Oecologia (2014) 174:1425–1435
DOI 10.1007/s00442-013-2839-9

GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Transplantation of subalpine wood-pasture turfs along a natural climatic gradient reveals lower resistance of unwooded pastures to climate change compared to wooded ones

Konstantin Gavazov · Thomas Spiegelberger · Alexandre Buttler

Received: 30 April 2013 / Accepted: 11 November 2013 / Published online: 4 December 2013

Abstract Climate change could impact strongly on cold-adapted mountain ecosystems, but little is known about its interaction with traditional land-use practices. We used an altitudinal gradient to simulate a year-round warmer and drier climate for semi-natural subalpine grasslands across a landscape of contrasting land-use management. Turf mesocosms from three pasture-woodland land-use types—unwooded pasture, sparsely wooded pasture, and densely wooded pasture—spanning a gradient from high to low management intensity were transplanted downslope to test their resistance to two intensities of climate change. We found strong overall effects of intensive (+4 K) experimental climate change (i.e., warming and reduced precipitation) on plant community structure and function, while moderate (+2 K) climate change did not substantially affect the studied land-use types, thus indicating an ecosystem response threshold to moderate climate perturbation. The individual land-use types were affected differently under the +4 K scenario, with a 60 % decrease in aboveground biomass (AGB) in unwooded pasture turfs, a 40 % decrease in sparsely wooded pasture turfs, and none in densely wooded ones. Similarly, unwooded pasture turfs experienced a 30 % loss of species, advanced (by 30 days) phenological development, and a mid-season senescence due to drought stress, while no such effects were recorded for the other land-use types. The observed contrasting effects of climate change across the pasture-woodland landscape have important implications for future decades. The reduced impact of climate change on wooded pastures as compared to unwooded ones should promote the sustainable land use of wooded pastures by maintaining low management intensity and a sparse forest canopy, which buffer the immediate impacts of climate change on herbaceous vegetation.

Keywords Climate change · Land use · ^{13}C · NDVI · Plant species richness · Plant growth form · Transplantation · Gradient · Mesocosm

Introduction

There is a rising awareness of climate change (Solomon et al. 2007) and ecological responses to it (Root et al. 2003; Walther et al. 2002). Recent studies of the impact of climate have reported plant community shifts in cold biomes due to current global warming (Elmendorf et al. 2012b)

Communicated by Jeremy Lichstein.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-013-2839-9) contains supplementary material, which is available to authorized users.

K. Gavazov · T. Spiegelberger · A. Buttler
Laboratory of Ecological Systems (ECOS), School of Architecture, Civil and Environmental Engineering (ENAC), Ecole Polytechnique Fédérale de Lausanne (EPFL), Station 2, 1015 Lausanne, Switzerland

K. Gavazov (✉) · A. Buttler
Research Unit Community Ecology, WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Site Lausanne, Station 2, 1015 Lausanne, Switzerland
e-mail: konstantin.gavazov@epfl.ch

T. Spiegelberger
UR EMGR Mountain Ecosystems, Irstea, 2 rue Papeterie, BP 76, 38402 Saint-Martin d'Hères, France

A. Buttler
UMR 6249 Chrono-Environnement, University of Franche-Comté - CNRS , 16 Route de Gray, 25030 Besançon Cedex, France

and the warmer climate that is predicted to occur in the future (Elmendorf et al. 2012a; Walker et al. 2006). Plants have been shown to track changes in temperature by shifting their distributions to either higher altitudes or to higher latitudes (Chen et al. 2011), thus forming new communities with species assemblages that are adapted to a warmer climate (Gottfried et al. 2012). The general conclusion drawn from these meta-analyses is that, overall, plant diversity and richness have not been significantly affected by the warming climate, although Klein et al. (2004) have shown there is the potential for rapid community responses depending on land-use practices.

Land-use changes that occur concomitantly with either management intensification or abandonment of mountain pastures are considered a major threat to these ecosystems worldwide (Körner et al. 2006), with strong negative implications for biodiversity (Niedrist et al. 2009; Tasser and Tappeiner 2002). Land-use practices can interact with the response of an ecosystem to climate change (Theurillat and Guisan 2001) by either accelerating it (forest encroachment, grazing overpressure, eutrophication) or counteracting it (traditional practices with low management intensity). Considering the daunting implications of biodiversity loss for the functioning of ecosystems, with a similar level of impact to those of most other anthropogenic impacts (Hooper et al. 2012), it is essential for ecologists to further investigate the mechanistic drivers of plant community shifts under climate change and their interaction with land use.

Subalpine pasture woodlands, such as those found on the crest of the Swiss Jura mountains, have been a traditional form of land use for millennia (Gillet and Gallandat 1996), providing equal shares of pastoral land and timber in a patterned landscape where forest encroachment is suppressed by livestock browsing and extensive pasture management (Buttler et al. 2009). The resulting heterogeneity of the landscape accommodates high floristic diversity (Dufour et al. 2006), which could potentially serve as a buffer to environmental and climate change (Grime et al. 2000; Lavorel et al. 2007). In addition, the lower evapotranspiration demand of wooded grasslands compared to unwooded ones is capable of mitigating the effects of heatwaves on forage production at the landscape scale (Gavazov et al. 2013) and this may also foster ecosystem resistance to the effects of climate change.

In this study, we present an integrative approach to investigating the responses of land-use-specific vegetation types with subalpine distributions to both moderate and high levels of climate change, corresponding to the A1B and A2 scenarios outlined by Meehl et al. (2007). Our aims were (1) to compare the diversity and biomass responses of plant communities shaped by contrasting land-use histories to different intensities of experimental climate change. To this end, we transplanted turfs with vegetation from three land-use types (spanning a gradient from open grassland to forest understory) along an altitudinal transect, thus simulating a year-round increase in temperature and decreases in precipitation and the period of snow cover. This setup allowed us to (2) determine the potential of each land use type to resist climate perturbations, and the changes in species composition and primary production. Measurements of plant phenology and tissue stable isotope signatures were intended to (3) provide a mechanistic explanation of the processes that were observed to lead to changes in community structure and function in response to climate change.

