Relationship between fundamental and realized niches in terms of frost and drought resistance

Vztah mezi fundamentální a realizovanou nikou s ohledem na odolnost vůči mrazu a suchu

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The objective of the present study was to relate the fundamental niches of 16 grassland species, defined in terms of their frost and drought tolerance, to their realized macroclimatic niches derived from the geographical distributions of the species. Eight species pairs each consisting of two congeneric species with different distributions and exposed to different levels of frost and drought stress were selected. The ranges of the two species in each genus differed in the degree to which their geographical ranges extended into cold or dry regions. Frost resistance was analysed by measuring electrolyte leakage and expressed as temperature at which 50% leakage occurred (LT_{50}). The genera investigated responded differently to frost stress. In two genera, the species with ranges extending into colder regions showed a lower LT_{50} than species confined to warmer regions. In two other genera, the opposite pattern was recorded and the species in the remaining genera did not differ in their frost resistance. Responses to drought stress were quantified by recording their responses to different moisture treatments in a glasshouse experiment. No differences in the responses to drought stress were recorded for species with geographical ranges that extended differently into dry regions. In general, there was only a poor match between fundamental and realized niches for only a few genera and only for resistance to frost and not drought. Thus, it is not possible to predict the geographical distribution ranges of two congeneric species based on their performance in experiments, and vice versa. Therefore, it is likely that the assumptions made in modelling species distributions are incorrect and as a consequence the forecasts of future distributions of species based on these models unreliable.

Keywords: biogeography, drought stress, electrolyte leakage, frost stress, geographical distribution range, grassland species, LT_{50}, macroclimatic niche, range boundary

Introduction

The distributional range of a species can be conceived as the geographical expression of its realized niche (Thompson et al. 1998, Holt et al. 2005). The realized niche is a subset of the fundamental niche, i.e. the range of environmental conditions the organism can tolerate when not restricted in its distribution by biotic interactions and dispersal (Hutchinson 1957, Pulliam 2000). In general, a causal link between fundamental and realized niche is expected because the limits of geographical ranges are supposed to be influenced by ecophysiological properties (Sakai & Larcher 1987, Jäger 1990, Milnes et al. 1998). Numerous concepts are based on this assumption and there is ample evidence of correlations between realized and fundamental niches. For example, Silvertown et al. (1999) showed that the hydrological realized niches of meadow species in the UK correspond to the fundamental niches determined experimentally by Ellenberg (1953). Among the environmental niche variables, climatic factors are important because they are thought to be the main limiting factor determining the patterns in large scale distributions of plants (e.g. Woodward 1987, Huntley et al. 1995, Sykes et al. 1996, Pearson & Dawson 2003, Svenning & Skov 2005). Since the influential study of Sykes et al. (1996), many studies on realized niches and models of the effect of climate change on distribution use variables like water balance and minimum temperatures (e.g. Normand et al. 2009, Kearney et al. 2010, Austin & Van Niel 2011).

In particular, frost and drought can be of paramount importance because their direct physiological effect on survival and growth (Larcher & Bauder 1981). For example, a reciprocal transplantation experiment along an altitudinal gradient in California revealed that frost restricted the distribution of *Mimulus cardinalis* (Angert 2006). Frost resistance is often reflected in a species' morphology. For example, leaves with a higher frost resistance usually have higher leaf dry matter content (LDMC) and leaf carbon content (LCC), less water available for freezing and are more resistant to dehydration (Morin et al. 2007). Furthermore, a lower specific leaf area (SLA) is associated with a reduction in the incidence of frost injury to leaves (Coopman et al. 2010).

Similarly, drought stress is invoked as a factor determining the limits of the distribution of plant species (e.g. Prince & Carter 1985). Depending on duration and intensity, drought stress limits the physiological activity of plants (Zavalloni et al. 2009). Extreme drought results in reduced rates of dry matter accumulation (Simane et al. 1993) and growth rates (Belaygue et al. 1996, Tardieu et al. 2000). Drought might result in the death of single plants as well as the extinction of whole populations (Xiang et al. 2007). Thus, many species of plants are adapted in different ways to drought stress. A higher investment in root biomass is required to improve water uptake in dry habitats, resulting in a higher root/shoot ratio (Schulze et al. 1996, Schwinning & Ehleringer 2001, Walck et al. 2001). Another way of reducing the incidence of drought stress is a low SLA, resulting in reduced area-based transpiration rates (Wright et al. 2004, Monclus et al. 2006, Matías et al. 2012).

The aim of the present study was to experimentally test whether there is a causal link between fundamental and realized niches in terms of frost resistance and drought tolerance. For this purpose, it is advantageous to compare congeneric species with similar habitat requirements and growth forms but with different types of ranges (Jäger 1992), thus, allowing phylogenetically valid comparisons. Phylogenetic relatedness has to be taken into consideration as closely related species tend to be more similar in their trait values, and thus also probably in their niches, than expected by chance (Felsenstein 1985, Villar et al. 2006). Confining comparisons to congeneric species, thus, avoids misinterpreting evolutionary heritage as adaptive characteristics.

