

The responses of grassland plants to experimentally simulated climate change depend on land use and region

ASTRID BÜTOF*, LARS R. VON RIEDMATTEN†‡, CARSTEN F. DORMANN†, MICHAEL SCHERER-LORENZEN‡, ERIK WELK* and HELGE BRUELHEIDE*

*Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, D-06108, Halle (Saale), Germany, †Helmholtz Centre for Environmental Research - UFZ, Department of Computational Landscape Ecology, Permoserstr. 15, D-04318, Leipzig, ‡Faculty of Biology/Geobotany, University of Freiburg, Schänzlestr. 1, D-79104, Freiburg, Germany

Abstract

Macroclimatic niche properties derived from species distribution ranges are fundamental for projections of climate change impacts on biodiversity. However, it has been recognized that changes in regional or local distribution patterns also depend on interactions with land use. The reliability and transferability of large scale geographic predictions to small scale plant performance need to be tested experimentally. Thus, we asked how grassland plant species pairs with different macroclimatic niche properties respond to increased spring temperature and decrease summer precipitation in three different land-use types. An experiment was carried out in the framework of the German Biodiversity Exploratories simulating climate change in 45 experimental plots in three geographical regions (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb) and three grassland management types (meadow, pasture, mown pasture). We planted six plant species as phytometers, each two of them representing congeneric species with contrasting macroclimatic niches and recorded plant survival and growth over 1 year. To quantify the species macroclimatic niches with respect to drought tolerance, the species' distribution ranges were mapped and combined with global climate data. The simulated climate change had a general negative effect on plant survival and plant growth, irrespective of the macroclimatic niche characteristics of the species. Against expectation, species with ranges extending into drier regions did not generally perform better under drier conditions. Growth performance and survival was best in mown pastures, representing a quite intensive type of land use in all study regions. Species with higher macroclimatic drought tolerance were generally characterized by lower growth rates and higher survival rates in land-use types with regular mowing regimes, probably because of reduced competition in the growing season. In conclusion, plant species with similar climatic niche characteristics cannot be expected to respond consistently over different regions owing to complex interactions of climate change with land use practices.

Keywords: Biodiversity Exploratories, climate change, field experiment, grassland management, plant distribution

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Introduction

The ongoing global climatic change might force many plant species to shift their geographical distribution ranges (Parmesan & Yohe, 2003; Walther *et al.*, 2005; Thuiller, 2007; Loarie *et al.*, 2009; Walther, 2010). Species distribution models (SDM) that predict future range shifts or species extinctions under climate change scenarios are built on the assumption that climate is the main driver of species distribution (Huntley *et al.*, 1995; Guisan & Zimmermann, 2000; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Hijmans & Graham, 2006; McKenney *et al.*, 2007). The reliability of such models has been repeatedly challenged (e.g. Dormann, 2007) and the

necessity to integrate interactions between global change factors has been stressed (Pereira *et al.*, 2010).

Since species responses to climatic changes are ultimately dependent on the fitness and performance of populations at much smaller spatial scales, the transferability of SDM predictions to local scales can be expected to be much more reliable when land-use variables are taken into account (Tubiello *et al.*, 2007; de Chazal & Rounsevell, 2009). Reliability is not only an issue in SDMs but also on models based on SDMs such as stacked SDMs, used to predict species richness in climate change scenarios. For instance, Pompe *et al.* (2008) could highly improve purely bioclimatic models of species richness in Germany by including land-use variables. Commonly, such models work with coarse land-use categories such as forest, grassland, agricultural land or urban area. However, these categories themselves comprise highly variable types of land use.

Correspondence: Astrid Bütof, tel. + 49 345 552 6198, fax + 49 345 552 7228, e-mail: astrid.buetof@botanik.uni-halle.de

Especially in grasslands, certain management practices can lead to significant differences in floristic and functional structure (Römermann *et al.*, 2009), since species have different tolerances to cutting, grazing and trampling (Briemle *et al.*, 2002; Stammel *et al.*, 2003; Scheidel & Bruelheide, 2004; Moog *et al.*, 2009). If such tolerances are linked to a species' macroclimatic niche characteristics, purely climatic SDMs will only be valid in certain land-use types. Different management regimes facilitate certain species with certain traits and affect species. For example, Kühner & Kleyer (2008) described a positive relationship of highly fertilized and frequently disturbed grassland habitats with species characterized by high specific leaf area and canopy height. Thus, species' local responses to climate change cannot be inferred from macroclimatic SDM alone but requires taking land use into account. As land-use patterns generally have a much finer grain than macroclimatic patterns, the problem arises that consistent information on both factors is not available at the same spatial scale. Actually, this difference in scale is the reason why macroecological approaches have rarely addressed land use so far. One obvious approach to bridge the different scales is experimental testing at the plot scale. Since such empirical studies are lacking so far we asked if and how different grassland management practices, like mowing, cutting or a combination of both, in interaction with regional climate change will affect plant species that differ in their macroclimatic niches.

