against the three-way interaction term, whereas both fixed factors were tested against their interactions with blocks, respectively. Based on the visual inspection of residuals for normal distribution, we log-transformed leaf width and bulbil mass prior to analysis. All analyses were carried out using the ANOVA procedure of Genstat 5 (Payne et al. 1993).

Results

Weather and temperature effect

Temperature conditions at the study site changed drastically within short time spans (data of 1995 shown as an example in Fig. 1) and strongly differed among years. Late snow melt with temperatures below freezing, coupled with early snow fall (August
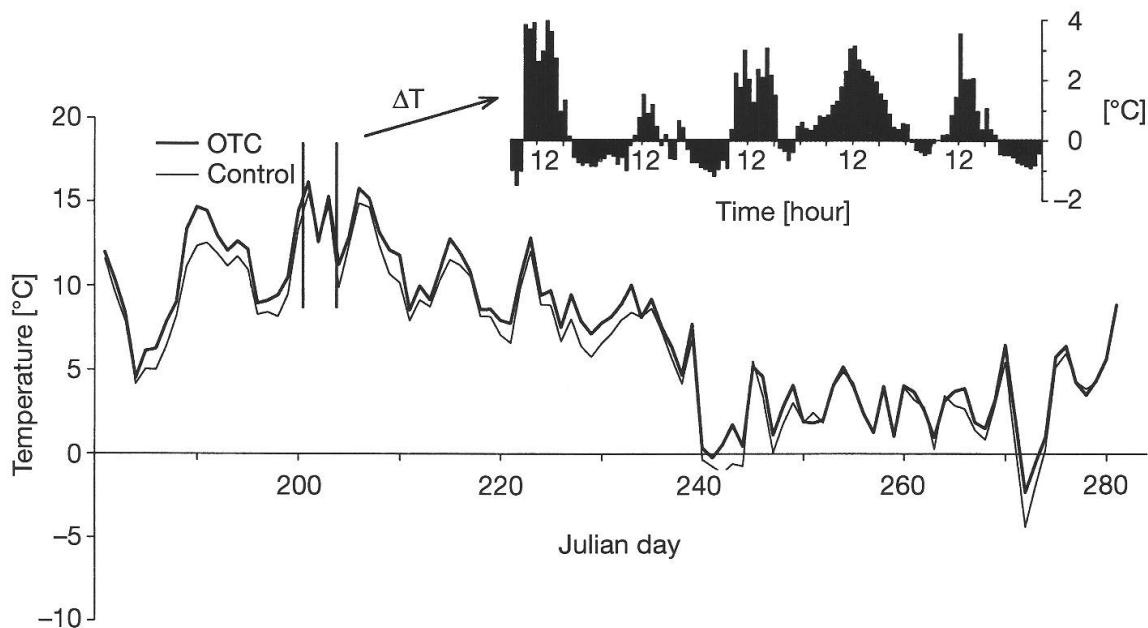
Fig. 1.   Daily mean temperature at the study site in Val Bercla, Switzerland, in 1995 measured in one pair of an open top chamber (OTC) and a control plot (15 cm above ground, starting on day 181 = 30 June). The inserted diagram shows nighttime cooling, illustrated as temperature difference of hourly means between OTC and control plot on a daily basis (days 201–206). Data were calculated from hourly means of five-minute interval recordings.

28), caused a lower mean temperature during the growing season in 1995 than in 1994, despite lost data during a warm July 1994 (Table 1). The third year had an even lower temperature mean over the whole growing season because of a cold period at the end of June and at the beginning of July. Accumulated daily global radiation during the growing season was similar to arctic sites (Molau 1993a). The high elevation and the steeper solar angle at lower latitudes may compensate for the darker nights in central Europe compared to those in the arctic summer.

On average, OTCs increased air temperature means per season by c. 1 °C at 15 cm above ground, and soil temperature was raised by almost 2 °C (Table 1). The daily means of air temperature inside OTCs were mostly above those of control plots (Fig. 1). On a daily basis, however, daytime air temperatures inside OTCs were clearly above those in control plots, whereas a decrease of air temperature was observed at night (Fig. 1, Table 1). Accordingly, hourly maxima were higher and hourly minima were equally low or lower inside OTCs than in control plots, and mean daytime temperatures over the entire growing season showed a higher increase in air and soil temperature inside OTCs than in control plots compared to means over the whole day (Table 1). Mean nighttime air temperatures were lower inside OTCs than in control plots in two of the three years of investigation, while soil temperatures were increased inside OTCs even during nighttime (Table 1). Nighttime temperature decrease thus lowered the effect of the OTCs on season means.