We tested the relationships between realized and fundamental niches both with respect to frost and drought resistance. The first hypothesis tested states that species with a geographic range extending into colder regions are more frost-resistant than species with a distribution range confined to warmer regions. In addition, we tested whether frost resistance was related to particular leaf traits. In particular, we expected that leaves with a tougher lamina, low specific leaf area (SLA), high leaf carbon content (LCC) and high leaf dry matter content (LDMC) would be less susceptible to freezing. Secondly, we hypothesized that species with a distribution range confined to more humid regions are more susceptible to drought stress than species with a distribution range extending into drier areas. In particular, we expected that drought adaptation will be reflected in a higher investment in root biomass and a lower specific leaf area (SLA) to reduce transpiration.

Material and methods

Species selection

We selected eight genera with two species each that were typical of grassland and had a similar growth form but differed in their geographical distributions (Jäger 1992) (Table 1, for distribution maps see Electronic Appendix 1–8). The macroclimatic features of the niches of the species were based on detailed digitized distribution maps of all species presented in ArcMap 9.1 (ESRI). The distribution dataset was based on information in Meusel et al. (1965) and Meusel & Jäger (1992) and completed and updated with data from online databases and floristic atlases (see Electronic Appendix 9). Values for the minimum temperature of the coldest period and annual precipitation per year were obtained from the WORLDCLIM dataset (Hijmans et al. 2005), which is presented in a 2.5 arc minutes grid (corresponding to a cell size of about 25 km^2 at the equator), for the distribution ranges of all species. Climate data were obtained for all grids cells where the species was present. Percentiles for the climate variables were derived from the resulting histograms. Macroclimatic frost niches were defined as the lowest 1%-percentile of the minimum temperature of the coldest period across all the cells where the species occurred. In the same way, drought niches were obtained by computing the lowest 1%-percentile of annual precipitation throughout the range (Table 1). In the following, we use the term "cold range type" for the species of a pair with the lower macroclimatic minimum temperature, whereas the species with the higher minimum temperature is referred to as "warm range type". Similarly, the species of a pair with low precipitation in the driest quarter throughout the distribution range is referred to as "dry range type", while the species growing in areas with high precipitation values is called "moist range type".

Seeds of all species were collected in summer 2007 in central Germany and the Czech Republic (Table 1). Every species was collected from one locality, except for *Achillea pannonica*, for which not enough seed germinated from a single provenance, and thus, plants from two closely located populations were used. The plants for both experiments were germinated in spring 2008 and then raised in 8.5 × 8.5 × 8 cm pots containing standardized soil (two parts compost and one part sand) without fertilizer and under controlled conditions in a glasshouse. Preceding trials had shown that the soil used was equally favourable for all the species studied. For Experiment 1 the plants were transferred in October 2008 to an outdoor bed in the Botanical Garden, thus allowing for acclimatization. For Experiment 2 the plants were transferred in September 2008 into an experimental chamber in the glasshouse.

Experiment 1: frost resistance

Frost resistance was expressed as tolerance of a single frost event and was tested in a climate test chamber (SANYO Atmos Chamber MTH-4400) for 9 hours starting at 8:00 a.m. and using 11 temperature treatments (control at +4°C, –6°C, –9°C, –12°C, –15°C, –18°C, –21°C, –24°C, –27°C, –30°C and –40°C) with eight replicates per treatment, resulting in a total of 88 replicates per species. Prior to the experiment, the plants were acclimated outdoors (October 2008 till February/March 2009). In all experiments, the two congeneric species of a pair (Table 1) were simultaneously exposed to the frost treatments, thus pooling any potential error of the temporal replication of the frost experiment with genus-specific differences.

Table 1. – Minimum temperature of the coldest period (from the WORLDCLIM dataset) and resulting range based on frost resistance (cold/warm), annual precipitation and resulting range type for drought resistance (dry/moist) and the location where the plant material was collected and type of experiments in which the species were used. Because of low germination rates of *Achillea pannonica* two closely located populations were used in these experiments.

Genus	Species	Minimum temperature of the coldest period [°C]		Annual precipitation [mm]		Location collected		Type of experiment	
						Latitude (°N)	Longitude (°E)	Frost	Drought
Achillea	*millefolium*	–43.6	cold	199	dry	52.510644	11.180309	x	x
	pannonica	–11.0	warm	396	moist	51.527867	11.890091	x	–
						51.534893	11.908932	–	x
Carlina	*biebersteinii*	–27.1	cold	–	–	48.805876	16.646231	x	–
	vulgaris	–13.1	warm	–	–	51.547828	11.946354	x	–
Centaurea	*scabiosa*	–	–	287	dry	51.528795	11.889641	–	x
	stoebe	–	–	324	moist	51.503299	11.945023	–	x
Dianthus	*carthusianorum*	–11.4	warm	505	moist	51.533204	11.981404	x	x
	deltoides	–23.0	cold	491	dry	52.510644	11.180309	x	x
Inula	*conyzae*	–	–	467	moist	50.963212	11.596487	–	x
	hirta	–	–	323	dry	51.534788	11.902825	–	x
Koeleria	*macrantha*	–36.7	cold	145	dry	51.532948	11.914366	x	x
	pyramidata	–10.0	warm	502	moist	51.592711	9.949324	x	x
Scabiosa	*columbaria*	–10.3	warm	416	moist	51.592711	9.949324	x	x
	ochroleuca	–34.3	cold	265	dry	51.533204	11.981404	x	x
Silene	*nutans*	–27.6	cold	252	moist	51.592302	9.948576	x	x
	otites	–22.7	warm	138	dry	51.527867	11.890091	x	x

