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Functional approach to xerothermic grasslands in Central Germany: trait composition, dominant grasses and soil factors

Tim Meier[1,2,*], Isabell Hensen[2,3] & Ingolf Kühn[1,2,3]

[1]Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Straße 4, D-06120 Halle (Saale), Germany; [2]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, D-06108 Halle (Saale), Germany; [3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Puschstraße 4, D-04103 Leipzig, Germany
*corresponding author: tim.meier@botanik.uni-halle.de

Abstract: Functional traits mediate how species and communities respond to (or affect) environmental gradients. These are impacted by global change, which has led to e.g. climate change and land-use change, affecting soil conditions, species richness and functional diversity in, among others, xerothermic (respectively dry or semidry) grasslands. Within the last decades, the dominance of grass species like *Bromus erectus* has increased in such grasslands in Central Germany, but factors driving their intraspecific trait variability (ITV) are not yet well understood. The aim of our study was, on the one hand, to compare the functional trait composition of two grassland types, namely dry and semidry, using multi- and single-trait approaches and to assess the effects of soil properties on these traits and, on the other hand, to reveal differences in functional traits and their ITV between the five dominant grasses *B. erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa capillata*. Based on vegetation relevés, functional traits (VPH – vegetative plant height, LDM – leaf dry mass, LA – leaf area, SLA – specific leaf area, LDMC – leaf dry matter content, LNC – leaf nitrogen concentration, LCC – leaf carbon concentration, leaf C/N ratio) were measured and soil factors (soil depth, pH value, $CaCO_3$ content, soil N and C content, soil C/N ratio) analysed. For each plot, the community weighted mean (CWM) of all functional traits was calculated to determine differences between the two grassland types and the coefficient of variation was used for interpreting differences in the ITV between the five grasses. There were minor differences between dry and semidry grasslands in the CWM of the functional traits LDM, LA, LNC and LCC, while other traits did not differ between the two grassland types. Soil factors had little effects on the trait composition of dry and semidry grasslands, although soil depth, $CaCO_3$ content and C/N ratio had the greatest influence on CWM and were potentially the strongest drivers for differentiation. The five grasses had species-specific trait distributions but showed relatively similar ITV, so we conclude that *B. erectus* was not more adapted to changing environmental conditions than the other grasses. Generally, we only found minor changes in the functional trait composition of dry and semidry grasslands in Central Germany and thus the environmental gradient was too small to derive clear differences in the ecosystem function between both grassland types, although the functional structure was largely determined by the dominant grasses.

Keywords: *Bromus erectus*, community weighted mean, dry grassland, functional traits, intraspecific trait variability, semidry grassland, soil factors

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Introduction

Ongoing global change (including climate warming, rising atmospheric nitrogen deposition, soil acidification, land-use change) does not only affect the species composition of grasslands (Bobbink et al. 2010, Duprè et al. 2010, Wesche et al. 2012, Diekmann et al. 2014, 2019), but also their functional trait composition (Garnier et al. 2007, Wellstein et al. 2013, Lewis et al. 2014, Helm et al. 2019, Pichon et al. 2022). Within the last decades, an increasingly dramatic loss of species (Bruelheide et al. 2020, Jandt et al. 2022, Meier et al. 2022b) and changes in functional diversity (Bernhardt-Römermann et al. 2011, Socher et al. 2012) have been found for species-rich, often endangered and protected xerothermic (dry or semidry, respectively) grasslands (Dengler et al. 2020).

Functional traits are defined as any measurable morphological, physiological or phenological characteristic of an individual that indirectly affects individual fitness (Violle et al. 2007). In particular, they are considered to reliably mediate species and community responses or effects to environmental gradients (Lavorel et al. 2008, Shipley 2009, Garnier et al. 2016) and thus influence ecosystem services, e.g. climate and water regulation, soil stability and protection from disturbance (de Bello et al. 2010). Vegetative plant height (VPH) and leaf traits are important key traits linked to plant resource acquisition and use, stress tolerance and competitive ability (Westoby et al. 2002, Díaz et al. 2016, Garnier et al. 2016). In this context, some leaf traits, such as specific leaf area (SLA), leaf dry matter content (LDMC) and leaf nitrogen concentration (LNC), are closely associated with leaf water and nutrient availability, photosynthetic rate, relative growth rate, leaf longevity and soil water content (Reich et al. 1999, Garnier et al. 2001, Wright et al. 2004, McGill et al. 2006). These three traits represent important components of the leaf economics spectrum, which captures relationships between several leaf traits and describes a gradient between traits of resource conservation and those of an acquisitive strategy, i.e. quick resource uptake and turnover (Wright et al. 2004). Fast-growing plants of nutrient-rich sites are characterized by high SLA and LNC but lower LDMC, resulting in faster turnover of nutrients, while slow-growing plants of nutrient-poor sites have low SLA and LNC but higher LDMC and are investing in conservation of nutrients (Díaz et al. 2004, Wright et al. 2004, Shipley et al. 2006).

