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Winners and Losers of Climate Change in a Central Alpine Glacier Foreland

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Abstract

The effects of microclimate change on the growth of fast- and slow-growing glacier foreland species were analyzed from 1996 to 2004 to test the following hypotheses: (1) plant growth and cover will increase due to experimental warming; (2) fast-growing species will respond the most; and (3) asexually and sexually reproducing forms of *Poa alpina* react differently—the asexually produced plantlets will respond the most due to their growth advantages in contrast to seedlings. Temperatures were increased with open top chambers (OTCs) by 1 ± 0.01 °C (soil surface) and 0.7 ± 0.03 °C (soil) during the growing seasons using a modified ITEX approach. Juvenile plants of *Artemisia genipi* (pioneer species), *Trifolium pallescens* (mid-successional species), *Anthyllis vulneraria* ssp. *alpestris* (late-successional species), *Poa alpina*, and *Poa alpina* ssp. *vivipara* (ubiquitous species) were planted into plots with OTCs and adjacent control plots and harvested after three, four, and five years, respectively. The *Artemisia* and *Poa* (R- and S-selected species) showed little response to changes in microclimate, whereas *Trifolium* and *Anthyllis* (plastic species, CSR/CS strategists) had significantly higher dry weights and enhanced reproduction.

Introduction

According to the IPCC (2001) scenario, global air temperatures are expected to increase by 1.4–5.8 K by 2100. On a regional scale, i.e. at the timberline ecotone of the Central Alps, a temperature increase of 1–2 °C during the last 100 years (Beniston, 1997; Beniston et al., 1997; Kuhn, 2005) and of 1 °C during the last 40 years (Wieser, 2002), respectively, has already been documented. Climate change has several implications for individual species' growth (Henry and Molau, 1997; Epstein et al., 2004) and ecosystem function in the Arctic and in alpine environments (Chapin et al., 1992; Körner, 1992; Chapin and Körner, 1995; Grabherr et al., 1994). At the species level, vegetative and reproductive growth processes will be affected. Snow melt will occur earlier in spring (Beniston, 1997; Henry and Molau, 1997), hence, the length of the growing season will be longer (Molau, 1996, 1997a; Kudo et al., 1999). At the ecosystem level vegetation zones may shift (Ozenda and Borel, 1995; Körner and Walther, 2001; Walther et al., 2002; Walther, 2003) and significant effects on diversity are suggested (Sala et al., 2000; Bakkenes et al., 2002). Species upward migration tendencies in the Alps are already observed (Gottfried et al., 1994, 1999; Grabherr et al., 1994, 2001; Pauli et al., 1996).

In alpine environments, glacial retreat is one of the most visible signals of warming (Haeberli, 1995). The colonization of newly exposed substrate in glacier forelands provides an opportunity to examine the influence of climate change on succession (Chapin et al., 1994; Matthews, 1992; Kaufmann, 2002), migration processes (Matthews, 1992), population, and community development (Erschbamer, 2001; Kaufmann, 2001; Kaufmann et al., 2002; Raffl and Erschbamer, 2004; Raffl et al., 2006). Plant species colonizing glacial forelands during different successional stages generally differ in functional traits (Caccianiga et al., 2006), and thus, they may differ also in their response to climate change (Chapin et al., 1997). Understanding the differential responses of the major functional plant types to climate change is essential to predict ecosystem development and future pathways of primary succession in the glacier foreland.

The aim of the present study was to examine the effects of warming on plant species inhabiting an alpine glacier foreland. A modified ITEX (International Tundra Experiment; Henry and Molau, 1997; Arft et al., 1999) approach was used. Seedlings of four selected species were planted into open top chambers (OTCs) and control plots (CTRLs) and harvested after three, four, and five years, respectively. The experiment was performed on recently exposed glacier foreland moraines. The questions addressed were: Will climate change affect all relevant successional groups equally? Which ecological strategies (fast- vs. slow-growing plants) are favored most? Three specific hypotheses were investigated: (1) species will exhibit significant vegetative and generative growth increase in response to warming; (2) fast-growing species will respond more to experimental warming than slow-growing species; and (3) asexually and sexually reproducing forms of *Poa alpina* react differently—the asexually produced plantlets are expected to have higher responses due to their growth advantages in contrast to seedlings.