We expected that (1) a simulated warmer and drier climate at lower altitude would result in a prolonged vegetation growing season with possible soil moisture limitation at its peak, which would (2) cause shifts in plant phenology, community composition, and ecosystem productivity. We also anticipated that (3) these effects would be more strongly expressed in the unwooded pastures due to their intensive land use and the resulting vegetation structure.

Materials and methods

Site description and design of the experimental climate change

The results presented in this study are from the second year of a climate manipulation study and reflect processes that occurred during the entire plant-growing season of 2011. Details regarding the choice of study sites, the pastoral management practices employed for each land-use type, and mesocosm construction are described by Gavazov et al. (2013). Briefly, in 2009, 45 mesocosms made of rectangular PVC boxes 60 × 80 and 35 cm in height were set up, containing soil monoliths of depth 30 cm and their intact herbaceous vegetation. This soil core depth was sufficient to contain most grassland roots. These turfs originated from Combe des Amburnex (N46°55′, E6°24′)—an area of subalpine pasture-woodland situated along the crest of the Swiss Jura Mountains, circa 1,350 m a.s.l. Each mesocosm contained one of the following three land-use types: a densely wooded (DW) pasture, a sparsely wooded (SW) pasture, or an unwooded (UW) pasture. This order reflects diminishing canopy cover of the dominant tree species *Picea abies* due to increasing intensity of pasture management, where ecosystem succession is kept in check by cattle grazing pressure. Unwooded pasture vegetation is of the rich grassland type, has a higher herbaceous productivity than its wooded pasture counterparts, and is characterized by a higher frequency of graminoids. Both wooded pasture types, in contrast, have higher frequencies of forbs. Sparsely wooded pasture vegetation has a characteristic

Table 1 Microclimate data overview for the plant-growing season (AMJJAS) of 2011. Mean parameter values for each altitude and pasture type are presented

Altitude (m a.s.l.)	1,350			1,010			570		
Air temperature (°C)	10.6			13.3			15.9		
Air humidity (%)	74.9			75.8			70.4		
Precipitation (mm)	733.3			624.1			467.4		
Land-use type*	UW	SW	DW	UW	SW	DW	UW	SW	DW
Soil temperature (°C)‡	12.4 ± 0.1 a	11.0 ± 0.2 b	10.4 ± 0.1 ab	15.6 ± 0.2 c	14.3 ± 0.2 d	13.2 ± 0.2 ae	18.4 ± 0.2 f	17.1 ± 0.1 g	16.0 ± 0.2 ch
Soil moisture (%)§	47.5 ± 4.7 a	39.2 ± 2.6 ab	30.3 ± 2.2 bc	26.3 ± 2.5 bc	31.6 ± 5.0 bc	25.3 ± 2.3 bc	15.9 ± 2.0 c	22.2 ± 1.9 c	15.8 ± 2.2 c

* Land-use type codes, where *UW* refers to unwooded pasture with 0 % canopy shading, *SW* to sparsely wooded pasture with 40 % canopy shading, and *DW* to densely wooded pasture with 80 % canopy shading

‡, § Reported values for soil temperature and moisture are means and standard errors for five replicate plots. Different letters indicate significant differences at the $P = 0.05$ threshold

dense moss layer (dominated by *Rhytidiadelphus triquetrus*), whereas densely wooded pasture vegetation is of the forest understory type, with patches of bare ground, accumulated litter, and occasional ligneous species. The three land-use types have a similar vascular plant diversity of ca. 30 species m^{-2}.

In order to create a year-round effect of climate warming and reduced precipitation with respect to the ambient climate at the mountain crest, mesocosms were transplanted to one of the three experimental sites: Combe des Amburnex (1,350 m a.s.l., N46°54′, E6°23′), Saint-George (1,010 m a.s.l., N46°52′, E6°26′), and Arboretum d'Aubonne (570 m a.s.l., N46°51′, E6°37′). The first site at 1,350 m a.s.l. served as a transplantation control site, with a mean annual rainfall of ca. 1,750 mm including more than 450 mm of snow, and a mean annual temperature of 4.5 °C. The other two sites were chosen to represent a combination of an annual temperature increase of +2 K and a precipitation decrease of −20 % at 1,010 m a.s.l. (referred to as the +2 K scenario hereon), and of +4 K and −40 % at 570 m a.s.l. (referred to as the +4 K scenario hereon). These data were spatially interpolated from nearby weather stations (source: MeteoSwiss). The temperature increments were chosen in accordance with the moderate A1B and the intensive A2 climate change scenarios outlined by the latest IPCC report (Meehl et al. 2007) and the predicted concurrent decrease in precipitation for temperate regions (C2SM et al. 2011; Frei et al. 2006). At each site, 15 mesocosms (i.e., five replicates of each land-use type) were transplanted to a common garden according to a completely randomized design. The boxes were dug down to surface level and placed in previously prepared trenches, thus preventing lateral heat exchange with the atmosphere. In order to limit seed rain from local plants into the plots, the area in immediate proximity to the mesocosm was covered with geotextile and the whole experimental site was mowed fortnightly.

Mesocosms with turfs from sparsely wooded pastures and densely wooded pastures were shaded using two types of UV-resistant nylon mesh, which reduced photosynthetically active radiation (PAR) by 40 and 80 % respectively, thereby simulating previously recorded light conditions in the corresponding land-use types during the 2009 growing season (unpublished data). The mesh fabric was suspended on wooden frames 50 cm above the ground surface. Whilst it did not alter rainfall input, it significantly reduced soil moisture evaporation and limited the incoming solar radiation heat flux (Table 1). The shades were positioned in the field only during the snow-free period of the year so as to avoid interference with snowpack. As a means of simulating the grazing pressure on the plots and to avoid a confounding effect of "abandonment" and accumulation of standing litter, vegetation was clipped close to ground level at the end of each growing season.

Climate measurements

Climate parameters were monitored continuously throughout the experiment by means of an automated weather station (Sensor Scope Sàrl, Lausanne, Switzerland) at each experimental site, which measured rain precipitation, air temperature, and humidity 2 m above the ground surface at 1 min intervals. ECH_2O EC-TM sensor probes coupled to Em50 data-loggers (Decagon Devices, Inc., Pullman, WA, USA) recorded soil temperature and volumetric water content in the topsoil (0 to −3 cm) every minute, and data were averaged over 1 h intervals. Data presented below are for the 6 months of the 2011 plant-growing season: April through September (AMJJAS).