Table 1. Weather data (2 m above ground) and temperature in the air (15 cm above ground; mean of two plots) and in the soil (3 cm; plot 4) inside open top chambers (OTCs) and in control plots at the study site in Val Bercla, Switzerland. Recorded from June 7 to September 27, 1994 (July 15–31 missing due to technical problems), June 18 to September 30, 1995 (OTC/control plot measurements starting June 29), and June 1 to September 30, 1996. Data are based on hourly means from five-minute interval recordings. Day: mean of daytime hourly means (7:30 a.m.–7:30 p.m.) over entire growing season; night: mean of nighttime hourly means (7:30 p.m.–7:30 a.m.) over entire growing season. Accumulated global radiation: values refer to 24 hours.

|	1994					1995					1996				
	Mean	Max	Min	Day	Night	Mean	Max	Min	Day	Night	Mean	Max	Min	Day	Night
Weather data															
Temperature [°C]	6.9	19.8	−7.9	8.6	5.2	5.7	20.2	−7.8	7.3	4.2	4.8	17.7	−6.0	6.5	3.2
Relative humidity [%]	76.3	100.0	21.5			82.9	100.0	17.0			81.2	100.0	19.0		
Wind speed [m/s]	2.3	9.3	0.0			1.7	7.2	0.0			1.8	9.5	0.0		
Accumulated global radiation [MJ/d]	14.7	30.9	1.0			13.0	30.3	2.6			14.5	29.6	2.8		
Temperature effects of OTCs															
Air															
OTC	8.4	36.1	−8.4	13.0	3.9	7.4	32.7	−8.6	11.5	3.3	6.8	31.8	−6.8	11.2	2.3
Control	7.4	27.0	−8.8	10.5	4.5	6.6	29.2	−8.9	9.9	3.4	5.5	25.5	−7.7	8.7	2.2
ΔT	+ 1.0			+ 2.5	− 0.6	+ 0.8			+ 1.6	− 0.1	+ 1.3			+ 2.5	+ 0.1
Soil															
OTC	9.1	29.2	−0.4	11.8	6.5	8.2	24.4	0.4	9.9	6.8	7.8	23.1	0.0	9.6	6.1
Control	7.4	22.8	−0.4	9.7	5.3	6.8	20.9	−0.4	8.3	5.3	5.1	20.3	−0.8	6.6	3.6
ΔT	+ 1.7			+ 2.1	+ 1.2	+ 1.4			+ 1.5	+ 1.5	+ 2.7			+ 3.0	+ 2.5
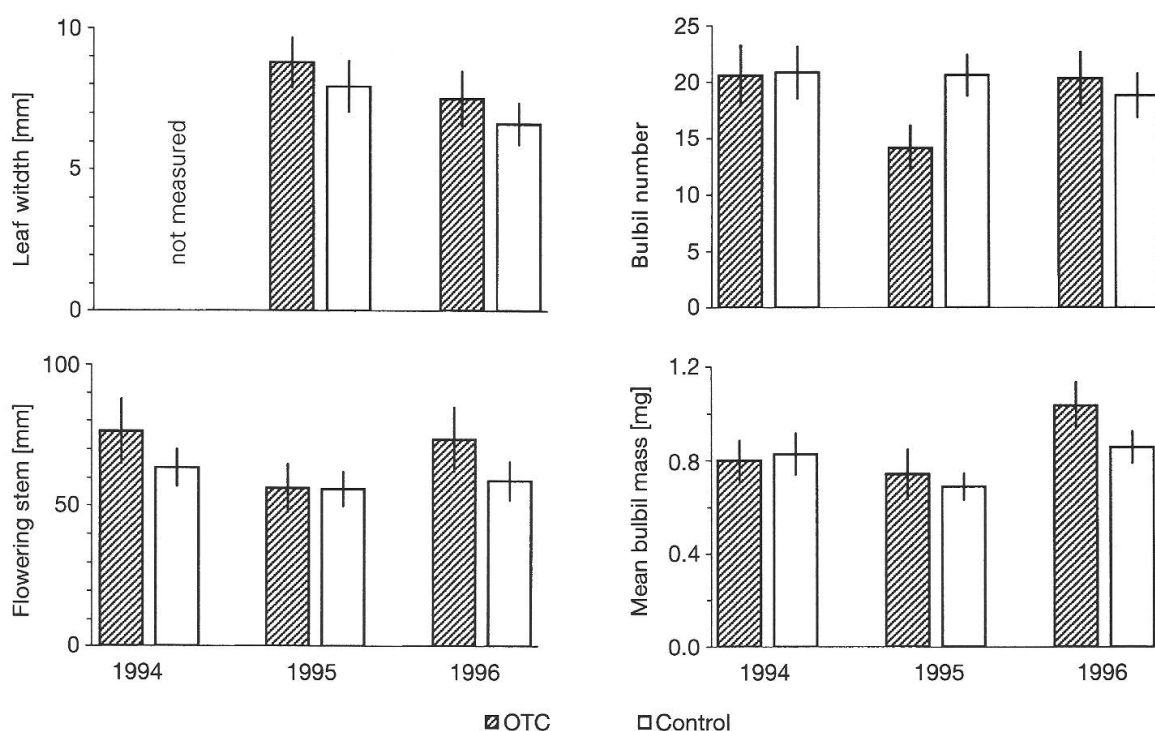
Fig. 2. Means (± SE) of vegetative and reproductive characters of *Polygonum viviparum* in open top chambers (OTCs) and control plots in three consecutive growing seasons (1994–1996; N = 40 with few missing values) at the study site Val Bercla, Switzerland.