Study Area, Material, and Methods

STUDY AREA

The Rotmoosferner glacier foreland (Obergurgl, Ötztal, Tyrol, Austria, 46°49′N, 11°02′E) was selected as the study site. The geological substrate belongs to the Ötztal-Stubai complex (Hoinkes and Thöni, 1993). Quartzofeldspathic and metapelitic strata intercalated by orthogneisses prevail. At the glacier foreland valley bottom, veins of metapelites, metacarbonates, metamarls, and amphibolites occur (Frank et al., 1987).

Vegetation mapping was carried out by Jochimsen (1970) and Rudolph (1991). The 1858 glacier stage can be easily recognized by the well-visible terminal moraine at 2300 a.s.l. On this moraine, an initial grassland with late successional species such as *Kobresia*

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TABLE 1

Species selected for the modified ITEX experiment in open top chambers and control plots on the Rotmoos glacier foreland (Obergurgl, Tyrol, Austria, 2400 m a.s.l.). The columns report the role of the species in the primary succession, the transplanted unit per species, the number of replicated blocks (= pairs of open chamber and control plot), the year of transplantation, and the year of harvest.

Species	Successional stage	Transplanted unit	No. of blocks	Year of transplantation	Year of harvest
Artemisia genipi	pioneer	juveniles	4	2001	2004
Trifolium pallescens	mid succession	juveniles	5	1996	2000
Anthyllis vulneraria ssp. *alpestris*	late succession	juveniles	4	2001	2004
Viviparous *Poa alpina*	ubiquitous	viviparous units	4	1998	2000
Seminiferous *Poa alpina*	ubiquitous	juveniles	3	2002	2004

myosuroides, *Agrostis alpina*, *Anthyllis vulneraria* ssp. *alpestris*, and *Poa alpina* is found (Raffl and Erschbamer, 2004). The 1923 moraine is mainly occupied by mid-successional species such as *Trifolium pallescens*, *Erigeron uniflorus*, *Salix* sp., and *Poa alpina.* A few *Anthyllis* individuals can already be observed there. The 1971 moraine at 2400 m a.s.l. shows a pioneer community of *Saxifraga aizoides*, *S. oppositifolia*, *Artemisia genipi*, and *Linaria alpina.* Also, *Poa alpina* and *Trifolium pallescens* individuals are already established, but no late successional species occur, and the vegetation cover remains rather sparse (17%; Mallaun, 2001). On the whole glacier foreland, *Poa alpina* occurs almost only in its viviparous form.

The soil development is rather poor, starting with a Syrozem on the youngest moraines. The first visible sign of soil development, i.e. an A horizon formation, was detected on the 1923 lateral moraine (Erschbamer et al., 1999). On the 1858 lateral and ground moraines, a differentiation between a brown-black A_{h1} and a dark brown A_{h2} was observed, although the soil profile exhibited only 4 cm depth (Erschbamer et al., 1999). No old soils are present in the investigated glacier foreland. For additional site descriptions see Erschbamer et al. (1999), Raffl and Erschbamer (2004), and Raffl et al. (2006).

MATERIAL

The investigated species are shown in Table 1 (nomenclature of the species from Flora Europaea, Royal Botanic Garden Edinburgh, http://193.62.154.38/FE/fe.html). They represent the main successional plant groups of the glacier foreland. *Artemisia genipi* and *Trifolium pallescens* are slow-growing, *Anthyllis vulneraria* ssp. *alpestris* and *Poa alpina* are fast-growing species (Niederfriniger Schlag, 2001).

Artemisia genipi Weber (Compositae) is an endemic perennial species from the alpine to the subnival belt of the Alps. It occurs on siliceous and rarely on calcareous scree sites, on glacier moraines, and in rock crevices. The species exhibited 65 to 99 seeds per shoot (Silvia Marcante, unpublished), low seed weights (0.21 mg; Schwienbacher and Erschbamer, 2002), and high germination rates under favorable conditions in the growth chamber (98.8 ± 4.0%; Schwienbacher and Erschbamer, 2002). According to these traits, *Artemisia* can be classified as ruderal strategist, although it was not among the glacier foreland species studied by Caccianiga et al. (2006). The total biomass per plant amounted to 144.3 ± 23.4 mg after 100 days in the growth chamber (Niederfriniger Schlag, 2001). In the Rotmoosferner glacier foreland, *Artemisia genipi* occurs only on the youngest moraines, rarely on recently eroded or disturbed areas of the older moraines. It may be characterized as a typical pioneer species (Schwienbacher, 2004).