Following regional climate changes predictions for Europe (Spekat *et al.*, 2006; Christensen & Christensen, 2007), two variables can be expected to have a paramount impact on the primary producers. One is the increase in spring temperatures, resulting in prolonged vegetation periods, which is an already observed phenomenon (Menzel *et al.*, 2006; IPCC, 2007). The other is a decline in summer precipitation involving more severe and prolonged drought periods (Christensen & Christensen, 2007; Knapp *et al.*, 2008). These two aspects of climate change have already been addressed in manipulative field experiments in grasslands. For example, earlier spring will result in earlier snow melt, which has been shown to reduce aboveground biomass of three common dwarf shrub species in a snow removal experiment in the Swiss Alps (Wipf *et al.*, 2009). Rain shelter (RS) experiments have shown that drought affects important ecosystem processes, such as productivity (Kahmen *et al.*, 2005; Engel *et al.*, 2009; Heisler-White *et al.*, 2009; Miranda *et al.*, 2009) and nutrient cycling (Sardans *et al.*, 2006).

So far most climate change experiments have only been carried out at single locations. Given the naturally limited number of treatment combinations between climate and land use, such single-site experiments will

not provide insight how land use will affect plant responses in different climates. One exception is a 7 years experimental warming project in shrublands along a north–south gradient in Europe (Peñuelas *et al.*, 2007) which found that the magnitude of responses depended greatly on the climatic differences between the six sites. Similarly, Heisler-White *et al.* (2009) detected differences in aboveground net primary productivity changes as response to altered precipitation events between three different grassland types in the Central Plains Region of North America. In contrast, in the International Tundra Experiment Walker *et al.* (2006) encountered similar responses of the plant community to increased temperatures between 11 experimental sites. The experiences from these experiments point out the value of manipulating climate simultaneously at different locations, but also show that the interaction with land use has to be addressed.

Experimental analyses of effects that are confined to the extant community have the disadvantage that comparisons with nonresident species, which have the potential to take over the role of the current residents in the future, are precluded. In field studies, such questions can only be addressed with phytometer approaches. Phytometers (*sensu* Gibson, 2002) can be chosen in a way to anticipate the putative effects of global change, i.e. by comparing species with macroclimatic niches that either better match the ambient or the manipulated climate regime. Using phytometers in replicated global change experiments distributed along climatic gradients also allows for evaluating site effects in a space-for-time approach.

Herein we make use of such a space-for-time approach, by carrying out highly replicated climate change experiments, covering three regions in Germany that differ in climate and three different types of land use in each region. Planting seedlings of species with contrasting distribution ranges and analysing their macroclimatic niches, we carried out a climate change experiment with increased spring temperatures and reduced summer precipitation in a total of 45 field greenhouses.

With this setup we tested the following hypotheses: (H1) The effects of simulated warming and drought on plant performance are similar to the effects of regional climatic differences among the study regions. More specifically, we tested whether or not the climatic differences between study regions result in effects are comparable to the climate change manipulations within each study region. (H2) The effects of climate change on plant performance are influenced by grassland land-use types. In particular, we tested whether climate change effects are mitigated or intensified in certain land-use types. Finally (H3) differences in the species'

performance in the experiment can be predicted from their macroclimatic niches, at least after having accounted for effects of region and land use. Testing this hypothesis is particularly important for global change research as it asks for the reliability and transferability of large scale geographic predictions to small scale plant performance.

Methods

Studied species and distribution data

Three pairs of species of contrasting distribution range were included in the study, each consisting of congeneric species,

one with a more oceanical and one with a more continental range (Table 1). All six species are native to European grasslands. Regarding habit and growth form, they are supposed to be intermediate in their grazing and mowing tolerance (Briemle *et al.*, 2002). In addition, the species pairs can be regarded to represent largely identical plant functional types (Box, 1996; Díaz & Cabido, 1997). The distribution data of the species were obtained from published range maps (Meusel *et al.*, 1965; Hultén & Fries, 1986; Meusel & Jäger, 1992) and updated with national and regional floristic data and internet databases. Climatic variables (mean temperature in April, precipitation in July) were extracted from the WORDCLIM dataset (Hijmans *et al.*, 2005) in a 2.5 arc minutes grid for the distribution ranges of all six species. As a proxy for macroclimatic summer drought tolerance we calculated the first

Table 1 Characteristics of the study species and description of the collection localities