Plant response

Experimental warming did not affect leaf width, but had a distinct effect on reproductive features in *Polygonum viviparum* at the study site. In the two years of measurement, leaf width was slightly higher in plants inside OTCs than outside, and it tended to decrease from 1995 to 1996; but neither of the treatment factors (temperature, year) resulted in a significant effect (Fig. 2, Table 2). The length of flowering stems, which were between 25 and 160 mm tall, was increased by 18% in plants inside compared with those outside OTCs (Fig. 2, Table 2). The number of bulbils greatly varied among plants, ranging from 1 to 36 bulbils per plant, and significantly correlated with the length of flowering stem (Pearson's correlation coefficient: $r = 0.463$, $P < 0.001$). Overall, plants inside OTCs had 10 % fewer bulbils than did those in control plots, which was mainly due to a very low number of bulbils in 1995 (Fig. 2, Table 2). However, bulbil number was slightly higher in plants inside OTCs than in control plants in the third year, resulting in a significant interaction of temperature × year (Fig. 2, Table 2). Mean bulbil mass per plant ranged from 0.35 to 1.73 mg, and the mass of individual bulbils ranged from 0.20 to 1.90 mg. Mainly the results of the third year of investigation led to a significantly positive effect of both treatment factors on bulbil mass (Fig. 2, Table 2).

Only few inflorescences bore flowers, and flower numbers were generally low, although there was one inflorescence with 16 flowers. As a consequence, relative bulbil number was 1.0 in most of the plants. Thus, the two variables flower number and relative bulbil number could not be included in the analyses.

Table 2. Responses of vegetative and reproductive characters of *Polygonum viviparum* to increased ambient temperature at the study site Val Bercla, Switzerland: results of mixed-model ANOVAs with "temperature" and "year" as fixed factors, and blocks as a random factor. Only the variation components of the main factors and the interaction term temperature × year (T × Y) are shown. Treatment factors were tested against their interactions with blocks (according to model 1 in Newman et al. 1997), block effects were tested against the three-way interaction (B × T × Y). df = degrees of freedom; MS = mean squares.

Character	Source of variation	df	MS	F-ratio
Leaf width (log-transformed)	Block	4	0.628	7.58*
	Temperature	1	0.248	0.39
	Year	1	0.700	4.06
	T × Y	1	0.003	0.04
Length of flowering stem	Block	4	1464.7	1.27
	Temperature	1	3363.7	17.43*
	Year	2	2259.1	3.45
	T × Y	2	939.1	0.81
Bulbil number	Block	4	45.0	2.86
	Temperature	1	112.8	9.26*
	Year	2	141.3	4.10
	T × Y	2	170.4	10.84**
Bulbil mass (log-transformed)	Block	4	0.053	1.31
	Temperature	1	0.016	8.01*
	Year	2	0.160	7.22*
	T × Y	2	0.023	0.56