Trifolium pallescens Schreb. (Leguminosae) is a perennial alpine and subnival species in Central and Southern European mountains. It occurs on scree sites, glacier moraines, alluvial areas, and open grasslands in the siliceous mountains. The species has up to 45 seeds per shoot (Kneringer, 1998), a relatively low seed weight (0.57 mg; Schwienbacher and Erschbamer, 2002), low germination rates without scarification (10.8 ± 2.5%), and high germination rates after scarification (92.0 ± 1.2%; Schwienbacher and Erschbamer, 2002). According to Caccianiga et al. (2006), it was defined as a CSR strategist. The total biomass per plant was 134.2 ± 67.3 mg after 100 days in the growth chamber (Niederfriniger Schlag, 2001). *Trifolium pallescens* is a typical mid-successional species with highest dominance on 40- to 50-year-old moraines (Mallaun, 2001).

Anthyllis vulneraria L. ssp. *alpestris* (Hegetschw.) Asch. & Graebn. (Leguminosae) is distributed in the subalpine and alpine belt of the Central and Southern European mountains, on calcareous scree or in stony grasslands and pastures. In the study area it dominates in the initial grasslands of the oldest moraine (Raffl et al., 2006) and spreads continuously toward the younger terrain. Presently, it has already reached the 1923 moraine; however, it is completely absent from the youngest moraines. The species exhibits about 15 seeds per shoot (Kneringer, 1998) which are quite heavy (3.75 mg; Schwienbacher and Erschbamer, 2002), the germination rate being low without scarification (22.0 ± 2.4%) and high with scarification (80.0 ± 6.3%; Schwienbacher and Erschbamer, 2002). *Anthyllis vulneraria* was classified as a CSR type (Grime, 1979); however, the alpine subspecies *alpestris* may rather be a CS strategist according to its dominance on the oldest moraine, the relatively large leaves and plant cover compared to other species on this site, and the high recruitment rate in the field (Silvia Marcante, unpublished data). The total biomass amounted to 160.5 ± 29.4 mg in the growth chamber (Niederfriniger Schlag, 2001).

Poa alpina L. (Poaceae) is an arctic-alpine grass with a circumpolar distribution. It is common in the subalpine and alpine belt of the Alps, mainly on nutrient- and base-rich soils, on resting places of wild or domestic animals, and also on pioneer sites and in gaps of alpine grasslands. The reproduction of *Poa alpina* is rather complex including allogamy, autogamy, and agamospermy (Bachmann, 1980, *in* Wilhalm, 1996). The species may reproduce also asexually by specialized vegetative propagules. These so-called "prolificated spikelets" or "leafy plantlets" (Pierce et al., 2000, 2003) dehisce from the mother plant and establish quickly during the short growing season in high altitudes (Pierce et al., 2000). The viviparous form, *Poa alpina* L. ssp. *vivipara* (L.) Arcang., is rather common along the whole chronosequence of the Rotmoosferner glacier foreland. Plantlets were regularly observed from the end of July onward. However, seminiferous *Poa alpina* plants and seeds in the seed bank were also present, mainly on the

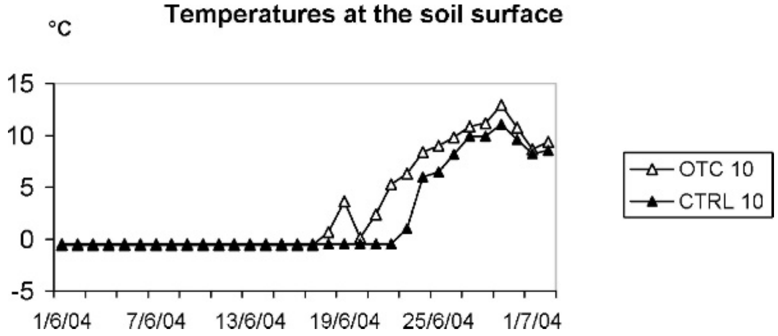

FIGURE 1. Mean temperature at the soil surface of block 10 in June 2004 showing the different melting time (i.e. temperature above 0 °C) in the open top chamber OTC 10 (melting date = 18 June 2004) compared to the control plot CTRL 10 (melting date = 23 June 2004) on the Rotmoos glacier foreland (Obergurgl, Tyrol, Austria, 2400 m a.s.l.).