Genus	Species	Minimum precipitation in July (mm)	Maximum aridity (growing season)	Maximum temperature in April (°C)	Growth form	Habitat type (in Central Germany)	Locality of collected seeds	
							Latitude	Longitude
<i>Achillea</i>	<i>millefolium</i>	7	0.25	16.9	Sg semirosulate, pl-polycarpic	Calcareous dry and semidry grasslands, dry meadows and shrubland	52.510644°N	11.180309°E
	<i>pannonica</i>	22	1.16	12.4	Eg semirosulate, pl-monocarpic	Dry and sandy, partly ruderal or rocky xerothermic grasslands	51.527867°N	11.890091°E
<i>Centaurea</i>	<i>scabiosa</i>	39	1.19	11.4	Sg semirosulate, pl-polycarpic	Calcareous dry and semidry grasslands, dry meadows and shrubland	51.528795°N	11.889641°E
	<i>stoebe</i>	35	1.56	11.6	Eg semirosulate, pl-monocarpic	Dry and sandy, partly ruderal or rocky xerothermic grasslands	51.528795°N	11.889641°E
<i>Dianthus</i>	<i>deltoides</i>	33	2.02	11.6	Eg erosulate, pl-polycarpic	Dry and sandy grasslands, rare in arid environment	52.510644°N	11.180309°E
	<i>carthusianorum</i>	50	3.42	10.7	Semi-eg semirosulate, pl-polycarpic	Xerothermic grasslands, dry slopes and borders of forests	51.534788°N	11.902825°E

Minimum precipitation in July, maximum aridity in the growing season, and mean temperature of April have been derived from a species macroclimatic niche analysis (see text). Growth form and habitat type are listed according Jäger & Werner (2005).

Sg, summergreen; eg, evergreen; pl, plurennial.

Table 2 Overview about the geographical location and the climate of the three study regions

Study region	Latitude	Longitude	Altitude a.s.l. (m)	Temperature in April (°C)			Summer precipitation (mm)		
				Mean	2009	Predicted	Mean	2008	Predicted
Schorfheide-Chorin	52°47'24.8"–53°13'26.0"N	13°23'27"–14°8'52.7"E	3–140	8.1	12.9	10.5	180	100	163
Hainich-Dün	50°56'14.5"–51°22'43.4"N	10°10'24.0"–10°46'45.0"E	285–550	7.1	11.5	9.8	215	136	175
Schwäbische Alb	48°20'60.0"–48°32'3.7"N	9°12'13.0"–9°34'48.9"E	460–860	6.8	10.2	9.4	290	316	270

Climate data are representative mean values for each region, derived from the WorldClim dataset (means between 1930 and 1990, Hijmans *et al.*, 2005; <http://www.worldclim.org>). Values for summer precipitation (June–August) in 2008 and mean temperature in April in 2009 were provided by local climate stations (Angermünde, Mühlhausen-Görmar, Münsingen-Apfelstetten). Predicted values refer to the period 2021–2050 according to the SRES-A1b climate change scenario from the CIAT database (Ramirez & Jarvis, 2008; <http://gisweb.ciat.cgiar.org/GCMPPage>).

percentile of July precipitation encountered throughout the distribution range. Alternatively, we estimated values for maximum drought in the growing season (mean monthly temperature >5 °C), by calculating monthly values of aridity (Trabucco & Zomer, 2009) to quantify precipitation availability over atmospheric water demand. Niche values for warm spring temperatures were calculated as the 99th percentile of mean April temperature values throughout the range.

Experimental sites (Exploratories, land use)

The experiment was set up in the framework of the German Biodiversity Exploratories (see <http://www.biodiversity-exploratories.de>; Fischer *et al.*, 2010). In three distant study regions in Germany (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb, for details see Table 2 and Fischer *et al.*, 2010), 45 experimental plots were used for this study, comprising three different grassland land-use types (meadows, pastures, mown pastures). Schorfheide-Chorin is located in NE Germany, Hainich-Dün is close to Germany's geographical centre and the Schwäbische Alb is located in SW Germany. The difference in current summer precipitation and spring temperature between the three regions is about two times larger than the expected changes according to the A1F1 climate change scenario (Table 2). In all three regions, each of the three land-use types was replicated five times (except in Schwäbische Alb: six pastures and four mown pastures). Meadows were mown twice or three times per year, and in addition, received fertilizer. Mown pastures were grazed and mown once per year and additionally fertilized in Hainich-Dün and Schwäbische Alb. Pastures were only grazed and received no additional fertilization.

Climate change manipulation

Since current regional climate change predictions for Central Europe (Spekat *et al.*, 2006) assume an earlier start of the growing season, as an effect of increasing spring temperatures, and prolonged summer drought periods, we decided to

simulate these two particular aspects of climate change. Two subplots were established in each plot, one was manipulated by placing open top chambers (OTCs) in spring (April 2009) and RSs in summer (July 2008), increasing temperatures in spring and drought in summer, the other subplot was used as nonmanipulated control.