*$P < 0.05$; **$P < 0.01$

Discussion

During the three seasons of investigation at a Swiss Alpine site, the reproductive characters of *Polygonum viviparum* showed distinct responses to experimentally increased mean ambient temperature (Fig. 2, Table 2). Manipulation resulted in longer flowering stems of plants inside OTCs compared with control plants. Despite this effect and though the length of flowering stems was significantly correlated with bulbil number, the latter variable showed the opposite effect to experimental warming. This was mainly due to a strongly reduced number of bulbils in treated plants in the second year of investigation. *Polygonum viviparum* is known for its extreme preformation of leaves and inflorescences: primordia need four years from initiation to maturity, which is assumed to delay measurable plant responses to environmental changes by at least one year (Diggle 1997). This could explain the effect of temperature increase on the length of flowering stems as a plastic character that may respond to actual environmental conditions, whereas bulbil number is predetermined and possibly rather mirrors the effects of the weather conditions of preceding years. Treated plants developed considerably heavier bulbils in the third year of the study, giving significant positive effects of the factors temperature and year (Fig. 2, Table 2). The reproductive behavior of treated

plants thus partly reacted to the modified environment as expected from the gradual changes that are found along elevational and latitudinal gradients (Bauert 1994). Since many plants produced no or only few flowers, we could not test our hypothesis on a shift from vegetative to sexual reproduction. Vegetative growth, estimated by the width of the largest leaf, tended to increase under elevated temperature (Fig. 2) and showed a slight decrease from the second to the third year of treatment. Thus, our hypothesis that a weak response of reproductive variables to our treatment might be due to increased vegetative growth could be partly supported with regard to the temperature effect, whereas the trend towards smaller leaves, in both OTCs and control plots, may be a response to natural climatic variation or increased interspecific competition within plots during the time of observation.

Our findings coincide with the positive response of *P. viviparum* to artificial temperature increase in a polar semi-desert on Svalbard (Wookey et al. 1994) and at a subarctic-alpine location in Norway (Totland and Nyléhn 1998). However, our study revealed weaker effects than those found in the Arctic or Subarctic. Several reasons may account for this difference. The temperature increase by 3.5 °C (at 36 cm above ground) in the experiment of Wookey et al. (1994) was markedly higher than that at our Alpine site, where OTCs only increased air temperature by about 1 °C (at 15 cm above ground; Table 1). The closed plastic tents used by Wookey et al. (1994) are generally more efficient in passive heating than are open top chambers (Marion et al. 1997). Nighttime cooling inside OTCs at the Alpine site (Fig. 1), which lowered the daily and seasonal means of temperature increase inside OTCs, additionally reduced the heating effect. This cooling effect is more pronounced at low-latitude sites, such as in the Alps, than at high-latitude sites. The diurnal pattern in temperate regions may cause an altered balance between photosynthesis during the warmer day and dark respiration during the colder night inside the chambers compared with control plots. However, our experimental design is not suitable for revealing specific daytime warming or nighttime cooling effects on plant performance, but merely considers an average temperature increase. Furthermore, mean temperatures during the growing seasons were higher at our Alpine site compared with the Arctic (Wookey et al. 1994), which implies that our population of *P. viviparum* grew under environmental conditions that were above the species' minimum requirements. This may explain the weaker response of plants found in our study than in the experiment carried out in the Arctic. On the other hand, we do not assume that there was a physiological constriction responsible for the limited temperature effect at our alpine study site as compared to the Arctic, because *Polygonum viviparum* occurs over a large elevational gradient and may frequently be found in the montane zone where the plants grow much larger than in alpine areas (Hegi 1981).

Vegetation cover at the investigated Alpine site was higher than that reported for the above mentioned location in the Arctic (Wookey et al. 1993). Vegetation covered less than 20% of the area at the study site on Svalbard compared to about 65% at our Alpine site. The canopy became even denser in some of our experimental plots during the study period, and many plant species grew taller inside OTCs than in control plots (Gugerli, pers. observation). Molau (1997) described a negative impact of shading on *Ranunculus nivalis*, another rhizomatous tundra forb under ITEX treatment, as do Stenström et al. (1997) in the case of the prostrate *Saxifraga oppositifolia*. Since most leaves of *P. viviparum* are close to the ground, above-ground competition might have been a limiting factor for *P. viviparum* at the Alpine site, whereas the high arctic population of *P. viviparum* appears to be more sensitive to temperature changes (cf. Arft et al. 1999).