The frost experiment lasted about 9 hours and the temperature levels were consecutively applied, lasting for 45 min per temperature treatment. At the end of each temperature treatment, plant material from all eight replicates per treatment was removed from the climate test chamber and stored at +4 °C, the remaining samples were cooled down to that of the next temperature treatment. The next day, disks (with a diameter of 5 to 15 mm) or pieces (with 8 mm length) were cut from the leaves and transferred into 10 ml 3% isopropanol solution. Subsequently, frost damage was measured as electrolyte leakage according to Kathke & Bruelheide (2011). Frost injury results in an increase in electrolyte conductivity because the formation of intracellular ice destroys the cell membrane and plasma escapes from the cell into the surrounding solution (Ashworth & Pearce 2002). In each sample, the temporal increase in electrical conductivity (C) in the solution over time was measured at six points in time using a laboratory roboter with a conductivity electrode (Metrohm). The initial conductivity C_0 (t = 0 h) recorded at the beginning of the measurement series was used to determine potential contamination of leaves, and thus, define the baseline for electrolyte leakage. Further conductivity measurements C_1, C_2, C_3 and C_4 were recorded on the four days following the exposure to frost (t = 4 h, 24 h, 48 h and 72 h, respectively). After the final measurement, the tissue samples were boiled for 20 minutes, which resulted in complete destruction of the cell membranes and maximum release of all ions into the isopropanol solution. This measurement is referred to as C_b and served as a tissue-specific reference for the maximum potential conductivity, thus allowing us to calculate the relative conductivities (RC) according to formula (1).

$$(1) \qquad RC = \frac{C_t - C_0}{C_b - C_0} = 1 - e^{-k \cdot t} \quad .$$

Based on the conductivity dataset, the rate of electrolyte leakage was determined for every species from the regression parameter k in a nonlinear regression according to Murray et al. (1989).

The slope k of the increase in electrolyte leakage with time (t) is a measure of the degree of cell injury from membrane damage, which is mostly brought about by intracellular ice formation. Thus, for every species, the differences between the k values recorded in all the temperature treatments and in the control were assessed using a one-factorial ANOVA. Then, the minimum frost resistance is the lowest temperature, at which it does not differ significantly from the control at +4°C. In addition, the k values were fitted to a four-parameter sigmoid regression using the following formula:

$$(2) \qquad k = f(T) = d + \frac{c}{1 + e^{-\left(\frac{T-a}{b}\right)}} \quad .$$

In formula (2) a, b, c and d are estimated regression parameters and T is the temperature in °C to which the samples were exposed. Formula (2) was used to calculate LT_{50} as the temperature at which 50% of the maximum k value was reached. The LT_{50} is the point of inflection of the sigmoid curve of k values regressed on freezing temperature.

Using six plants per species from the same batch as used in the experiment and not exposing them to any treatment, we measured specific leaf area (SLA) according to Cornelissen et al. (2003), and leaf carbon content (LCC) and leaf dry matter content (LDMC) using total CN analysis (Elementar Vario EL).

Experiment 2: drought tolerance

The responses of the target species to drought stress were quantified experimentally in a glasshouse. We established five linearly increasing soil moisture treatments (5%, 10%, 15%, 20% and 25% gravimetric water content) up to the maximum water content (field capacity, 25% on average) of the standardized soil used (in the following all percentages refer to g water per 100g dry soil). Seven species pairs were used in the experiment (Table 1), with six replicates per species and per moisture level (n = 420 individuals in total). Each individual was planted in a pot (8.5 × 8.5 × 8 cm) filled with standard soil without fertilizer and placed randomly in a climate chamber and kept under the following conditions: 12 hours light at 20°C and 12 hours dark at 15°C. The plants were watered every second day to maintain the weight of a particular moisture treatment. The experiment lasted eight weeks. At the end, all plants were harvested and dry matter determined (dried at 70°C for 48 h). We calculated relative growth rates (RGR) of shoot, root and total biomass for each plant according to Hunt (1989) as well as the root/shoot ratio. Some cases of root rot resulted in a final individual number of n = 399 included in the statistical analysis. In addition, SLA was assessed using three randomly chosen intact leaves for each individual analysed, resulting in n = 337 individuals in the statistical analysis.