oldest moraines of the glacier foreland (Silvia Marcante, unpublished). In the literature it was generally assumed that the species can switch from sexual to asexual reproduction and *vice versa* (Wilhalm, 1996). Experiments have shown that the viviparous forms remain viviparous also under favorable lowland conditions in the Botanical Garden in Innsbruck and that sexually produced plants remain sexually in the lowland as well as at the typical glacier foreland site (Brigitta Erschbamer and Ruth Niederfriniger Schlag, unpublished). Thus, in this study the seminiferous *Poa alpina* and the viviparous *Poa alpina* ssp. *vivipara* were treated as two distinct species. The seminiferous *Poa alpina* produces between 19 and 46 seeds per shoot with mean seed weights of 0.41 mg (Silvia Marcante, unpublished), the germination rate was 78%, and the total biomass 445.2 ± 55.4 mg after 100 days in the growth chamber (Niederfriniger Schlag, 2001). Compared to other target species of the glacier foreland, *Poa alpina* exhibited the highest growth rate (Niederfriniger Schlag, 2001).

METHODS

In 1996, 10 tetragonal open top chambers constructed according to the guidelines of ITEX (Molau and Mølgaard, 1993) were established together with adjacent control plots (CTRLs), forming a total of 10 blocks on the 1971 moraine. In 1998, two other OTCs and two CTRLs were added. The research area had to be protected against horse and sheep grazing by electric fences. The dimensions of the OTCs were: 30 cm height, lower diameter 84.6 cm, upper diameter 50 cm. The OTCs remained in the field site year-round. Temperatures were measured using dataloggers (Optic StowAway Temp, StowAway TidbiT, Onset Computer Corporation, Pocasset, Massachusetts) at the soil surface and in 3 cm soil depth in the OTCs and in the CTRLs. Up to five blocks were furnished with dataloggers. Snow melting date was deduced from daily soil surface temperatures rising above 0 °C. The start and the end of the growing season were indicated by daily mean temperatures being above 0 °C. During the growing season differences in volumetric water content of the soil were measured in two OTCs and two CTRLs using CYCLOBIOS sensors (R. Kaufmann, Institute of Ecology, University of Innsbruck).

One hundred juvenile plants of *Trifolium pallescens* (i.e. seedlings with two or three leaves) were collected on an older, 48-year ice-free moraine and immediately transplanted into five OTCs and five CTRLs, 10 individuals each. Viviparous plantlets of *Poa alpina* and seeds of *Anthyllis*, *Artemisia*, and *Poa* were collected in the glacier foreland and propagated/germinated during winter-/springtime in a growth chamber and later in a greenhouse at the Innsbruck Botanical Garden. For acclimatization the young plants were transported to Obergurgl (1930 m a.s.l.) at the beginning of July and then transplanted to the field site at the end of July of the respective year (Table 1). Ten individuals per species were planted in the OTCs and CTRLs, respectively.

Vegetative and generative shoot numbers were counted every growing season. After harvest, the individuals were washed, divided into vegetative and generative above- and below-ground parts, dried at 80 °C for 48 hours, and weighed.

STATISTICAL ANALYSES

Data analyses were performed using the SPSS 11.0 programs. Multivariate ANOVAs with randomized complete block design (Sokal and Rohlf, 1987) were performed for temperature as well as for species data with "treatment" and "year" as fixed factors and "blocks" (= pairs of OTC/CTRL) as random factor. The temperature data was log10-transformed. Univariate ANOVAs were performed to compare treatment effects on vegetative and flowering shoot numbers.

Results

MICROCLIMATE

Mean daily soil surface temperature was slightly below 0 °C in winter. The snow melting date was easily observable from the soil surface temperature curve (Fig. 1). In most CTRLs snow and ice cover stayed several days longer in spring compared to the OTCs. A considerable heterogeneity was observed between the blocks, and no significant extension of the growing season could be shown in the OTCs.

During the growing season mean soil surface temperatures were constantly 1 ± 0.01 °C higher ($P < 0.0001$; Fig. 2), maxima were 1.88 °C higher ($P = 0.005$), and minima 0.65 °C higher in the OTCs ($P = 0.006$). Considerable differences were observed between the years ($P < 0.001$). No block effects were detected ($P = 0.079$). The mean soil temperature was 0.71 ± 0.03 °C higher in the OTCs ($P = 0.069$) than in the CTRLs. Volumetric soil water content was slightly higher in the OTCs with exception of 1997 (see figure in Erschbamer, 2001), though no significant differences resulted.