Allocation to or depletion of below-ground organs and herbivory are factors which also influence the response of experimental plants and could blur observed above-ground changes. Since ITEX observations have to be non-destructive, no information could be gathered on below-ground organs. Invertebrates appeared to prefer the vegetation in sheltered plots. In the second year of investigation, 74% of the marked plants inside OTCs exhibited traces of herbivore activity (larvae of beetles, snails), whereas only 27% of control plants were affected (Gugerli, unpubl. data). The thereby reduced leaf area for photosynthetic activity could lead to an underestimation of a possible positive growth effect of *P. viviparum* plants under elevated temperature.

In a meta-analysis on the reaction of tundra plants to experimentally increased summer temperature, Arft et al. (1999) explored a large data set from 13 arctic and alpine ITEX sites. They show that vegetative growth increased in the early years of treatment, which was mainly due to a strong response of herbaceous species, whereas sexual reproduction only gradually increased in the course of experimentation (Arft et al. 1999). These authors concluded that the differential responses among sites, life forms, and in time are due to the variation of the primary forces, e.g. climate, responsible for these effects across spatial, temporal, and genetic gradients. In the long run, however, changes in nutrient availability through temperature effects on decomposition and mineralization rates may strongly influence the response patterns of individuals, species, and the vegetation as a whole. This became evident in a study of experimental temperature manipulation, where short-term responses after three years proved to be poor indicators of community changes observed after nine years of treatment (Chapin et al. 1995). Only long-term experiments will thus provide the necessary information on community changes resulting from individualistic responses due to climate warming.

Zusammenfassung

Vorkommen und Verhalten von Pflanzen in arktischen und alpinen Gebieten werden hauptsächlich durch abiotische Faktoren, wie zum Beispiel die Temperatur, limitiert. Es ist deshalb zu erwarten, dass eine globale Klimaänderung das Wachstum von Tundrapflanzen beeinflussen wird. An einem Schweizer Standort haben wir während drei Jahren *Polygonum viviparum*, eine in der Tundravegetation weit verbreitete und häufig vorkommende krautige Art, unter experimentell erhöhter Temperatur untersucht. Es wurde postuliert, dass fortpflanzungsbezogene Merkmale bei *P. viviparum* gleich auf die Temperaturerhöhung reagieren würden, wie sie sich den sich verändernden Umweltbedingungen entlang von Höhen- und Breitengradienten ändern: längere Blütenstandstriebe mit mehr und grösseren reproduktiven Organen sowie eine Verlagerung von der Bildung von vegetativen, d.h. Bulbillen, zu sexuellen Fortpflanzungsorganen. Zusätzlich wurde vegetatives Wachstum, ausgedrückt als Breite des grössten Blattes, erfasst. Oben offene Klimakammern (OTCs) erhöhten die mittlere Lufttemperatur um ca. 1 °C. Während die mittlere Lufttemperatur in den Kammern tagsüber deutlich höher war als in der Umgebung, wurde der Effekt über die gesamte Wachstumsperiode reduziert durch die in den Kammern erfolgte erhöhte Auskühlung während der Nacht. Bei einem Teil der gemessenen reproduktiven Variablen stellten wir

signifikante Behandlungseffekte fest: Pflanzen in den OTCs entwickelten längere Blütenstandstriebe und ein erhöhtes Bulbillengewicht im Vergleich mit frei wachsenden Kontrollpflanzen. Wir konnten jedoch keinen signifikanten Effekt der erhöhten Umgebungstemperatur auf die Blattbreite als Zielvariable für oberirdisches vegetatives Wachstum feststellen. Die im zweiten Untersuchungsjahr gefundene geringe Anzahl Bulbillen auf behandelten Pflanzen führte zu einem signifikant negativen Effekt auf diese Variable bezüglich der Temperatur, und auch die Interaktion von Temperatur × Jahr war signifikant. Dies wird als "carry-over"-Effekt interpretiert, welcher als Folge von bereits in Vorjahren entwickelter Blütenstandsanlagen entsteht und dadurch eine mögliche kurzfristige Reaktion auf experimentelle Behandlung verschleiern kann. Zusätzlich werden Allokation in unterirdische Organe sowie biotische Interaktionen, z.B. oberirdische Konkurrenz oder reduziertes photosynthetisch aktives Gewebe wegen erhöhter Aktivität von Herbivoren innerhalb der Kammern, als mögliche Erklärungen für die beobachteten Reaktionsmuster erläutert.

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