The OTCs measured 2 m × 3 m, had a height of 1.4 m and were made of a PVC tube construction with a 0.2 mm thick greenhouse plastic (UV 5 coex-foil made of ethylene vinyl acetate copolymers; folitec Agrarfolien-Vertriebs GmbH, Westerbürg, Germany) enclosing all four sides. The same tube construction was used for the RSs, removing the greenhouse plastic from the sides and using it as a top cover. Soil moisture and temperature (aboveground and at 10 cm soil depth) were measured every half an hour by moisture sensors (ECH2O, type EC-5; Decagon Devices, Inc., Pullman, WA, USA) and temperature sensors (Thermochron® iButton; Maxim Integrated Products, Inc., Sunnyvale, CA, USA) in three plots per exploratory region and recorded by a data logger (Em5b; Decagon Devices, Inc.). Differences between the control and climate change plots were tested for significance with pair wise *t*-tests.

Phytometers

Seeds of all species were collected in summer 2007 in Central Germany (for sampling locations, see Table 1) and seedlings were raised under controlled standardized conditions in a glasshouse in spring 2008. We refrained from accounting for putative intra-specific variation in species responses because evidence for different responses in provenance at this geographic scale has been found to be of minor importance (Weißhuhn *et al.*, 2011). Instead we aimed at using a single provenance of each species that was sampled from closely adjacent sites, thus avoiding the additional complexity of differences in local adaptations of target species. Accordingly, the seeds were sampled in climatically very similar lowland sites in Saxony-Anhalt, covering two adjacent soil-climate-regions (Roßberg *et al.*, 2007). The climate data from the two meteorological station closest to the respective sampling sites

(ca. 20 km) only differ by 7 mm in monthly precipitation (SD 5.42) and by 0.075 K in monthly mean temperature (SD 0.28).

In June 2008, the raised individuals had reached an age of 16 weeks and were planted in the plots (one individual per species in each subplot) and watered once to ensure initial establishment. At the time of planting, eight individuals of each plant species were harvested to obtain initial dry biomass data for calculating relative growth rates (RGR). Roots and shoots were separated and dried for 42 h at 70 °C. The same procedure was carried out for each planted individual at the end of the experiment in May 2009. Survival of each individual plant, RGR according to Hunt (1990) and shoot–root ratios were used for further statistical analyses.

Statistics

The data (survival, RGR of total biomass and shoot–root ratio) were analysed with generalized linear mixed effect models (GLMM). For survival, a logit-link function and binomial error distribution were used, while the GLMM for all other response variables had an identity-link function and Gaussian error distribution. The fixed factors were study region (Alb, Hainich, Schorfheide), climate change treatment (climate change, control) and land use (meadow, pasture, mown pasture). Minimum July precipitation, maximum monthly aridity in the growing season and maximum April temperature as obtained from the species' macroclimatic niche served as continuous covariable in separate models. Plot identity (nested within study region and land-use type) and genus entered the models as random factors. In a first step, linear mixed effect models were fitted that included the following interactions according to our hypotheses: study regions \times climate change manipulation (Hypothesis 1), land use \times study region and land use \times climate change manipulation (Hypothesis 2), and the interaction of the minimum July precipitation, maximum monthly aridity and the maximum April temperature as derived from the macroclimatic niche analysis with climate change, study region and land use (Hypothesis 3). In a second step, each model was optimized by removing insignificant interactions. Optimization was based on maximum-likelihood parameter estimation and continued until the lowest Akaike Information Criterion value was reached or when only the

main effects remained in the model (Zuur *et al.*, 2009). The probabilities and estimates of the final models were then calculated using restricted maximum likelihood estimation, as recommended by Zuur *et al.* (2009). All statistical analyses were computed in SAS 9.1 (proc glimmix; SAS Institute Inc., 2002, Cary, NC, USA). Graphs were produced with R 2.10.1 (R Development Core Team 2009, Vienna, Austria), using the least square estimates and standard errors from proc glimmix.

Results

Climate change manipulation

The OTCs in spring 2009 increased soil and air temperature between 0.2 and 0.69 K (Table 3). Soil moisture was merely affected (Hainich-Dün and Schorfheide-Chorin) or even slightly increased on the climate change plots (Schwäbische Alb).

The treatment effect of the RSs in summer 2008 was much more pronounced and also resulted in larger differences between the study regions (Table 3). Soil moisture reduction on the climate change plots ranged between 14.1 and 3.7 percentage points in water content (i.e. percentage soil water content in the control minus percentage soil water content in the climate change treatment) in the Schwäbische Alb and Hainich-Dün, respectively. In the Schwäbische Alb, the RSs also increased soil and air temperature at a higher level than the OTC's in spring 2009 (Table 3).