The mass ratio hypothesis (Grime 1998) states that trait values of the dominant species of a community (those that contribute most to the biomass) have a higher influence on ecosystem functions. Therefore, to calculate the functional composition of a community, the trait values of the single species are multiplied by their relative abundance and then summed up, resulting in the community weighted mean (CWM) (Garnier et al. 2004). Environmental changes can cause not only a shift in the abundance of species but also a shift in their intraspecific trait variability, leading to a new functional composition of a community (Lepš et al. 2011).

Intraspecific trait variability (ITV) usually describes the variability of functional traits of individuals within a species (Albert et al. 2010) but can also be studied between and within populations (Jung et al. 2010, Pakeman 2013, Mitchell & Bakker 2014). This variability can, for example, have implications for species coexistence and ecosystem functions (Jung et al. 2010, Siefert et al. 2015) and represents the result of genetic differentiation and phenotypic plasticity (Nicotra et al. 2010, Albert et al. 2011). In particular, phenotypic plasticity, i.e. the emergence of multiple phenotypes from a single genotype

(Miner et al. 2005, Violle et al. 2012), allows the plant to respond to changing environmental conditions by morphological and physiological adaptations throughout its life span (Stark et al. 2017).

Dry grasslands are characterized by a steeper slope, shallower soil depth and lower water and nutrient availability than semidry grasslands and are therefore subject to slower successional processes (Ellenberg & Leuschner 2010), causing differences in species composition (Meier et al. 2021) and probably functional trait composition between both grassland types. Thus, drought-adapted species may have a higher abundance in dry grasslands, which implies a stronger influence on their functional trait composition (sensu Grime 1998), whereby, for example, the same species could have a lower VPH and SLA in dry grasslands due to a higher water limitation than in semidry grasslands.

In xerothermic grasslands, competitive grasses produce more biomass than dicotyledonous species (Del-Val & Crawley 2005) and can thus contribute considerably to the functional composition of these communities, which has already been demonstrated for *Stipa* grasslands (Meier et al. 2019). In addition, the increasing abundance of dominant grasses is promoted by nitrogen inputs and the loss in traditional land use (e.g. grazing or mowing) (Diekmann et al. 2014, Lemmer et al. 2021), that are mainly responsible for the conversion of previously species-rich to species-poor grassland communities due to increasing competition effects (Wesche et al. 2012).

Within the last three decades, various studies revealed an increasing dominance of grass species in xerothermic grasslands, such as *Bromus erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* and *Stipa* sp. (Bobbink et al. 1998, Bornkamm 2006, 2008, Meier et al. 2021, 2022b), which often co-occur in different plant communities (Meier & Partzsch 2018, Meier et al. 2021, 2022b). Particularly for Central Germany, in more than two decades, there was a significant increase in the presence of *B. erectus*, which tripled to quintupled in cover in the dry and semidry grasslands, depending on the different study regions (Meier et al. 2021, 2022b). Moreover, *B. erectus* and *Stipa* species are relatively similar in their functional traits (Meier et al. 2019). Accordingly, it has been experimentally shown that under nutrient addition, the growth performance and competitive ability of *B. erectus* had negative effects on *S. capillata* and *S. tirsa*, which could lead to the displacement of both *Stipa* species in the future (Meier et al. 2022a).