Vegetation analyses

Herbaceous vegetation was harvested at peak biomass in July 2011 during the second year following the transplantation and served as an estimate of the annual AGB production. At each mesocosm, a permanently marked area 35 × 35 cm was cut down to ca. 1 cm above the soil surface, determined to species level, dried at 70 °C for 48 h, and weighed. Biomass of individual species was allocated to one of the following plant growth forms (PGF): shrub, graminoid, forb, or moss.

Plant diversity was assessed on the basis of the presence/absence of vascular plant species in/from the entire mesocosm area. The Shannon diversity index was calculated from individual species abundance in terms of biomass within the 35 × 35 cm area.

Plant phenological development was monitored in situ throughout the 2011 vegetation season by means of a remote sensing device that captured the normalized difference vegetation index (NDVI) (Pontailler and Soudani 2012). Pilot work supported the use of this approach in grasslands, as a strong linear relationship ($R^2 = 0.97$) was seen between AGB and the NDVI signal (Landolt 2010). A tripod-held NDVI sensor (Laboratoire Écologie-Systématique-Évolution, CNRS, Orsay, France) coupled to a CR10X data-logger (Campbell Scientific, Inc., Logan, UT, USA) was used during a total of 12 campaigns between 11 April 2011 and 18 October 2011, spanning the time window between snowmelt and first frost at the control site at 1350 m a.s.l. No NDVI measurements were taken for a month (July–August) following the plant biomass harvest in order to allow for vegetation regrowth.

Isotopic analyses of plant tissue

Drought stress during the plant-growing season was investigated by the $\delta^{13}C$ enrichment technique, based on isotopic discrimination arising from water limitation during photosynthesis (Farquhar et al. 1989). Higher $\delta^{13}C$ values result from nonpreferential fixation of the heavier ^{13}C isotope during the prolonged closure of leaf stomata associated with high vapor pressure deficit. This process is independent of an altitudinal gradient in $\delta^{13}C$ natural abundance in plants, which results from a decrease in $^{13}CO_2$ discrimination during carboxylation at higher altitudes (Körner et al. 1988). To this end, four dominant vascular plant species, represented across all experimental treatments, had their stable carbon isotope compositions measured. These were two graminoids (*Agrostis capillaris* and *Festuca rubra aggr.*) and two forbs (*Alchemilla monticola* and *Taraxacum officinale*).

Nitrogen deposition along the transplantation gradient was investigated by determining the nitrogen isotopic composition of a common bryophyte species *Rhytidiadelphus triquetrus* which, due to a lack of root organs, relies on an airborne supply of nutrients, and is therefore a sensitive indicator of N input and signature (Harmens et al. 2011). Mean N concentration and $\delta^{15}N$ in the moss tissue were determined for each mesocosm. The former reflected the total level of nitrogen deposition and the latter the predominant type of deposition, with higher $\delta^{15}N$ values related to wet and lower ones to dry deposition (Bragazza et al. 2005).

The entire dried (as above) biomass per mesocosm of each species was homogenized, ground using a ball mill, and analyzed for isotopic composition using a DELTA V Advantage isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany).

Data analysis

All data were analyzed according to our completely randomized block design, where block was matched with the transplantation altitude treatment and was treated as a categorical variable (Quinn and Keough 2002). Total and individual PGF biomass, plant species richness, and Shannon diversity were analyzed using a type I analysis of variance (ANOVA), with fixed factors of altitude and land use. Significant differences between the levels of each treatment factor and their interactions were examined using pairwise comparisons, where family-wise error rate was controlled using the Bonferroni procedure.

Data on the isotopic compositions of the plant tissue from the five species mentioned above were analyzed using a type I analysis of variance. A linear mixed effects model was fitted to the data, using the restricted maximum likelihood method (REML) to account for cases where species were not present in each plot (Zuur et al. 2009). The model for all tested plants included plant species, altitude, and land use, as well as all two- and three-way interactions as fixed effects. Based on the results of

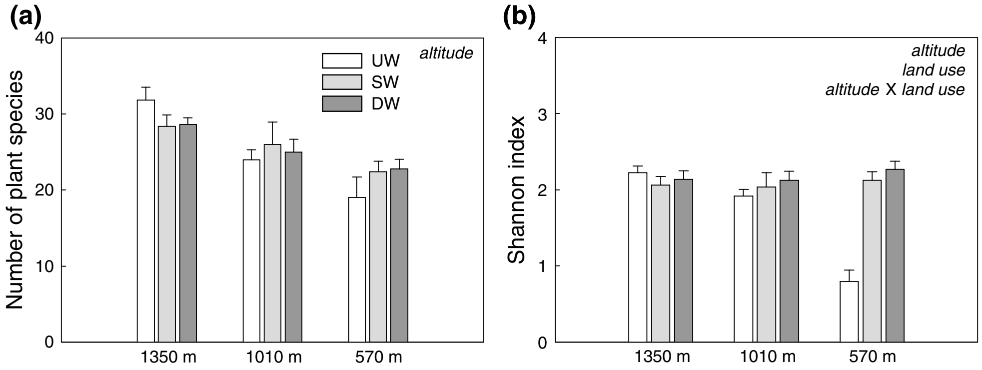

Fig. 1 Plant species **a** richness and **b** Shannon diversity for the vegetation communities in the three land-use types: unwooded pasture (*UW*), sparsely wooded pasture (*SW*), and densely wooded pasture (*DW*). Significant ($P < 0.05$) factors (*in italics*) and interactions (*marked with an X*) are shown for each response variable

this overall analysis, we also tested for treatment effects on each plant species individually. Subsequent pairwise comparisons of between-treatment factor levels for each species were executed according to the Bonferroni method.

A repeated measures linear mixed effects model, using type I analysis of variance and the REML estimation method, was used to test the evolution of the NDVI signal through the plant-growing season. Altitude, land use, and their interaction were treated as between-subject fixed factors, and sampling date (categorical variable) and all two- and three-way interactions with date as within-subject fixed factors. Significant differences between levels of the fixed factors were detected using predefined linear combinations of contrasts, thus accounting for the model's structure.