Plant responses

Table 4 shows all effects of the optimized models for survival, RGR of total biomass and shoot–root ratio, using region, climate change treatment, land use and the first percentile of July precipitation in the species' distribution range as predictors. In general, the models based on maximum monthly aridity instead of summer drought (mean first percentile of July precipitation)

Table 3 Mean differences between plots with simulated climate change and control plots

Manipulation	Study region	Temperature (in K)		Moisture (in Δ vol.%)
		Air (10 cm height)	Soil (10 cm depth)	Soil (10 cm depth)
Increased spring temperature (OTC)	Alb	0.69 \pm 0.06***	0.45 \pm 0.02***	1.7 \pm 0.6*
	Hainich	0.39 \pm 0.01***	0.30 \pm 0.01***	0.8 \pm 0.5
	Schorfheide	0.36 \pm 0.01***	0.20 \pm 0.01***	–0.2 \pm 0.8
Summer drought (RS)	Alb	1.15 \pm 0.06***	0.84 \pm 0.04***	–14.1 \pm 1.5***
	Hainich	0.32 \pm 0.06***	–0.03 \pm 0.01	–3.7 \pm 0.5**
	Schorfheide	0.53 \pm 0.06***	0.08 \pm 0.01*	–6.3 \pm 2.9*

Moisture refers to the difference in per cent soil water content between the climate change and the control treatment. Significant differences are indicated as follows: *** P < 0.001, ** P \leq 0.01, * P \leq 0.05.

OTC, open top chamber; RS, rain shelter.

Table 4 Results of the generalized mixed models for survival (with logit-link function and binomial error distribution) as well as relative growth rate (RGR) of total biomass ($\text{g g}^{-1} \text{ week}^{-1}$) and shoot–root ratio (g g^{-1}) (with identity-link function and Gaussian error distribution), based on REML parameter estimation

Source of variation	df	Survival	RGR total biomass	Shoot–root ratio
		F-value	F-value	F-value
Region	2	15.10***	1.95	0.30
Climate change	1	25.52***	4.71*	0.46
Region × climate change	2	11.30***	0.92	–
Land use	2	3.35*	3.97*	0.91
Region × land use	4	2.57†	1.23	–
Climate change × land use	2	–	3.62*	–
Region × climate change × land use	3	–	2.71*	–
JulyPrec	1	3.39†	34.07***	18.33***
Region × JulyPrec	1	–	–	–
Climate change × JulyPrec	1	–	–	–
Land use × JulyPrec	1	4.06*	–	–

Plot (nested in study region and land-use type) and genus were considered random factors in the models. Significant effects are indicated as follows: *** $P < 0.001$, * $P \leq 0.05$, † $P \leq 0.1$.

JulyPrec, first percentile of July precipitation in the species' distribution range; REML, restricted maximum likelihood.

gave nearly identical results (minor differences in a few significance values), as both variables were strongly correlated ($r = 0.864$, $P = 0.026$). The inclusion of spring warmth (mean maximum April temperature) revealed even smaller differences in the model results since the

correlation with July drought ($r = -0.915$, $P = 0.011$) is even higher.

Thus, in Table 4 and in the following discussion only the results based on tolerated macroclimatic summer drought (minimum July precipitation) as macroclimatic niche property are given.

Survival

The survival of the plants differed strongly between study region and climate change treatment (Table 4). Survival in the Alb with a mean survival rate of 81.9% was about two times larger than in the Schorfheide (38.9%) and four times larger than in the Hainich (18.8%; Fig. 1a). The climate change treatment had an overall negative impact on survival compared to the control, reducing survival rates to more than half (Fig. 1b). However, the effect differed between study regions, indicated by a significant interaction of study region with climate change (Table 4). At the coldest and wettest site (Alb), survival rates were highest and did not differ between climate change treatments, whereas summer drought and spring warming had negative effects at the other sites, in particular in the Hainich, where only a few individuals survived in the climate change treatment (Fig. 1c).

Survival also differed between land-use types (Table 4). Most individuals survived in mown pastures (53.5%) compared to uniform land use in pure pastures (42.6%) or meadows (43.8%). In contrast, summer drought resistance, measured as the first percentile of July precipitation in the geographical distribution range, had only marginal effects on the species' survival rate, but showed significant interactions with land use (Table 4). Species that had niches extending into drier areas survived better in land-use types with a regular mowing regime, i.e. in meadows and mown