To predict the outcome of environmental changes on xerothermic grasslands, the underlying mechanisms of plant adaptation based on functional traits are an important prerequisite (Wellstein et al. 2013). In particular, soil properties (e.g. soil depth, pH value, $CaCO_3$ content, C/N ratio) cause strong changes in functional traits (Jager et al. 2015). The aim of our study was to compare the functional trait composition (CWM) of dry and semidry grasslands in Central Germany based on published vegetation relevés (Meier et al. 2021, 2022b) using multi- and single-trait approaches, and to assess the effects of the abiotic conditions on these traits using different soil properties (cf. Le Bagousse-Pinguet et al. 2014). On the other hand, functional differences between the dominant grasses *B. erectus*, *B. pinnatum*, *F. rupicola*, *H. pratense* and *S. capillata* should be revealed, as these could negatively influence the species richness of xerothermic grasslands due to their competitive and stress-tolerant strategy type (CS) (Grime 2001). We expected a higher ITV for *B. erectus* compared to the other grasses, as this species benefits from climate change and nitrogen depositions (Meier et al. 2022a, b).

We asked the following questions: (i) Does the functional trait composition of dry grasslands clearly differ from that of semidry grasslands? (ii) What is the effect of soil factors on the composition of functional traits, and which ones have the largest influence? (iii) Do the five dominant xerothermic grasses differ in their functional traits? (iv) Does *Bromus erectus* show a higher adaptation in functional traits to environmental changes compared to the other grasses?

Material and methods

Study areas

The study region is in Central Germany within the federal states of Saxony-Anhalt and Thuringia. Vegetation relevés, soil samples and functional traits of the xerothermic grasslands of the Kyffhäuser, the Porphyry outcrops near Halle (Saale) and the Saale-Unstrut-Triasland were investigated in 2018 and 2019. The vegetation relevés were published in Meier et al. (2021) and Meier et al. (2022b) (see there for detailed information), while species abundance was used for functional trait analyses. Most of the sites were grazed (with varying grazing intensity), while only a few sites were abandoned (porphyry outcrops). The proportion of grazed plots and the grazing intensity were similar among dry and semidry grasslands. A total of 101 relevés were included in this analysis, whereas the plant communities belong to the class *Festuco-Brometea* and were here classified into dry and semidry grasslands. The same classification was already used by Meier et al. (2021), who assigned different plant communities to these grassland types (see further information in that study). In contrast, the different plant communities *Gentiano-Koelerietum*, *Carici-Seslerietum*, *Trinio-Caricetum*, *Festuco-Stipetum* were not subdivided into dry and semidry grasslands in Meier et al. (2022b), so we assigned these plant communities to the two grassland types based on the EuroVegChecklist (cf. Bergmeier 2020): *Carici-Seslerietum*, *Trinio-Caricetum* and *Festuco-Stipetum* were classified here as dry grassland and *Gentiano-Koelerietum* as semidry grassland.

Soil analyses

For each plot, the soil depth [cm; SO] was measured with the help of a metal rod, with five punctures per plot. Moreover, a mixed sample of the mineral topsoil (A-horizon) was taken from each plot with five punctures and the soil samples were dried in the laboratory at room temperature. Subsequently, the pH_{H_2O} value (Microprocessor pH-Meter – pH537 WTW, Schütt Labortechnik GmbH), C content [%], N content [%], C/N ratio (C/N analyser; vario EL cube, Elementar Analysensysteme GmbH) and $CaCO_3$ content [%] (Scheibler apparatus) were measured.

Measurement of functional traits

In all plots, functional traits of the most abundant species were quantified, which together accounted for 80% of the biomass present in each community (Grime 1998, Garnier et al. 2004). For an overview of measured functional traits and their ecological functions, see Table 1. From 10 individuals per species, vegetative plant height [cm; VPH] was measured, which is defined as the distance between the highest photosynthetic organ and the

Table 1. Summary of all investigated functional traits with their definitions and ecological functions that were used as predictor for community weighted mean (CWM) and intraspecific trait variability (ITV).

Functional trait	Abbreviation	Unit	Definition	Ecological function
vegetative plant height	VPH	cm	distance between highest photosynthetic organ and base of the plant	light interception, competitive ability
leaf dry mass	LDM	mg	dry weight of an individual leaf	relative growth rate, metabolic rate
leaf area	LA	mm^2	one-sided projected surface area of an individual leaf	relative growth rate, metabolic rate
specific leaf area	SLA	mm^2/mg	ratio of fresh leaf area to leaf dry mass	relative growth rate, photosynthesis rate
leaf dry matter content	LDMC	mg/g	ratio of leaf dry mass to leaf fresh mass	metabolic rate, biomass production
leaf nitrogen concentration	LNC	%	total amount of N per unit of leaf dry mass	relative growth rate, resource acquisition and use
leaf carbon concentration	LCC	%	total amount of C per unit of leaf dry mass	relative growth rate, resource acquisition and use
leaf carbon/nitrogen ratio	C/N	–	ratio of C per unit of leaf dry mass to N per unit of leaf dry mass	resource acquisition and use