Statistics

In Experiment 1, across all species the effects of genus (six genera) and either the lowest 1%-percentile of mean minimum temperature in the coldest period or range type (cold versus warm, as derived from the lowest 1%-percentile of mean minimum temperature in the coldest period) were assessed for the LT_{50} value using ANCOVA with minimum temperature of the coldest period, obtained from the species' macroclimatic niche, as a covariable. For every genus, the effect of range type (cold vs warm) was tested for SLA and LCC using one-factorial ANOVAs.

In Experiment 2, the effects of range type (dry versus moist, as derived from the 1%-percentile of annual precipitation) and species nested in range type (14 species) were factorial predictors, while soil moisture treatments (gravimetric water content) entered the analysis as a continuous predictor. To account for unimodal relationships to water content, the square of soil moisture was also used in the statistical model, as well as all interactions between the main factors. In the ANOVA, the effect of range was tested against species nested in range type, while all other terms were tested against the error term. This model was applied to every measured response variable (RGR of shoot dry weight, RGR of root dry weight, RGR of total dry weight, root/shoot ratio and SLA). The full model was used to predict the responses of every species at all five levels of moisture content. Statistical tests for differences between the two species with contrasting ranges at each moisture level were derived from least square means and standard errors, using Tukey-Kramer post-hoc tests. All statistics were calculated using SAS 9.2, the glm procedure and type III SS. Graphs were produced using R 2.12.0 (R Development Core Team 2010).

Results

Experiment 1: frost resistance

Only in the two genera *Achillea* and *Carlina* were the species of the cold range type more frost-resistant than the congeneric species with a geographical distribution range in warmer regions, evident in lower LT_{50} values (Table 2). Conversely, the species of the warm range type of the genera *Koeleria* and *Scabiosa* were more frost-resistant than their cold range counterparts. The two species pairs of the genera *Dianthus* and *Silene* did not differ in frost resistance. Across all species, the ANCOVA showed no relationship between LT_{50} values and the minimum temperatures experienced by the species, neither when expressed as a 1%-percentile of the minimum temperature of the coldest period, nor when then the classification of cold vs warm range type was used (Table 3). Instead, we only recorded a significant effect of genus, with *Silene* and *Koeleria* being the least and the most frost-resistant genera, respectively (Table 2, 3).

Testing for morphological differences within every genus, we found a significantly higher specific leaf area (SLA) for species of the cold compared to the warm range type in *Achillea* ($P = 0.020$), *Dianthus* ($P < 0.001$) and *Silene* ($P < 0.001$) (Fig. 1). The species of the genera *Carlina*, *Koeleria* and *Scabiosa* did not differ significantly in SLA. A significantly higher leaf carbon content (LCC) was recorded for the species of the cold range type in the genus *Koeleria* ($P = 0.003$) and with range type in *Silene* ($P < 0.001$) (Fig. 2). The results for leaf dry matter content (LDMC) reflected those for LCC, with an additional significant difference in the genus *Dianthus* ($P = 0.015$) (Fig. 3).

Table 2. – Range type based on the minimum temperature of the coldest period and LT_{50}-values (mean ± standard error) obtained from Experiment 1. Minimum frost resistance refers to the lowest temperature in the experiment, at which the slopes of the increases in electrolyte leakage (the k values) did not differ from those of the control at +4C.

Genus	Species	Range type	LT_{50} [° C]		Minimum frost resistance [° C]
Achillea	*millefolium*	cold	–22.45	± 0.92	–15
	pannonica	warm	–17.85	± 1.65	–15
Carlina	*biebersteinii*	cold	–30.34	± 3.77	–12
	vulgaris	warm	–16.56	± 1.01	–15
Dianthus	*deltoides*	cold	–30.66	± 0.77	–27
	carthusianorum	warm	–29.77	± 0.47	–18
Koeleria	*macrantha*	cold	–30.91	± 4.66	–21
	pyramidata	warm	–36.02	± 8.35	–24
Scabiosa	*ochroleuca*	cold	–17.24	± 0.94	–15
	columbaria	warm	–19.92	± 1.27	–18
Silene	*nutans*	cold	–12.13	± 0.30	–9
	otites	warm	–11.11	± 0.41	–6

Table 3. – ANCOVA type SS III of LT_{50} values from Experiment 1 as a function of (A) the minimum temperature of the coldest period or (B) the classification cold vs warm range type (see Table 1) and genus. Df – degrees of freedom. Significant results are indicated in bold.

		df	F-value	P
A	Minimum temperature of the coldest quarter	1	0.21	0.665
	Genus	5	**5.64**	**0.040**
B	Range type	1	0.57	0.484
	Genus	5	**6.00**	**0.036**