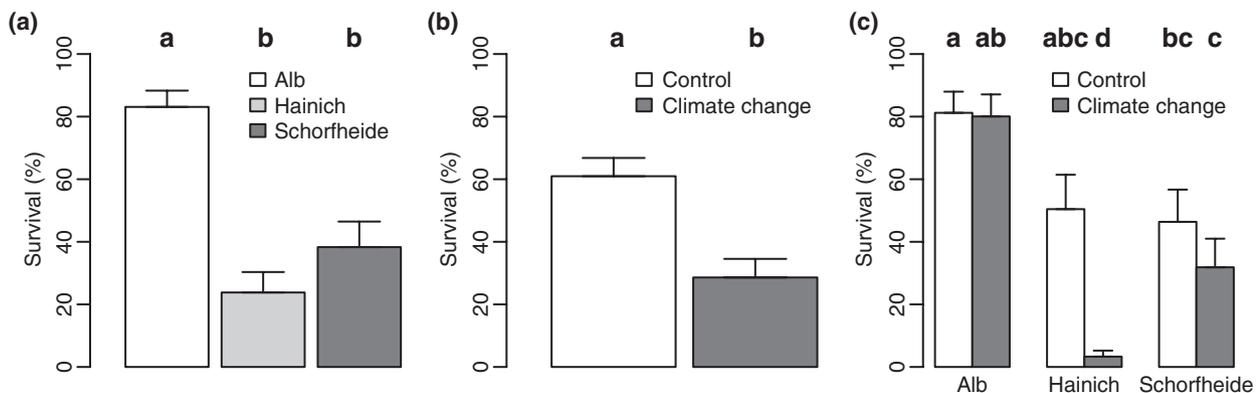


Fig. 1 Survival rates (\pm SE) of the transplanted species (a) in the three different study regions, (b) under simulated climate change and in the control plots and (c) under simulated climate change and in the control plots, separately by regions. Small letters indicate significant differences according the Tukey *post hoc* test. For statistical details, see Table 4.

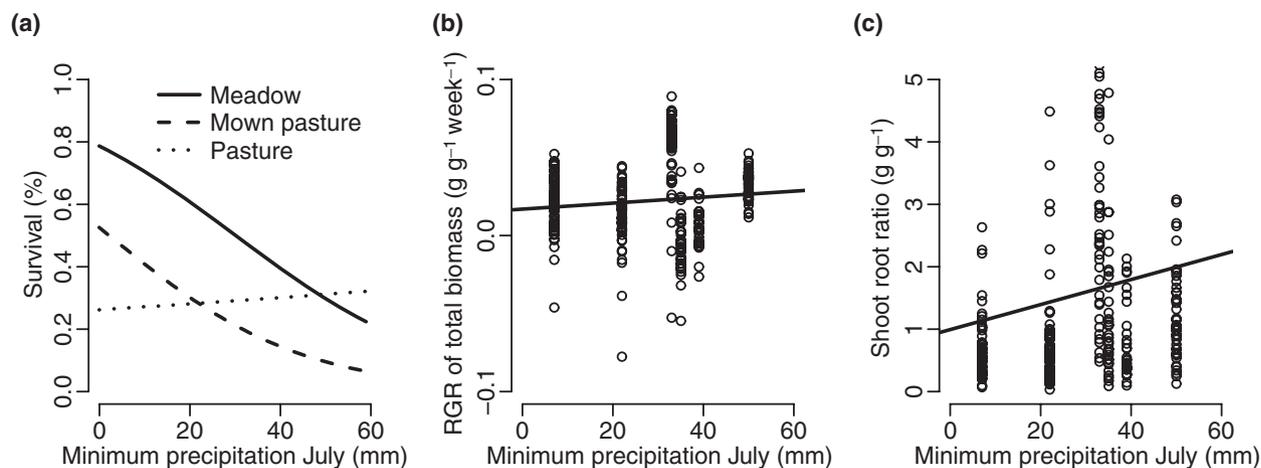


Fig. 2 Effect of the species' macroclimatic drought tolerance, expressed as the first percentile of July precipitation in the species' geographical distribution, on (a) plant survival rates in the three different land-use types, as estimated by the generalized linear mixed model with logit-link function, (b) relative growth rates (RGR) of total biomass and (c) shoot-root ratio of the phytometer species, showing raw data and regression lines as estimated by the generalized linear mixed model with identity-link function. For statistical details, see Table 4.

pastures (Fig. 2a). In contrast, macroclimatic summer drought tolerance seemed not to play any role for survival in pastures (Fig. 2a).

Growth performance

Study region was not decisive for growth performance of the plants (Table 4). Similar to the results for survival, the climate change manipulation was detrimental and reduced RGR of total biomass to about 21.1% compared to the control. Furthermore, type of land use resulted in differences in RGR of total biomass (Table 4). The RGR of total biomass of the survived plants was significantly higher in mown pastures (mean \pm SE, $0.0298 \pm 0.0031 \text{ g g}^{-1} \text{ week}^{-1}$) compared to pastures ($0.0201 \pm 0.0025 \text{ g g}^{-1} \text{ week}^{-1}$) and meadows ($0.0171 \pm 0.0029 \text{ g g}^{-1} \text{ week}^{-1}$). In addition, the effect of the climate change manipulation on RGR of total biomass differed between land-use types (Table 4; Fig. 3a). The relative reduction in growth caused by the climate change manipulation was lowest in mown pastures (-9.2%) compared to pastures (-34.4%) and meadows (-26.9%). However, the amount of growth reduction caused by simulated climate change was different in the three study regions with respect to land-use types (Table 4). In the Alb, the largest growth reduction was recorded for meadows (Fig. 3b). In contrast, in the Hainich and the Schorfheide, growth reduction caused by the climate change manipulation was highest in pastures (Fig. 3c and d).