EFFECTS ON PLANT GROWTH

More leaves and shoots, respectively, were produced by *Artemisia*, *Trifolium*, and *Anthyllis* within the OTCs in contrast to the CTRLs (Table 2), although the effects were significant only for *Trifolium.* Dry weight was clearly enhanced in OTC plants of *Trifolium* and *Anthyllis* (Fig. 3). The viviparous *Poa* was negatively affected in the OTCs with a significantly lower shoot number and lower dry weights (Table 2, Fig. 3). For the

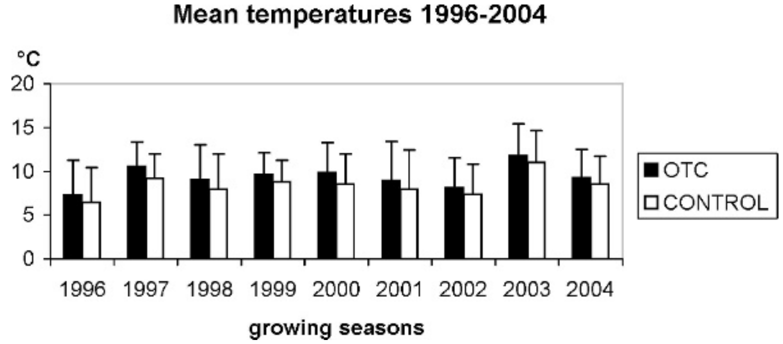

FIGURE 2. Mean soil surface temperatures (°C) in the open top chambers (OTC) and in the control plots (CTRL) during the growing seasons 1996–2004 on the Rotmoos glacier foreland (Obergurgl, Tyrol, Austria, 2400 m a.s.l.).

seminiferous *Poa*, no significant effects were detected, neither on the number of shoots (Table 2) nor on dry weight (Fig. 3).

The total amount of flowering shoots was significantly enhanced for *Trifolium* and *Anthyllis* within the OTCs (Table 3). The increase of flowering shoots observed for *Anthyllis* from 2002 to 2004 shows progressive development from the first flowering (1.5-year-old plants) to adult plants (3.5-year-old plants). The viviparous *Poa* had higher numbers of flowering shoots in the CTRLs, although the differences were not significant. No flowering differences were detected for the seminiferous *Poa.* The individuals of *Artemisia* were still not flowering.

Discussion

The individualistic nature of species responses to environmental warming (Chapin and Shaver, 1985; Press et al., 1998; Dormann and Woodin, 2002; Dormann et al., 2004) was confirmed by the present study. The pioneer species *Artemisia genipi* and the seminiferous *Poa* were quite unaffected by warming, the two legumes *Trifolium* and *Anthyllis* enhanced their growth and reproduction, and the viviparous *Poa* was negatively affected.

Comparably to *Artemisia*, the very first glacier foreland colonizer, *Saxifraga aizoides* (Erschbamer et al., 1999), did not show any response (Marcante et al., 2007). *Saxifraga* was classified as a ruderal strategist by Caccianiga et al. (2006) and the same may apply to *Artemisia.* It seems that these alpine ruderal strategists are not able to adapt to climate warming. Sørensen (1941, *in* Henry and Molau, 1997) defined periodic and aperiodic species for Greenland, the periodic being constrained by genetic traits, the aperiodic profiting from an extension of the growing season. A more appropriate terminology for species reactions to environmental change may be suggested here: "inflexible" vs. "plastic." Thus, *Artemisia* is a rather inflexible type comparable to those arctic-alpine species lacking plasticity during experimental warming (Jones et al., 1997; Stenström et al., 1997; Suzuki and Kudo, 1997; Gugerli, 1998; Starr et al., 2000).