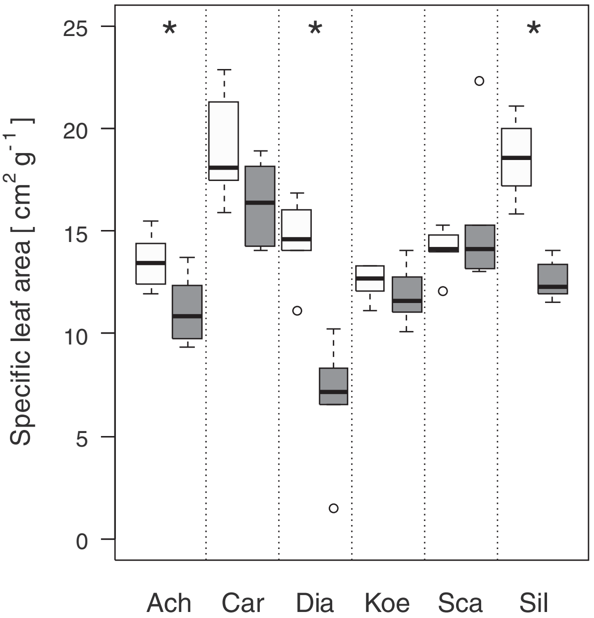

Fig. 1. – Box-and-whisker plots of specific leaf area (SLA) for all species pairs investigated in Experiment 1. Species of the cold range type are shown in dark grey; species of the warm range type in white. Ach – *Achillea*, Car – *Carlina*, Dia – *Dianthus*, Koe – *Koeleria*, Sca – *Scabiosa*, Sil – *Silene*. Box-and-whisker plots show median, upper and lower quartile and outliers (i.e. values > 1.5 times interquartile distance) of the response variable. Significant results are indicated by asterisks.

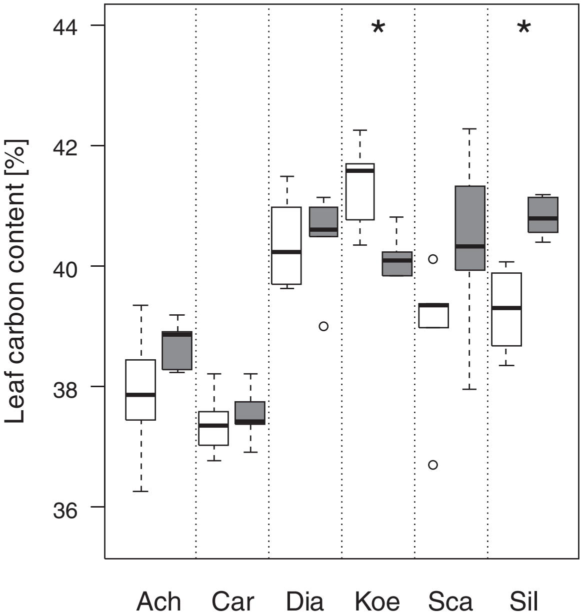

Fig. 2. – Box-and-whisker plots of leaf carbon content (LCC) for all species pairs investigated in Experiment 1. Species of the cold range type are shown in dark grey; species of the warm range type in white. Ach – *Achillea*, Car – *Carlina*, Dia – *Dianthus*, Koe – *Koeleria*, Sca – *Scabiosa*, Sil – *Silene*. Box-and-whisker plots show median, upper and lower quartile and outliers (i.e. values > 1.5 times interquartile distance) of the response variable. Significant results are indicated by asterisks.

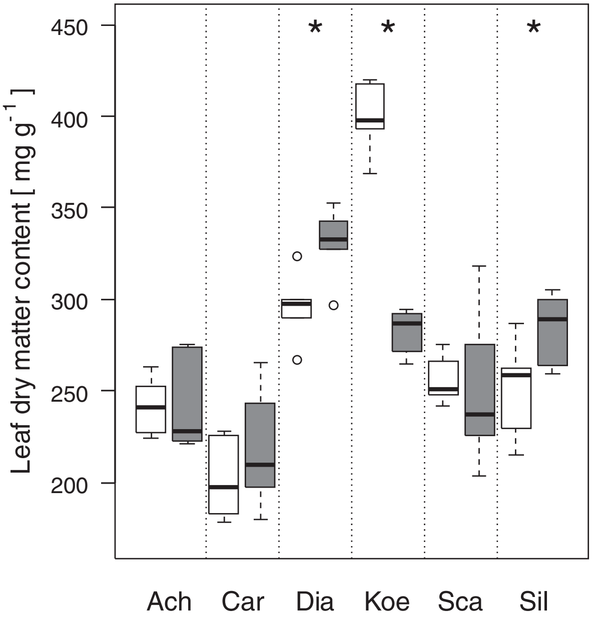

Fig. 3. – Box-and-whisker plots of leaf dry matter content (LDMC) for all species pairs investigated in Experiment 1. Species of the cold range type are shown in dark grey; species of the warm range type in white. Ach – *Achillea*, Car – *Carlina*, Dia – *Dianthus*, Koe – *Koeleria*, Sca – *Scabiosa*, Sil – *Silene*. Box-and-whisker plots show median, upper and lower quartile and outliers (i.e. values > 1.5 times interquartile distance) of the response variable. Significant results are indicated by asterisks.