Assumptions of normality and homoscedasticity of the residuals in all final models were verified visually using diagnostic plots. For all statistical tests, effects were considered significant at $P < 0.05$. All statistical analyses were performed using R version 2.14.1 (R Development Core Team 2012), and mixed effects models were run using the nlme package (Pinheiro et al. 2012).

Results

Climate change simulation

During the second year following transplantation to lower altitudes with a warmer and drier climate, all of the mesocosms experienced tight coupling between soil and air temperatures during the plant-growing season, with significantly warmer soils at lower altitudes (Table 1). In addition, decreasing canopy cover (shading) across the land-use types stimulated warmer soil temperatures due to the increase in irradiance. Mean seasonal soil moisture values for unwooded pastures decreased significantly under both of the simulated climate change scenarios, whereas in sparsely wooded pastures it decreased only under the +4 K scenario, and in densely wooded pastures it remained unchanged (Table 1).

Plant diversity

Plant communities that were transplanted in mesocosms to the warmer and drier climate experienced a marked loss in species richness (Fig. 1a). The number of species decreased by up to 30 % ($F_{2,36} = 15.2$, $P < 0.001$), with a significant effect observed at both transplantation altitudes, 1,010 m a.s.l. ($P < 0.001$) and 570 m a.s.l. ($P = 0.011$), compared to the control site at 1,350 m a.s.l. Species richness was the same among the land-use types and did not show a significant interaction with the transplantation treatment. The greatest losses were observed for graminoid and leguminous species. In contrast to species richness, the Shannon diversity index (Fig. 1b) varied significantly across both altitude ($F_{2,36} = 9.2$, $P < 0.001$) and land use ($F_{2,36} = 16.0$, $P < 0.001$), with a significant interaction noted between these two factors ($F_{4,36} = 14.7$, $P < 0.001$). This pattern was mainly driven by the significant ($P < 0.001$) decrease in the Shannon index of unwooded pasture mesocosms that were transplanted to 570 m a.s.l. (Fig. 1b). This drastic decline was attributed to both the loss of common species (see Resource 1 in the Electronic supplementary material, ESM), and to the reduction in their abundance (see Resource 2 in the ESM). A single graminoid species, *Agrostis capillaris*, remained unaffected by the transplantation treatment and thus became dominant in the plant community, representing 59 % of the total AGB per mesocosm (compared to 22 % in the control plots).

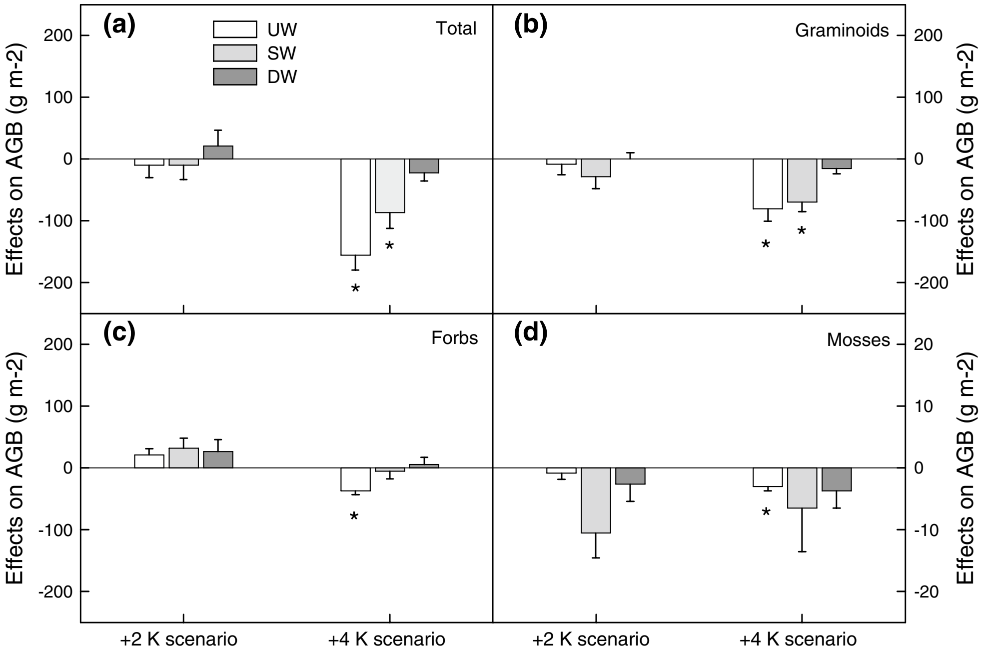

Fig. 2 Effect of transplantation to a warmer and drier climate at 1,010 m a.s.l. (+2 K scenario) and 570 m a.s.l. (+4 K scenario) on aboveground biomass (AGB) production. Data presented in the plots are for **a** the total biomass and the biomasses of **b** graminoids, **c** forbs, and **d** mosses (*y*-axis scale varies). The three land-use types are: unwooded (*UW*), sparsely wooded (*SW*), and densely wooded (*DW*) pastures. *Asterisks* indicate significant differences (from controls at 1,350 m a.s.l.) when using the threshold $P < 0.05$

Plant biomass

Total herbaceous AGB across all three land-use types decreased to 45 % of that of the control site following the transplantation to the warmer and drier climate ($F_{2,36} = 29.3$, $P < 0.001$), with a significant effect observed at the lowest site at 570 m a.s.l. ($P < 0.001$). Land use also exerted a strong effect ($F_{2,36} = 21.0$, $P < 0.001$) and interacted significantly with the transplantation treatment ($F_{4,36} = 4.7$, $P = 0.004$). This manifested as a significant effect of climate change on unwooded pasture ($P < 0.001$) and on sparsely wooded pasture vegetation ($P = 0.012$) at the lowest altitude, but not on the densely wooded pasture type (Fig. 2a).

Different PGFs reacted with different intensities and directions in response to the experimental climate change. Graminoid AGB from all three land-use types was strongly negatively affected by the transplantation to lower altitude ($F_{2,36} = 18.7$, $P < 0.001$). The response of graminoid AGB to the treatment was land-use-type dependent, as indicated by a significant interaction term ($F_{4,36} = 2.8$, $P = 0.042$), and was strongly expressed at the lowest altitude in the unwooded pasture ($P = 0.006$) and sparsely wooded pasture ($P = 0.005$) mesocosms (Fig. 2b).