base of the plant (Weiher et al. 1999). Compared to upright-growing plants, the plant height of rosette plants was measured directly on the leaves of the rosette. The leaf traits were investigated according to a standardized protocol (Pérez-Harguindeguy et al. 2013). If possible, attention was paid to the fact that the leaf traits were studied on the same individuals on which the plant height was also measured. A total of 10 leaves were harvested for each species per plot, i.e. one leaf per individual (preferably the highest young but fully developed leaf). However, if fewer individuals were present, two leaves per individual were harvested (a minimum of five individuals). Only intact, fully developed leaves were taken, which were oriented preferably towards the sunlight. The leaf samples were kept moist with water in plastic bags and stored in a cool box for further analyses. In the laboratory, the leaves were scanned with a flatbed scanner with a resolution of 300 dpi and their leaf areas [mm^2; LA] were analysed using WinFOLIA Pro S, version 2004a. If some leaves were too large, they were cut up and the cumulative area of all parts was determined. Then, the leaves were freshly weighed individually, dried in a drying cabinet at 80 °C for 24 h and weighed again to determine the leaf dry mass [mg; LDM]. Based on these parameters, SLA (ratio between leaf area and leaf dry mass in mm^2/mg) and LDMC (ratio between leaf dry mass and water-saturated fresh mass of the leaf in mg/g) were calculated. Afterward, a C and N analysis of the leaves was performed. For this purpose, the leaf samples were milled beforehand (Vibratory Mill MM 400, Retsch GmbH) and then transferred to the C/N analyser. Only mixed leaf samples were analysed, i.e. one sample for each species per plot. However, an exception was made for the five dominant grasses *B. erectus*, *B. pinnatum*, *F. rupicola*, *H. pratense* and *S. capillata*, where single leaf samples were analysed (10 samples per plot). Resulting from this analysis, LCC [%] and LNC [%], as well as the C/N ratio, could be determined. The functional traits were deliberately collected on the plot level in the field, as trait values from databases do not take ITV into account (Cordlandwehr et al. 2013). To draw clearer conclusions about the functional adaptation of *B. erectus*, additional functional traits were collected for this species in 2019. Therefore, 93 existing vegetation relevés of the Kyffhäuser (Leonhardt 2019) were revisited, and only functional traits of *B. erectus* were sampled.

Data analysis

Statistical analyses were performed in R 3.6.0 (R Core Team 2019). The soil factors and functional traits that represented the dependent variables were checked graphically for normal distribution and homoscedasticity, and all were logarithmically transformed to achieve normality for subsequent analyses. For each relevé, the CWM (log-transformed data) was calculated for all functional traits: $\mathrm{CWM} = \sum_{i=1}^{S} \left(p_{ic} \times t_{ic} \right)$. Here, the mean value of trait t of species i was weighted by the relative species abundance p in community c, with a total of S species (Garnier et al. 2004). Therefore, the relative abundances of the species (transformed Braun-Blanquet coverage values) of both vegetation datasets were harmonized, whereby the estimate values 2a and 2b were previously combined into estimate value 2 (cf. Meier et al. 2021). The packages dplyr (Wickham et al. 2021) and tidyr (Wickham 2021) and the function weighted.mean were used to help calculate the CWM.

A principal component analysis (PCA) should reveal functional gradients between communities of dry and semidry grasslands. For this purpose, the CWM values were scaled to zero mean and unit variances, and the results were presented graphically in a biplot over the trait composition. As a complement to PCA, multivariate analysis of variance (MANOVA) with Pillai's trace as a test statistic was used for directly testing the difference between all functional traits together as response variables and the grassland type as a predictor. Mean values of the CWM (log-transformed values were back-transformed) of different functional traits were compared between dry and semidry grasslands with paired t-tests. To determine gradients between functional traits (CWM) and soil factors (see variables above), a redundancy analysis (RDA) was performed and tested for significance using a Monte-Carlo test (9,999 permutations). Forward selection was performed using the 'ordistep' function to reduce the number of soil factors of the RDA, which contributed significantly to explaining the functional trait composition. The results were visualized in a triplot together with the trait composition and the soil factors. All multi-trait analyses were performed using the package vegan (Oksanen et al. 2020).