Experiment 2: drought tolerance

In the drought stress experiment, no significant range type effect was recorded for any of the five response variables (Table 4). Except for the root/shoot ratio, all response variables strongly responded to soil moisture (Table 4). In all cases, the relationship with soil moisture was unimodal, as indicated by a significant effect of soil moisture squared (Table 4). As an example, RGR of root dry weight, Fig. 4 shows that 11 out of the 14 species showed higher root growth at intermediate soil water contents, a pattern that was also recorded for shoot dry weight and total dry weight (not shown). None of the response variables showed a significant interaction between moisture treatment or moisture treatment squared and range type (Table 4). In contrast, there were significant species × range type interactions for RGR of shoot dry weight, RGR of root dry weight and RGR of total dry weight. Additionally, a significant interaction was recorded between moisture treatment × species × range type for RGR of root dry weight (Table 4). In Fig. 4 these interactions are reflected in a higher RGR of root dry weight for the species of the dry range type in the genera *Centaurea*, *Inula* and *Scabiosa*, while higher root growth was recorded for the species of the moist range type in *Dianthus* and *Silene* (here only at 5% soil water content). The genera *Achillea* and *Koeleria* did not show any significant differences between range types (Fig. 4).

Table 4. – Three-way ANOVA type III SS for species pairs for the five response variables RGR of shoot dry weight, RGR of root dry weight, RGR of total dry weight, root/shoot ratio and specific leaf area as a function of soil moisture (M), soil moisture squared (M^2) and range type (R, moist vs dry) and interactions between species (S) × range type, moisture treatment × range type and moisture treatment × species × range type. Df_{num} – degrees of freedom of the numerator, df of the denominator = 12 for range and the residual error term for all other predictors, i.e. 374, 358, 357, 357 and 295 for RGR of shoot dry weight, RGR of root dry weight, RGR of total dry weight, root/shoot ratio and SLA, respectively. Significant results are indicated in bold.

Factor	df_{num}	RGR shoot dry weight [g·g^{-1}·week^{-1}]		RGR root dry weight [g·g^{-1}·week^{-1}]		RGR total dry weight [g·g^{-1}·week^{-1}]		Root/shoot ratio [g·g^{-1}]		SLA [cm^2·g^{-1}]	
		F-value	p	F-value	P	F-value	P	F-value	p	F-value	P
R	1	0.55	0.474	0.32	0.581	0.01	0.930	0.62	0.446	0.00	0.976
M	1	**7.92**	**0.005**	**14.31**	<0.001	**15.40**	<0.001	2.94	0.087	**9.03**	0.003
M^2	1	**4.12**	**0.043**	**9.20**	0.003	**9.16**	0.003	2.46	0.118	**4.89**	0.028
S × R	12	**2.63**	**0.002**	**3.34**	<0.001	**2.62**	0.002	1.17	0.303	1.13	0.335
M × R	1	0.73	0.394	1.21	0.273	0.00	0.954	1.30	0.254	0.63	0.429
M^2 × R	1	0.34	0.561	1.23	0.269	0.03	0.864	0.90	0.342	0.76	0.384
M × S × R	12	1.62	0.085	**2.46**	0.004	1.73	0.059	1.70	0.065	1.16	0.311
M^2 × S × R	12	1.35	0.186	**1.88**	0.035	1.31	0.209	1.37	0.180	1.20	0.283

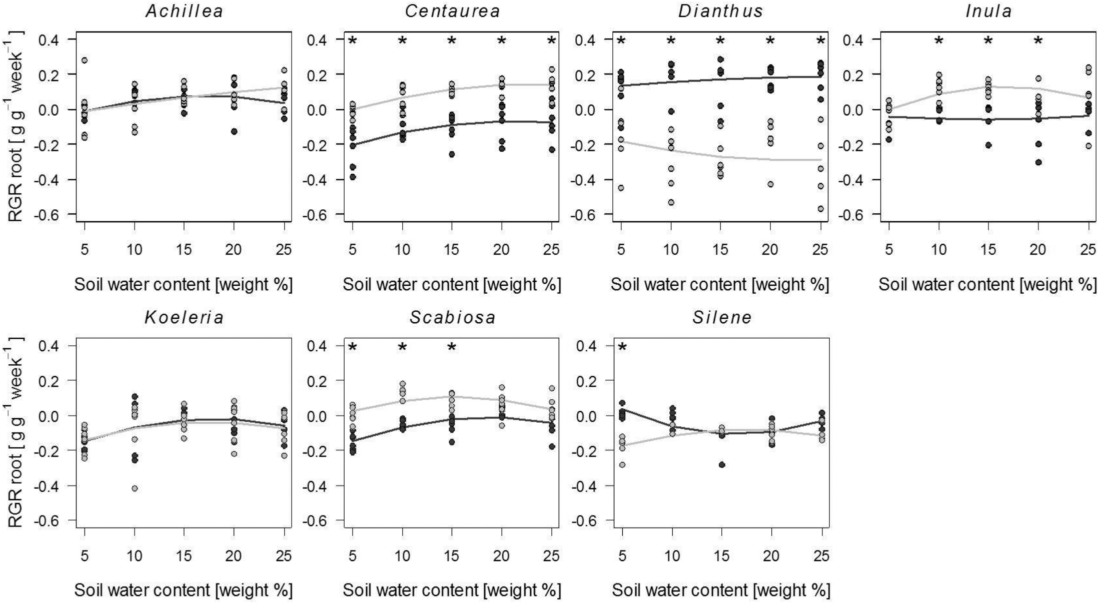

Fig. 4. – Relative growth rate of root dry weight (RGR root) as a function of soil water content for all species pairs investigated in Experiment 2. Species of the dry range type are shown in dark grey; species of the wet range type in light grey. Regression lines were obtained using least square means and whether the differences between the two species of contrasting range type were significant were determined using Tukey-Kramer post-hoc tests and significant differences are indicated by asterisks.