Forbs in the three land-use types were significantly affected by the altitude of transplantation ($F_{2,36} = 10.7$, $P < 0.001$) and, overall, showed an increase in AGB with moderate climate change at 1,010 m a.s.l. ($P = 0.033$). Nevertheless, none of the individual pasture types showed a significant effect on forb AGB after transplantation to this altitude (Fig. 2c). To the contrary, the unwooded pasture vegetation at 570 m a.s.l. had a significantly lower ($P = 0.005$) forb AGB than the controls.

The moss AGB, almost exclusively represented by *Rhytidiadelphus triquetrus*, showed a significant reduction following transplantation to the lower altitude ($F_{2,36} = 6.2$, $P < 0.005$). Pooled across land-use types, this was evident for the sites at 1,010 m a.s.l. ($P = 0.047$) and at 570 m a.s.l. ($P = 0.004$); however, within individual land-use types, only unwooded pastures differed significantly ($P = 0.002$) from the controls (Fig. 2d).

Because ligneous species were only occasionally represented in our mesocosms, and exclusively in those from the densely wooded pasture type, it was not possible to build a robust statistical model describing their response to the altered climate following the transplantation.

NDVI

The phenological development of herbaceous vegetation in the mesocosms, determined by means of NDVI sensing, showed marked seasonality (Fig. 3), with most of the variation in the NDVI signal being explained by the date of sampling ($F_{11,395} = 202.5$, $P < 0.001$). Sampling date was

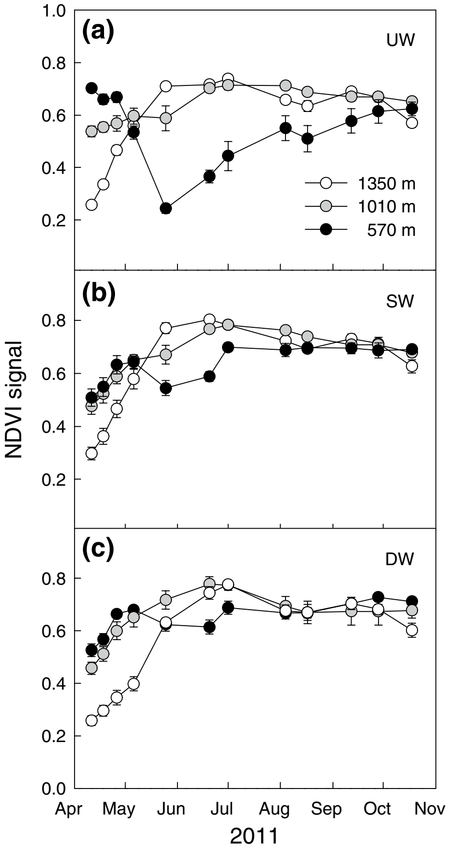

Fig. 3 Normalized difference vegetation index (NDVI) during the growing season months of 2011 for each of the three pasture types, **a** unwooded (*UW*), **b** sparsely wooded (*SW*), and **c** densely wooded (*DW*), along the altitude transplantation gradient

also significant in its two-way interactions with altitude ($F_{22,395} = 80.9$, $P < 0.001$) and land use ($F_{22,395} = 15.0$, $P < 0.001$), and the three-way interaction of these factors ($F_{44,395} = 7.9$, $P < 0.001$). This is readily observed in Fig. 3, where the NDVI signal curves follow different trajectories depending on the land use and the altitude of transplantation. Altitude alone had a strong and significant effect on plant phenology ($F_{2,36} = 9.7$, $P < 0.001$), causing an advance of up to 30 days in the development of the vegetation and a midseason senescence (Fig. 3). NDVI differed significantly across land-use types ($F_{2,36} = 7.6$, $P = 0.002$), and this pattern was significantly influenced by its interaction with altitude ($F_{4,36} = 3.7$, $P = 0.013$). Individual land-use types responded differently to the transplantation treatment. Unwooded pasture mesocosms (Fig. 3a) experienced a significant decrease in NDVI values at 570 m a.s.l. ($t = -3.1$, $P = 0.003$) and a significant increase at 1,010 m a.s.l. ($t = 3.4$, $P = 0.002$) in comparison to the controls at 1,350 m a.s.l. Those of sparsely wooded pasture type (Fig. 3b) were not affected significantly, whereas those of densely wooded pasture type (Fig. 3c) showed a significant increase at 1,010 m a.s.l. ($t = 2.1$, $P = 0.038$). All pasture types recovered to control conditions during the second part of the growing season following a series of rewetting events, which allowed for herbaceous vegetation regrowth.

Plant isotopic signatures

All of the tested vascular plant species experienced a significant increase in δ^{13}C ($F_{2,36} = 92.6$, $P < 0.001$) following their transplantation to a lower altitude (Fig. 4). Inherent differences between species in their δ^{13}C signatures were present ($F_{3,91} = 184.6$, $P < 0.001$), and those showed significant interactions with land use ($F_{6,91} = 14.9$, $P < 0.001$), altitude ($F_{6,91} = 6.4$, $P < 0.001$), and the combination of land use and altitude ($F_{12,91} = 2.0$, $P = 0.030$). Significant δ^{13}C enrichment ($P < 0.001$) was observed in all species from mesocosms transplanted to 570 m a.s.l. in comparison to the controls at 1,350 m a.s.l. In addition, *Agrostis capillaris* (Fig. 4a) showed significant δ^{13}C enrichment ($P = 0.011$) at 1,010 m a.s.l. compared to the control.

Nitrogen concentration in the green tissue of the moss *Rhytidiadelphus triquetrus* did not exhibit any significant differences among the three altitudes of transplantation (Table 2), leading to the conclusion that the levels of aerial nitrogen deposition were similar at the three altitudes. The δ^{15}N signature was, however, significantly affected by altitude ($F_{2,36} = 33.0$, $P < 0.001$), as it was more depleted in ^{15}N at the lower elevation in comparison to the control site, thus indicating that the predominant type of N deposition is dry deposition.