Among all response variables, the species' macroclimatic drought tolerance, derived from minimum July precipitation in the species distribution range, was

found to have the largest general effect on RGR (Table 4). The RGR of total biomass decreased with increasing macroclimatic drought tolerance (Fig. 2b). This relationship between growth performance of species and macroclimatic drought tolerance did not differ between study regions, land-use types or climate change treatments, as seen in the absence of significant interactions in Table 4. For example plant growth responses to experimental climate change simulation were quite species specific (Fig. S1).

Allocation pattern

Shoot-root ratios did not differ between study regions, land-use types or climate change treatments (Table 4). The species differed solely in shoot-root ratio in relation to macroclimatic drought tolerance measured as minimum July precipitation encountered in their distribution range (Table 4). Species with a higher macroclimatic drought tolerance showed smaller shoot-root ratios than species that were macro-climatically less drought tolerant (Fig. 2c). As for RGR of total biomass, there were no significant interactions with regions, land-use types or the climate change treatments (Table 4).

Discussion

The survival of phytometer plants was affected by both the climatic differences between the three exploratory regions and the climate change treatment effects. As assumed in the first hypothesis, both treatments had similar effects on the plants, as survival rates decreased

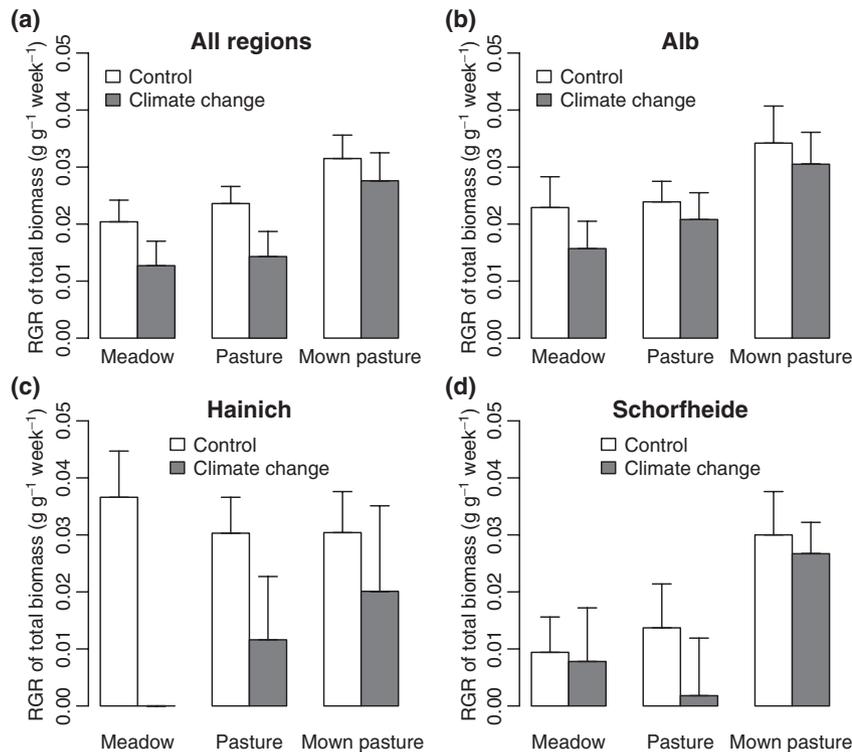


Fig. 3 Relative growth rates of total biomass (\pm SE) as a function of land use and climate change treatment for (a) all regions, (b) Schwäbische Alb, (c) Hainich-Dün, and (d) Schorfheide-Chorin. For statistical details, see Table 4.

with increasing mean annual temperature and decreasing precipitation in the three study regions (control plots) as well as under manipulated climate change resulting in summer drought. Hence, this is a justification for space-for-time approaches, complementing manipulative climate change experiments. However, as hypothesized we detected regional differences in effect sizes of the climate change treatments. While the climate change treatment had no effect on survival at the wettest site (Schwäbische Alb), there was a significant reduction at the other two sites. As all planted species naturally occur in mesic to semidry grasslands (Jäger & Werner, 2005), the consistently higher mortality cannot be attributed to the species' particular sensitivity. On the contrary, from the results we can conclude that increasing summer drought in regions with low precipitation might present a risk also to populations of rather drought tolerant plant species. Although the effects of manipulated climate change on the abiotic environment (soil moisture and temperature) were greatest in the Schwäbische Alb, it can be assumed that the general moister conditions have buffered the impact of the experimental drought.