Discussion

Frost resistance

The frost resistance of the leaves of the species investigated did not coincide with the differences in their macroclimatic niches. Although most congeneric species differed in their fundamental niches, the extent and direction of the differences were not reflected in their realized niches. As only two genera showed the hypothesized trend, the first hypothesis predicting a higher frost resistance of the cold range species compared with that of warm range species has to be rejected. Although the results for *Carlina* confirm previous interpretations of Meusel & Kästner (1990), who had assumed that the absence of *C. vulgaris* from eastern parts of Europe was because it could not survive the cold winter temperatures recorded there, the majority of genera did not conform with the expectations. Similarly, we did not find evidence for the supposed relationship between frost resistance and leaf morphology.

The possible explanations for the unexpected results fall into two main categories, which question either the validity of realized niche-based approaches (see below) or the adequacy of the methods used here. Using LT_{50} values has the advantage of using a highly standardized procedure, but the temperature obtained might both under- or overestimate frost resistance. On the one hand, it is possible that plants can survive lower temperatures than that indicated by the LT_{50} because plants can shed damaged leaves. On the other hand, even slight damage might be lethal because of ensuing pathogen damage (e.g. Hernádez et al. 1998, Pukacki & Przybyl 2005). Furthermore, the leaves might not be the most crucial organs for winter survival as plants might survive winter belowground as rhizomes or root organs. In the case of *Digitalis purpurea*, Bruelheide & Heinemeyer (2002) report that the different plant organs differ in their resistance to frost, with leaves more susceptible than buds and roots. Thus, frost resistance of other tissues might be different. We have also disregarded the effect of life stage on frost resistance. It is known that seedlings of the target species are much more sensitive to frost damage than adult plants (N. Stahl & H. Bruelheide, own observations). In adult plants, frost resistance also depends on the phenological stage, e.g. on the age of leaves (Pop et al. 2000). As young leaves shortly after bud burst in spring are the most sensitive to damage by frost (Cannell & Smith 1984, Dittmar et al. 2006, Augspurger 2009) we have considered repeating our experiments in other seasons of the year. In addition, surviving exposure to frost depends not only on frost avoidance mechanisms but also the regeneration potential of the plants (Taschler & Neuner 2004). Taking these factors into consideration the results have to be interpreted with great care. Nevertheless, the results clearly show that frost resistance of leaves cannot be assumed to be a simple reflection of the species' distribution range.

Drought tolerance

In none of the genera investigated was there any support for the hypothesized differences in performance between the range types. As most species responded similarly to water limitation the second hypothesis was rejected. Only for two genera (*Dianthus* and *Silene*) was there some indication that the species with a range extending into drier regions were more drought-resistant than the species of the moist range type. Interestingly, we found no indication of a higher allocation of biomass to roots, a feature commonly associated with resistance to drought in species of the dry range type (Ashenden et al. 1975, Kato et al. 2006, Hund et al. 2009).

Assuming that the realized niche approach is valid (see below), the failure to find differences in drought resistance might again be due to various methodological reasons. The pots used might have provided a too artificial setting for revealing differences in root systems as deep-rooting species are unlikely to be able to respond when grown in pots measuring only 8 cm.

In contrast, drought damage is not caused by single events but develops over time. Possibly, an experiment lasting more than eight weeks might be more successful in identifying differences between the two range types. For example, Landolt et al. (1974) report differences in performance between three closely related species belonging to the *Scabiosa columbaria* species complex when recorded over two vegetation periods. Not only the time of exposure to drought but also the ensuing period of recovery from the effects of drought might be important, as Milnes et al. (1998) state that *Koeleria macrantha* can fully recover from the effects of a severe drought. Finally, a reason for the absence of significant differences in drought resistance might be the neglect of its interaction with other factors (Bauder 1989, Milnes et al. 1998). For example, drought stress in plants might be increased by competition (Barton 1993, Brooker 2006). However, following the same argument as for frost resistance, we have to conclude that the resistance of whole plants to drought is also not a simple function of the species' distribution range.

Correspondence between fundamental and realized niche

Both the frost and the drought experiments did not result in a match between the species' fundamental and realized niches. While large differences were found in the species' distribution ranges, the interspecific variability in growth and responses to stress was generally low in the experiments. Thus the species investigated of each pair exhibited very similar fundamental niches but dissimilar realized niches. These findings differ from those of other niche studies. For example, a general agreement of fundamental and realized niche with respect to frost is reported for different species of *Ericaceae* in the British Isles (Bannister & Polwart 2001).