Discussion

Responses of the vegetation to their transplantation along an altitudinal gradient simulating a warmer climate and reduced precipitation were driven to a large extent by the magnitude of the treatment. Significant deviations from control conditions in plant aboveground biomass, phenology, richness, and diversity were observed primarily for the communities exposed to the intensive climate change treatment (+4 K scenario), with little to no effect of the moderate climate change treatment noted (+2 K scenario). The directions of these responses were, however, the same, indicating a threshold (see Beier et al. 2012) in the physiological tolerances of plants to simulated climate change. Another major finding from this experimental manipulation was that, across land-use types, intensively used unwooded pastures were consistently more responsive to climate change than their counterparts from extensively used wooded pastures of either sparsely or densely wooded type.

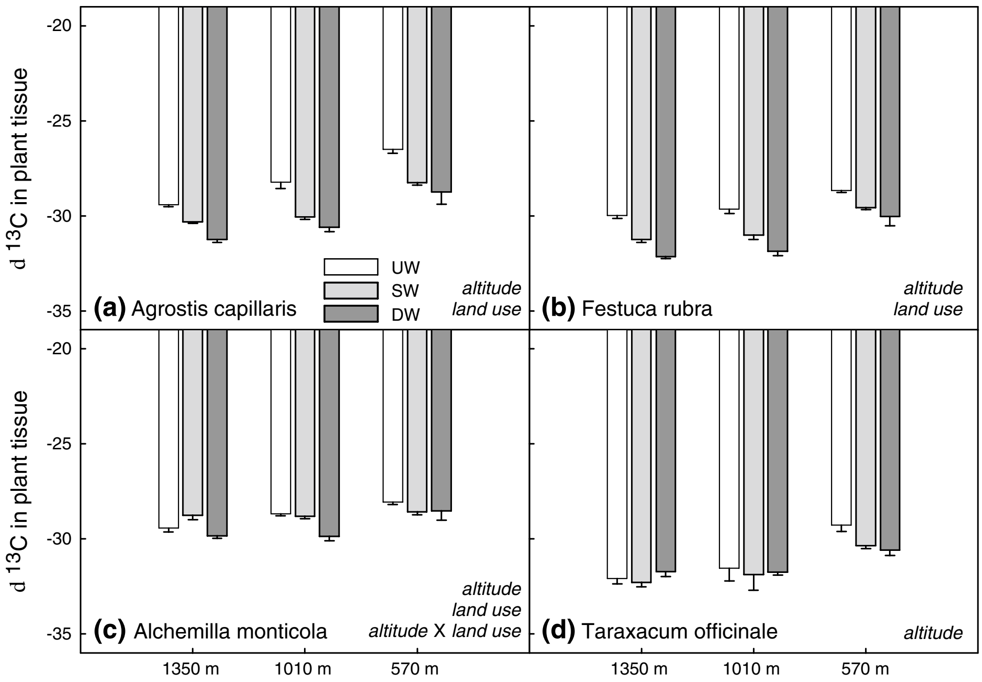

Fig. 4 Carbon isotope signatures of the four most common vascular plant species sampled from each of the three studied land-use types: unwooded pasture (*UW*), sparsely wooded pasture (*SW*), and densely wooded pasture (*DW*). Higher δ^{13}C values within a given species are an indication of water limitation during the vegetation season. Significant ($P < 0.05$) factors (*in italics*) and interactions (*marked with an X*) are shown for each species tested

Table 2 Concentration of N and δ^{15}N of green moss tissue from the species *Rhytidiadelphus triquestrus* collected from the transplanted mesocosms in July 2011

Altitude (m a.s.l.)	1,350	1,010	570
N content (%)	1.80 ± 0.10 a	1.72 ± 0.09 a	1.98 ± 0.14 a
δ^{15}N	−5.77 ± 0.27 a	−8.14 ± 0.21 b	−8.34 ± 0.27 b

Mean parameter values are presented (reported values are means and standard errors for up to 15 replicates; different letters indicate significant differences at the $P = 0.05$ threshold) for each altitude

Plant community attributes

The observed rapid decrease in species richness and diversity in response to climate change is comparable to experimental findings for other mountain grassland ecosystems (Klein et al. 2004; Sebastia et al. 2008). We found a reduction in the total number of vascular plant species in the warmer and drier climate for all three studied land-use types, with a stronger effect size at a stronger treatment intensity. The decrease in Shannon diversity was, however, only expressed in the unwooded pasture vegetation, reflecting a combined loss of species richness, reduction in individual species abundance, and increased dominance of a single graminoid species—*Agrostis capillaris*. Both the total biomass and the biomasses of individual plant growth forms decreased substantially following their transplantation to lower altitudes. The strong increase in the mean annual temperature and the reduction in precipitation (+4 K scenario) halved the aboveground biomass in unwooded pasture mesocosms, which were associated with the strongest deficiency in soil moisture content during the plant growing season, and experienced the most pronounced enrichment in plant tissue δ^{13}C, a legacy of drought stress. These experimental findings corroborate modeling evidence (see Engler et al. 2011) indicating a strong dependence of mountain plant performance and floristic composition on the severity of drought episodes during projected climate change this century.

Plant growth forms

Regarding PGFs, we expected that plants with different morphologies and life strategies would respond differently under changing environmental conditions (Lavorel et al. 2007). Indeed, we observed that the graminoid PGF was more strongly affected by the simulated warmer and drier climate than either forbs or bryophytes, a finding that is in line with previous results of studies of plant communities from subalpine grasslands (Gilgen and Buchmann 2009; Sebastia 2007) and from an alpine snowbed (Johnson et al.

2011). Graminoids presented a consistent decrease in biomass in both unwooded and sparsely wooded pastures, and contributed substantially to the overall decrease in the total aboveground biomass in these land-use types. We believe that inherent differences in the morphology, growth, and ecophysiology between graminoids and forbs could have driven the dichotomous responses of these growth forms. First, it has been shown that, in cold-adapted biomes, forbs exhibit a capacity for belowground resource storage and leaf bud preformation, which could grant them a competitive advantage over graminoids under climatic perturbation (Wookey et al. 2009). Both the large tap roots and the rhizomes of the mountain forbs at our pasture-woodland field site seem to be more beneficial than the near-surface fine roots of the graminoids under prolonged periods without precipitation. Second, preliminary results from our transplantation experiment (Hildbrand and Wohlgemuth 2013) suggest a shortened leaf lifespan and intensified production of leaf cohorts in forbs during the growing season, which indicates their method of regrowth following extended periods without precipitation. Third, forbs from a range of subalpine grasslands have been reported to exhibit a higher water-use efficiency than graminoids due to tighter regulation of stomatal conductance (Signarbieux and Feller 2012). Indirect evidence for the latter could be found in the carbon isotope ratios of green plant tissues collected from the mesocosms: whereas forbs did not show a consistent response to climate manipulation according to the land use of origin, graminoids were consistently more enriched in δ^{13}C in more open canopy pastures and at a higher intensity of climate change. We interpret this as a capacity of subalpine forbs to minimize water loss under unfavorably dry conditions. All of these mechanisms point to the advantageous growth form of forbs in a warmer and drier subalpine climate, thus also demonstrating the usefulness of the PGF classification (see Dorrepaal 2007) for predicting ecosystem response to climate change.