Positive growth responses were recorded for *Trifolium* and *Anthyllis.* This is corresponding to the ITEX program results (Arft et al., 1999, Walker et al., 1999) and the Van Wijk et al. (2003) meta-analysis showing a clear trend of biomass increases for vascular plants. The two legumes are plastic species with high growth increases under changed microclimate, similar to some tundra forbs (Chapin et al., 1995; Henry and Molau, 1997). Both are nitrogen-fixing species. This functional group plays an essential role in the early successional stages of glacier forelands because of their rapid growth rates, though they are not first colonizers (Chapin et al., 1994; Matthews, 1992). Moreover, they initiate biological mineral cycling (Matthews, 1992), enhance above-ground production (Thomas and Bowmann, 1998), and facilitate establishment of late successional species (Chapin et al., 1994). Tscherko et al. (2003) demonstrated the increasing enzyme activity and functional diversity in the soil up to a moraine age of 50 years, where *Trifolium pallescens* reaches the highest abundance (Erschbamer et al., 1999; Raffl et al., 2006). In the experiment presented here the samples of both the legumes were visibly nodulated. Higher temperatures might have increased nodule activity. In this case enhanced growth of the legumes has to be interpreted as an indirect warming effect. The results suggest that *Trifolium pallescens*, the early successional species, and *Anthyllis alpestris*, the late successional species, are clear winners of climate change in the glacier foreland. Under climate warming, they will gain competitive advantage over non nitrogen-fixing species. Similar hypotheses were drawn for legumes under elevated CO_2 (Warwick et al., 1998).

Flowering of the legumes seemed to depend on the individual's age: *Trifolium* started only in the fourth year after transplantation, *Anthyllis* already in the second year. Kuen and Erschbamer (2002) showed clearly that reproduction of *Trifolium pallescens* growing in the glacier foreland is size- and not age-dependent. The *Anthyllis* individuals of the experiment had already a larger size at transplantation and thus flowering occurred much earlier compared to the *Trifolium* individuals transplanted as tiny juveniles. The size of the *Artemisia* was obviously too small for reproduction.

Positive effects on phenology and/or on reproductive output under enhanced temperatures have been confirmed repeatedly, i.e. for *Dryas octopetala* (Wookey et al., 1993; Welker et al., 1997), *Polygonum viviparum* (Wookey et al., 1994), *Vaccinium uliginosum* and *Ledum palustre* (Suzuki and Kudo, 1997), *Eriophorum vaginatum* (Molau and Shaver, 1997), *Cassiope tetragona* and *Ranunculus nivalis* (Molau, 1997b), *Silene acaulis* (Alatalo and Totland, 1997), *Papaver radicatum* (Mølgaard and Christensen, 1997), *Carex bigelowii* (Stenström and Jónsdóttir, 1997), *Ranunculus acris* (Totland, 1999), *Saxifraga stellaris* (Sandvik and

TABLE 2

Number of shoots or number of leaves (*) per individual at the end of the experiment in the open top chambers (OTCs) and in the control plots (CTRLs) of the Rotmoos glacier foreland (Obergurgl, Tyrol, Austria, 2400 m a.s.l.). The results of the univariate ANOVA *(P)* are given: bold numbers show significant differences.

	Shoots or leaves (*) per individual		
	OTCs	CTRLs	*P*
Artemisia genipi	2.600	2.375	0.846
*Trifolium pallescens**	6.082	3.901	**0.001**
Anthyllis alpestris	21.711	19.357	0.415
Viviparous *Poa alpine*	1.889	2.923	**0.006**
Seminiferous *Poa alpina*	4.536	4.966	0.241

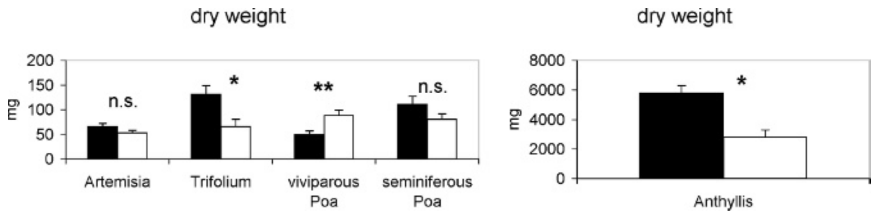

FIGURE 3. Total dry weight (mg) per individual in the open top chambers (black bars) and in the control plots (white bars) and results of the multivariate ANOVA (P = 0.01, *P = 0.05, n.s. = not significant). Block effects were detected only for viviparous *Poa*, P = 0.05.**

Totland, 2000), and *Rubus chamaemorus* under spring warming experiments (Aerts et al., 2004; whereas under summer warming this species produced less flowers). These studies and partly the results of the present investigation (*Trifolium*, *Anthyllis*) show that reproduction of most arctic/alpine species is temperature-limited (Henry and Molau, 1997).