Overall, these results point out the necessity to consider regional variation of climate change effects below the spatial scale of biomes, for which already strongly

different responses have been reported (Parmesan, 2006; IPCC, 2007). Ecoregion- or even landscape-specific response patterns have also been reported by Heisler-White *et al.* (2009) from three different grassland sites in the Central Plains Region of North America. The authors showed that changes in aboveground net primary productivity as response to simulated extreme rainfall regimes differed between study sites according to differences in the sites' mean annual precipitation. Our findings also explain contrasting findings in monitoring studies on climate change effects. For example, while Vittoz *et al.* (2009) found comparably low impacts of climate change on subalpine grasslands in the Swiss Northern Alps, Pauli *et al.* (2007) showed rapid range shifts of plant species in Tyrol in Austria. According to our results, changes in species survival, and thus in occurrence, can be expected to be more rapid and to occur to a greater extent even in climatically slightly stressful regions. As we have shown, this does not only apply to extreme biomes such as alpine or desert habitats (Brown *et al.*, 1997; IPCC, 2007; Pauli *et al.*, 2007; Kelly & Goulden, 2008), but also to regional differences within mesophilous grasslands. However, the overall survival rate was not lowest at the driest site, which shows that there is some variation not accounted for by region alone, such as for example variation in soil

properties or differences in land-use intensity within regions.

The planted phytometers showed also differences in survival and growth rates between land-use types. As hypothesized, we encountered interactive effects of land-use management with manipulated climate change. Across all regions plants grew better in mown pastures and additionally, in this land-use type the negative effect of simulated climate change was lower than in grasslands that were uniformly managed as meadows or pastures.

Among all studied land-use types mown pastures receive the highest management intensity as they were mown, grazed and additionally fertilized. Fertilization might have partly compensated for the negative climate change effects. In a warming experiment Sardans *et al.* (2008) have shown that warming by 1 °C decreased N leaf concentrations of shrub species by 25%. The underlying causes were not altered allocation patterns but probably changes in soil N availability. Consequently, the comparably high N supply in mown pastures might mitigate climate warming effects. Although the meadows in the three study regions received even higher levels of fertilizers than the mown pastures, they might have provided less favourable conditions for the phytometers due to stronger competition effects from a higher and denser stand structure. In contrast, disturbance in pastures was higher and biomass removal was more selective than in mown pastures. Higher disturbances can not only lead directly to plant mortality but overgrazed microsites are also more susceptible to drought (Ryser, 1993). This might be particularly problematic in very intensively grazed sites with high stocking rates (Kemp & Michalk, 2007).

As both, grazing and mowing are combined in mown pastures, the discussed negative effects for herb species survival might have been less detrimental compared to plots with a uniform management. Probably the mitigating effect of mown pastures has been the combination of resource supply with lower competition intensity and lower physical disturbance. In consequence, if mown pastures provided a more balanced habitat for mesophilous grassland species, this land-use type might be generally more able to buffer climate change effects. In contrast, for pastures and meadows, local aspects might play a more important role in mitigating climate change impacts. Climate change effects were better buffered in meadows in the Schorfheide-Chorin and in pastures in the Schwäbische Alb. In conclusion, for conservation strategies concerning changing climatic conditions, potential land-use changes between grassland management types should be considered very carefully.

In contrast to our third hypothesis, the measured plant species responses along the environmental gradient of the exploratory regions and under simulated climate change were not clearly predictable from their macroclimatic niche properties. No evidences were found that species with a higher summer drought tolerance in their geographical range performed better under drier conditions and *vice versa*. Consequently, we have to conclude that species' local responses to changing climate cannot by default be derived from their macroclimatic niche characteristics but might be strongly affected by further drivers in a complex manner. Macroclimatic niche properties seemed to be related to some extent to general growth performance patterns. Species with a higher summer drought tolerance in their geographic range did not only show lower growth rates and lower shoot-root ratios but also performed better in land-use types with a regular mowing regime. Drought-adapted species have often been shown to allocate more resources to belowground biomass (Jackson *et al.*, 1996; Schulze *et al.*, 1996), especially in early developmental stages (Padilla *et al.*, 2007, 2009). In addition, being stress tolerators, these species also display lower growth rates, thus representing inferior competitors *sensu* Grime (1977). In grasslands with regular cuts, strong herbaceous competitors are less frequent. Consequently, drought tolerant species might take advantage of reduced competition, which in this study seem to be reflected in higher survival rates in meadows and mown pastures. In contrast, the more randomly occurring disturbances in form of trampling and grazing in pastures may have led to the observed overall average survival rates of both, geographically drought tolerant and drought sensitive species. In consequence, our results indicate that on smaller spatial and temporal scales, the competitive and probably compensative abilities of species might play a more important role for survival and growth under climate change than the macroclimatic niche properties of a plant species.

Conclusion

Macroclimatic niche properties were found to be related to general growth patterns, but were not sufficient to directly predict plant responses to global climate change. Depending on ecoregion, landscape, or even management practices, species might show strongly varying, yet partly contrary local responses. Consequentially, anticipatory conservation and management strategies require improved climate change predictions with stronger model regionalization and consideration of interactions with land use variables.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Effect of the climate change treatment to relative growth rates of total biomass. Am, *Achillea millefolium*; Ap, *Achillea pannonica*; Csc, *Centaurea scabiosa*; Cst, *Centaurea stoebe*; Dc, *Dianthus carthusianorum*; Dd, *Dianthus deltoides*. For species characteristic, see Table 1.

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