Plant phenology

Plant phenological development was controlled to a large extent by the magnitude of the simulated climate change. At the onset of the growing season, mesocosms exposed to the +4 K scenario were considerably "greener" than the controls at the top of the gradient. This result confirmed our expectations that shorter snow cover duration and warmer soils in spring advance plant phenological development, corroborating findings relating to annual variations in winter climate (Inouye 2008) and experimental snow manipulations (Wipf and Rixen 2010). However, subsequent soil moisture limitation due to the absence of a spring snow melt and a pronounced reduction in growing season precipitation exposed these turfs to drought stress, as reflected by the premature senescence of the vegetation. This was particularly evident in the unwooded pastures, which were subjected to the direct effects of sun irradiation and wind.

Land use

The land-use types chosen for study in this work have been shaped through a history of different pasture management intensities, and there could be many reasons why the vegetation from unwooded pastures was significantly more affected by the warmer and drier climate than that from both wooded pasture types. Above, we explored the hypothesis for a differential PGF response; hence, considering the higher frequency of forbs in wooded pastures and their conservative use of water, this may contribute to the observed land-use pattern. We believe, however, that other factors also play a role, and their individual effects are hard to tease apart. First, in accordance with our results, highly productive early successional grassland communities have been shown to be more responsive to simulated climate warming and reduced precipitation than late successional ones, which are typically found in areas of low intensity management (Grime et al. 2000). Second, drought resistance and the recovery potential of a plant community have been also attributed to species richness (van Ruijven and Berendse 2010), with an important role played by subordinate plant species (Mariotte et al. 2013). Our results do not support such a hypothesis, since unwooded pastures hosted some of the richest communities, with over 30 vascular plant species within a single mesocosm (0.5 m^{-2} of surface). Third, at the landscape scale, both trees (Teuling et al. 2010) and herbaceous undergrowth (Gavazov et al. 2013) exhibit lower evapotranspiration as compared to grasslands, thus conserving soil moisture content, which in turn allows them to cope better with long-lasting heat and drought stress. Our data suggest that under simulated climate change, shaded wooded pasture types retained higher soil moisture levels throughout the growing season. This was also reflected by the within-species δ^{13}C enrichment, which was significantly lower in shaded plots for three of the four tested species, indicating a lower vapor pressure deficit.

Experimental considerations

The experimental design employed in this study allowed for the direct comparison of the responses of the vegetation of three distinct land-use types to two levels of climate change with warmer and drier climates (+2 and +4 K scenarios), as predicted for temperate mountain systems. Our results may not, however, apply to other cold-adapted ecosystems, particularly in higher latitude regions where precipitation is not expected to decline as climate warms.

Mesocosm transplantation to lower altitudes tended to introduce some confounding factors besides the desired gradient in temperature and precipitation. Due to its direct effects on plant growth and species diversity, atmospheric nitrogen deposition was investigated by sampling the tissue nitrogen concentration in the ubiquitous moss species *Rhytidiadelphus triquetrus* (Harmens et al. 2011). The lack of treatment effects, in addition to the mapped information (FOEN 2009) for comparable loads of nitrogen deposition along the slopes of the Jura Mountains, provided evidence that enabled us to eliminate a potential confounding factor related to N emissions along the gradient. Additionally, informal comparisons of control plots with neighboring intact grasslands (unpublished data) suggested that turf transplantation had no effect on the composition of the vegetation after two years of treatment, similar to other findings in the literature (MacGillivray et al. 1995; Sebastia et al. 2008). We did not detect any incoming species in the plots at lower altitudes over the two experimental years.

In conclusion, our findings provide unequivocal evidence that the studied temperate subalpine pastures have a resistance potential at moderate levels of climate change (+2 K scenario) in terms of productivity and plant diversity. The observed negative impact of the high level of climate change (+4 K scenario) was strongest in the intensively managed unwooded pasture system and only minimal in the extensively used sparsely and densely wooded pastures. This indicates that the pasture-woodlands of the Jura Mountains are internally buffered to moderate climate perturbations, and that stronger impacts of climate change in the future can be circumvented through sustainable land use and by preserving the diversity of the landscape.

Acknowledgments This work was supported by the CCES (Competence Center Environment and Sustainability of the ETH Domain, Switzerland) as part of the Mountland Project. We thank Arboretum National d'Aubonne, Commune of St-George (VD), Parc Jurassien Vaudois, and Fondation Les Bois Chamblard for their logistical and infrastructural support. Special thanks go to Arturo Knecht for his assistance in sorting the plant biomass and to Robert Mills for proofreading. The manuscript improved considerably in terms of focus and clarity after it was assessed by two anonymous referees.