As we confined our analyses to intrageneric comparison, we can exclude phylogeny as a reason for the discrepancy between fundamental and realized niches. Nevertheless, it is likely that the time required for the evolution of different degrees of frost or drought tolerance differs among genera. However, even taking phylogenetically corrected contrasts of responses into account, we do not think that this explanation holds. For example, the two very closely related *Carlina* species (separated about 9.8 million years ago) differed more in frost resistance than the more distantly related *Dianthus* species (separated about 27.6 million years ago) (Durka 2002, personal communication of node ages from S. Michalski). It is also possible that frost and drought are not the limiting factors for the majority of species studied. Summer temperatures (Hennenberg & Bruelheide 2003) or length of the growing season and seasonality of the climate (Jäger 1968) might also limit the geographical distribution of species. Furthermore, there are several other environmental factors that might interact and limit the geographical ranges of plant species. Equally important might be soil conditions. Clearly, soil conditions are very variable even within a single grid cell used in the macroclimatic niche analysis and soils with a high water storage capacity might compensate for a drier macroclimate. Still, even when admitting that we restricted the analysis to only two axes of the multidimensional realized niche, an important conclusion is that these axes might be irrelevant in terms of determining limits of ranges.

Finally, it might be concluded that biotic factors that result in the fundamental niche of a species conforming with its realized niche, such as competition (Walck et al. 2001), herbivory (Bruelheide & Scheidel 1999) or pathogens (Bütof & Bruelheide 2011) might be more decisive than abiotic factors in determining the ranges of species. This would fully comply with early ideas on this topic, pointed out by H. Ellenberg, competition results in species with similar fundamental niches occupying different realized niches which came from his so-called Hohenheim experiment, in which he grew different grass species along an experimental gradients of depth to the water table in monocultures and in mixtures (Ellenberg 1954, Hector et al. 2012). Further support comes from recent findings on niches of tropical tree species, such as those of Baltzer et al. (2007) who report no relationship between the fundamental and realized niches with respect to the seasonality of the rainfall.

Irrespective of which of these explanations is correct, one important conclusion is that species distribution models that exclusively rely on climate envelopes might be unrealistic. This conclusion also holds even when we take within-species differentiation into account. We can expect that individuals from different provenances of the same species respond differently to frost and drought (Erfmeier & Bruelheide 2005, Kathke & Bruelheide 2011). However, in this case it would no longer be justified to calculate one single climate envelope for the whole species. Species distribution models are a popular method for predicting the potential effect of climate change on species range shifts (e.g. Iverson & Prasad 1998, Thomas et al. 2004, Pompe et al. 2010) and species invasion (e.g. Peterson 2003, Thuiller et al. 2005). The risk when using distribution data is that the species' fundamental niches are underestimated and therefore also the species' potential distribution (Anderson & Raza 2010). Thus, species distribution models run the risk that species might react differently to changing climatic conditions than generally predicted. In the future models should combine data on realized niche from species occurrences with results of experimental studies on species fundamental niches (Bruelheide 1999, Kearney 2006, Pearson et al. 2007). In addition, macroclimatic characteristics of niches should be also be compared with ecophysiological performance along well resolved phylogenetic relationships to enhance the understanding of the degree to which the properties of the fundamental niche are conserved.

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Souhrn

Cílem práce je srovnání fundamentálních nik 16 druhů travinných společenstev, definovaných na základě jejich tolerance vůči mrazu a suchu, s realizovanými makroklimatickými nikami, odvozenými z geografického rozšíření. Bylo studováno 8 dvojic druhů téhož rodu, lišících se rozšířením a vystavených různé míře stresu z mrazu a sucha. Tolerance vůči mrazu byla stanovena pomocí nárůstu elektrické vodivosti poškozených pletiv a vyjádřena jako teplota, při níž vodivost dosáhla 50 % (LT50). Rody se v reakci na stres vyvolaný mrazem lišily; u dvou rodů vykazovaly druhy, jejichž rozšíření zasahuje do chladnějších oblastí, nižší hodnoty LT50, než druhy vázané na teplé oblasti, u dalších dvou byly výsledky opačné a zástupci zbývajících rodů se v toleranci vůči mrazu nelišili. Reakce na stres vyvolaný suchem byla měřena vystavením druhů různým hladinám vlhkosti ve skleníkovém experimentu a nelišila se v závislosti na tom, nakolik rozšíření studovaných druhů zasahovalo do klimaticky suchých oblastí. Obecně vzato byl soulad mezi fundamentálními a realizovanými nikami slabý, zjištěný pouze v několika rodech a jen pokud jde o toleranci vůči mrazu, nikoli suchu. Geografické rozšíření dvou druhů téhož rodu tudíž nelze předpovědět na základě jejich experimentálně zjištěné reakce. Je proto pravděpodobné, že předpoklady, na nichž je založeno modelování rozšíření rostlinných druhů, jsou chybné, což vede k nespolehlivosti modelů předpovídajích budoucí rozšíření.

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