The negative reaction of the viviparous *Poa alpina* was unexpected. However, already Woodward et al. (1986) reported that leaf extension of *Poa alpina* ssp. *vivipara* was insensitive to temperature variations, whereas the seminiferous *Poa alpina* exhibited enhanced extension rates. Differences between the two reproductive forms of *Poa alpina* were also shown in the study presented here.

According to the high growth potential of *Poa alpina*, growth stimulations due to warming were expected. The negative response of the viviparous *Poa* and the weak, not significant growth increase of the seminiferous *Poa* are not in line with the initial hypothesis. A shift from viviparous propagation to seed production may be therefore assumed. Gugerli and Bauert (2001) detected a lower number of bulbils under increased temperatures for the viviparous *Polygonum viviparum*, and they therefore suggested a transition from bulbils to sexual reproduction.

It has also to be considered that *Poa* may be nutrient- rather than temperature-limited, as was found for several arctic species (see review *in* Dormann et al., 2004). *Poa alpina* showed a massive response to fertilizer treatments in glacier forelands already after two years (Körner, 1999); however, the species was not affected by CO_2 enrichment (Körner et al., 1996, 1997; Schäppi and Körner, 1996; Baxter and Farrar, 1999; Pierce et al., 2003). For *Poa alpina* ssp. *vivipara* in both the vegetative and the reproductive stage, long-term exposure to elevated CO_2 was proved to be a disadvantage (Pierce et al., 2003). A lack of reasonable explanations has to be admitted and probably for alpine species unknown stoichiometric constraints (Körner et al., 2005) have also to be considered.

TABLE 3

Number of flowering shoots per individual in the open top chambers (OTCs) and in the control plots (CTRLs) for *Trifolium*, the viviparous *Poa*, and the seminiferous *Poa* at the end of the experiment and for *Anthyllis* in the years 2002–2004. The results of the univariate ANOVA *(P)* are given: bold numbers show significant differences.

	Number of flowering shoots per individual		
Species	OTCs	CTRLs	*P*
Trifolium pallescens	0.800	0.238	**0.019**
Anthyllis alpestris 2002	3.579	1.800	**0.049**
Anthyllis alpestris 2003	4.868	1.900	**<0.0001**
Anthyllis alpestris 2004	25.316	14.214	**0.002**
Viviparous *Poa alpina*	1.000	1.235	0.334
Semniferous *Poa alpina*	0.250	0.103	0.375

CONSEQUENCES OF WARMING FOR ALPINE PRIMARY SUCCESSIONS

Legumes (CSR/CS species) are assumed to be the winners of climate change in alpine environments, whereas R- (*Artemisia*) and S-selected species (*Poa*) seem to be unaffected or even negatively affected. Among the losers, also more prominent pioneer species such as *Saxifraga aizoides* (Marcante et al., 2007) and *Saxifraga oppositifolia* (Stenström et al., 1997) have to be mentioned. Due to the accelerated growth and reproductive output of relatively competitive, plastic species such as the investigated legumes, it may be predicted that the successional replacement speed will be enhanced. Species with inflexible growth strategies such as the pioneers may suffer from enhanced competition. Under continuous warming the pioneers and the non-legumes may be replaced by fast-growing legumes (*Trifolium*, *Anthyllis*) much faster than happens presently. These plastic species are expected to have a larger and more stable seed production (Marcante et al., 2007) and subsequently a more efficient population development. The only critical point in this scenario could be the seed size. Large seeds such as those of *Anthyllis* are dispersal-limited; thus, the species cannot fully profit by growth dynamic accelerations.

The actual occurrence of *Poa alpina* ssp. *vivipara* in the whole glacier foreland could be brought to a halt (Erschbamer, 2001) or the viviparous form could shift to the seed-producing form due to warming effects. In general, *Poa alpina* could probably only profit if nitrogen deposition increases substantially. Berendse and Jonasson (1992) and Rustad et al. (2001) suggested increases of nutrient supply and nitrogen availability due to global change. However, these effects could even be higher for *Trifolium pallescens*, which was able to multiply growth 50-fold in a fertilizing experiment at a field site under ambient temperature conditions (Niederfriniger Schlag, 2001). Thus, the speed of successional replacement by *Trifolium* may increase linearly due to warming and contemporaneous nitrogen deposition.

One of the important issues for the future will be the investigation of competitive interactions under changed microclimate conditions in order to elucidate the successional pathways and their changes in the glacier foreland.

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