References

Beier C et al (2012) Precipitation manipulation experiments—challenges and recommendations for the future. Ecol Lett 15:899–911

Bragazza L et al (2005) Nitrogen concentration and delta N-15 signature of ombrotrophic *Sphagnum* mosses at different N deposition levels in Europe. Glob Change Biol 11:106–114

Buttler A, Kohler F, Gillet F (2009) The Swiss Mountain wooded pastures: patterns and processes. In: Rigueiro-Rodrigues A, McAdam J, Mosquera-Losada MR (eds) Agroforestry in Europe, current status and future prospects, vol 6. Springer, Dordrecht, pp 377–396

C2SM et al. (2011) Swiss Climate Change Scenarios CH2011. C2SM/MeteoSwiss/ETH/NCCR Climate/OcCC, Zurich

Chen IC, Hill JK, Ohlemueller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Dorrepaal E (2007) Are plant growth-form-based classifications useful in predicting northern ecosystem carbon cycling feedbacks to climate change? J Ecol 95:1167–1180

Dufour A, Gadallah F, Wagner HH, Guisan A, Buttler A (2006) Plant species richness and environmental heterogeneity in a mountain landscape: effects of variability and spatial configuration. Ecography 29:573–584

Elmendorf SC et al (2012a) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. Ecol Lett 15:164–175

Elmendorf SC et al (2012b) Plot-scale evidence of tundra vegetation change and links to recent summer warming. Nat Clim Change 2:453–457

Engler R et al (2011) 21st century climate change threatens mountain flora unequally across Europe. Glob Change Biol 17:2330–2341

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Ann Rev Plant Physiol Plant Mol Biol 40:503–537

FOEN (2009) Nitrogen deposition 2000. Federal Office of the Environment (FOEN), Bern

Frei C, Scholl R, Fukutome S, Schmidli J, Vidale PL (2006) Future change of precipitation extremes in Europe: an intercomparison of scenarios from regional climate models. J Geophys Res Atmospheres 111:D06105

Gavazov K, Peringer A, Buttler A, Gillet F, Spiegelberger T (2013) Dynamics of forage production in pasture-woodlands of the Swiss Jura Mountains under projected climate change scenarios. Ecol Soc 18:38

Gilgen AK, Buchmann N (2009) Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. Biogeosciences 6:2525–2539

Gillet F, Gallandat JD (1996) Wooded pastures of the Jura Mountains. In: Etienne M (ed) Western European silvopastoral systems. INRA Editions, Paris, pp 37–53

Gottfried M et al (2012) Continent-wide response of mountain vegetation to climate change. Nat Clim Change 2:111–115

Grime JP et al (2000) The response of two contrasting limestone grasslands to simulated climate change. Science 289:762–765

Harmens H et al (2011) Nitrogen concentrations in mosses indicate the spatial distribution of atmospheric nitrogen deposition in Europe. Environ Pollut 159:2852–2860

Hildbrand G, Wohlgemuth T (2013) Functional responses of two dominant species of pasture-woodlands to simulated climate change. In: ClimTree 2013 (Int Conf on Climate Change and Tree Responses in Central European Forests), Zürich, Switzerland, 1–5 Sept 2013

Hooper DU et al (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108

Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. Ecology 89:353–362

Johnson D, Vachon J, Britton AJ, Helliwell RC (2011) Drought alters carbon fluxes in alpine snowbed ecosystems through contrasting impacts on graminoids and forbs. New Phytol 190:740–749

Klein JA, Harte J, Zhao XQ (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. Ecol Lett 7:1170–1179

Körner C, Farquhar GD, Roksandic Z (1988) A global survey of carbon isotope discrimination in plants from high-altitude. Oecologia 74:623–632

Körner C, Nakhutsrishvili G, Spehn E (2006) High-elevation land use, biodiversity, and ecosystem functioning. In: Spehn E, Liberman

M, Körner C (eds) Land use change and mountain biodiversity. CRC, Boca Raton

Landolt P (2010) Calibration of a NDVI sensor. MSc thesis. Ecole Polytechnique Fédéral de Lausanne (EPFL), Lausanne, p 20

Lavorel S, Diaz S, Cornelissen JHC, Garnier E, Harrison SP, McIntyre S, Pausas JG, Perez-Harguindeguy N, Urcelay C (2007) Plant functional types: are we getting any closer to the Holy Grail? In: Canadell J, Pereira LFP, Pataki D (eds) Terrestrial ecosystems in a changing world. Springer, Berlin, pp 171–186

MacGillivray CW, Grime JP, Team TISP (1995) Testing predictions of the resistance and resilience of vegetation subjected to extreme events. Funct Ecol 9:640–649

Mariotte P, Vandenberghe C, Kardol P, Hagedorn F, Buttler A (2013) Subordinate plant species enhance community resistance against drought in semi-natural grasslands. J Ecol 101:763–773

Meehl GA et al (2007) Global climate projections. In: Solomon S et al (eds) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Niedrist G, Tasser E, Luth C, Dalla Via J, Tappeiner U (2009) Plant diversity declines with recent land use changes in European Alps. Plant Ecol 202:195–210

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2012) nlme: linear and nonlinear mixed effects models. R package version 3.1-104. R Foundation for Statistical Computing, Vienna

Pontailler JY, Soudani K (2012) Tracking canopy phenology and structure using ground-based remote sensed NDVI measurements. In: Le Galliard JF, Guarini JM, Gaill F (eds) Sensors for ecology. Towards integrated knowledge of ecosystems. CNRS, Paris, pp 243–257

Quinn GP, Keough GP (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA (2003) Fingerprints of global warming on wild animals and plants. Nature 421:57–60

R Development Core Team (2012) R version 2.15.1. R Development Core Team, Vienna

Sebastia MT (2007) Plant guilds drive biomass response to global warming and water availability in subalpine grassland. J Appl Ecol 44:158–167

Sebastia MT, Kirwan L, Connolly J (2008) Strong shifts in plant diversity and vegetation composition in grassland shortly after climatic change. J Veg Sci 19:299–306

Signarbieux C, Feller U (2012) Effects of an extended drought period on physiological properties of grassland species in the field. J Plant Res 125:251–261

Solomon S et al (2007) Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Tasser E, Tappeiner U (2002) Impact of land use changes on mountain vegetation. Appl Veg Sci 5:173–184

Teuling AJ et al (2010) Contrasting response of European forest and grassland energy exchange to heatwaves. Nat Geosci 3:722–727

Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. Clim Change 50:77–109

van Ruijven J, Berendse F (2010) Diversity enhances community recovery, but not resistance, after drought. J Ecol 98:81–86

Walker MD et al (2006) Plant community responses to experimental warming across the tundra biome. Proc Natl Acad Sci USA 103:1342–1346

Walther GR et al (2002) Ecological responses to recent climate change. Nature 416:389–395

Wipf S, Rixen C (2010) A review of snow manipulation experiments in Arctic and alpine tundra ecosystems. Polar Res 29:95–109

Wookey PA et al (2009) Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. Glob Change Biol 15:1153–1172

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York