Furthermore, the package corrplot (Wei & Simko 2021) was used to generate a correlation matrix of the pairwise correlations of all functional traits, which was calculated across the most common species of the dry and semidry grasslands (Supplementary Table S1). In addition, mean functional traits were calculated for the functional groups of grasses and forbs.

Analysis of covariance (ANCOVA), conducted with the package car (Fox & Weisberg 2019), was used to investigate the effect of each soil factor on each functional trait (CWM) between the dry and semidry grasslands. The CWMs of each functional trait represented the response variables, while the soil factors and the grassland type (dry and semidry) were the fixed factors. In addition, interactions between metric and categorical predictors were included in the models (soil factor × grassland type), but model simplification was performed if there were no significant interactions. To avoid pseudoreplication, the nested random effect of the vegetation plot was included in the models, as many species were sampled over several plots and within a plot several individuals of a species had different trait values. These results were visualized by using the package ggplot2 (Wickham 2016).

To characterize the ITV of the five dominant grasses, the coefficient of variation (CV) was calculated (Everitt 1998). Higher CV values indicate that species have a high ITV and thus their traits are more strongly influenced by environmental factors (according to

Wellstein et al. 2013 a very high variability if CV > 0.51). We applied one-way analysis of variance (ANOVA) with subsequent Tukey's post-hoc test using the multcomp package (Hothorn et al. 2008) to determine differences in both the unweighted functional traits (normally distributed data) and their CV between the five dominant grass species and additionally for *B. erectus* between dry and semidry grasslands. All statistical analyses were considered significant if P < 0.05.

Results

Functional trait composition of dry and semidry grasslands

The first two axes of the PCA explained ~72% of the variation and revealed a strong positive covariation between the traits VPH, LDM and LA, resulting in a slight differentiation of CWMs between dry and semidry grasslands (Fig. 1). In addition, SLA and LNC were positively correlated with each other, negatively with C/N and to a lesser degree with LDMC and LCC. MANOVA revealed significant differences between all functional traits together and the grassland type (Supplementary Table S2). The semidry grasslands had significantly higher LDM and LA, but significantly lower LNC and LCC compared to the dry grasslands (Fig. 2). There were no significant differences in VPH, SLA, LDMC and C/N between the two grassland types. Comparing functional groups, grasses had higher VPH, LDMC and LCC than forbs (Supplementary Table S1). Across all species, functional traits showed both strongly significant negative (e.g. LNC and C/N, SLA and C/N) and positive (e.g. LDM and LA, LDMC and C/N) correlations (Supplementary Fig. S1).

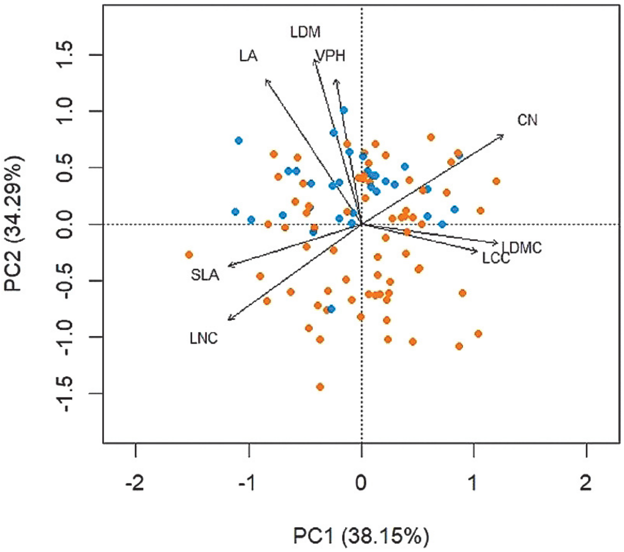


Fig. 1. Principal component analysis (PCA) of the distribution of the community weighted mean (CWM) within the dry (orange symbols) and semidry (blue symbols) grasslands (in a total of 101 relevés). Functional traits (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; for abbreviations see Table 1) are shown as vectors. The proportions of declared variability are given on the axes.

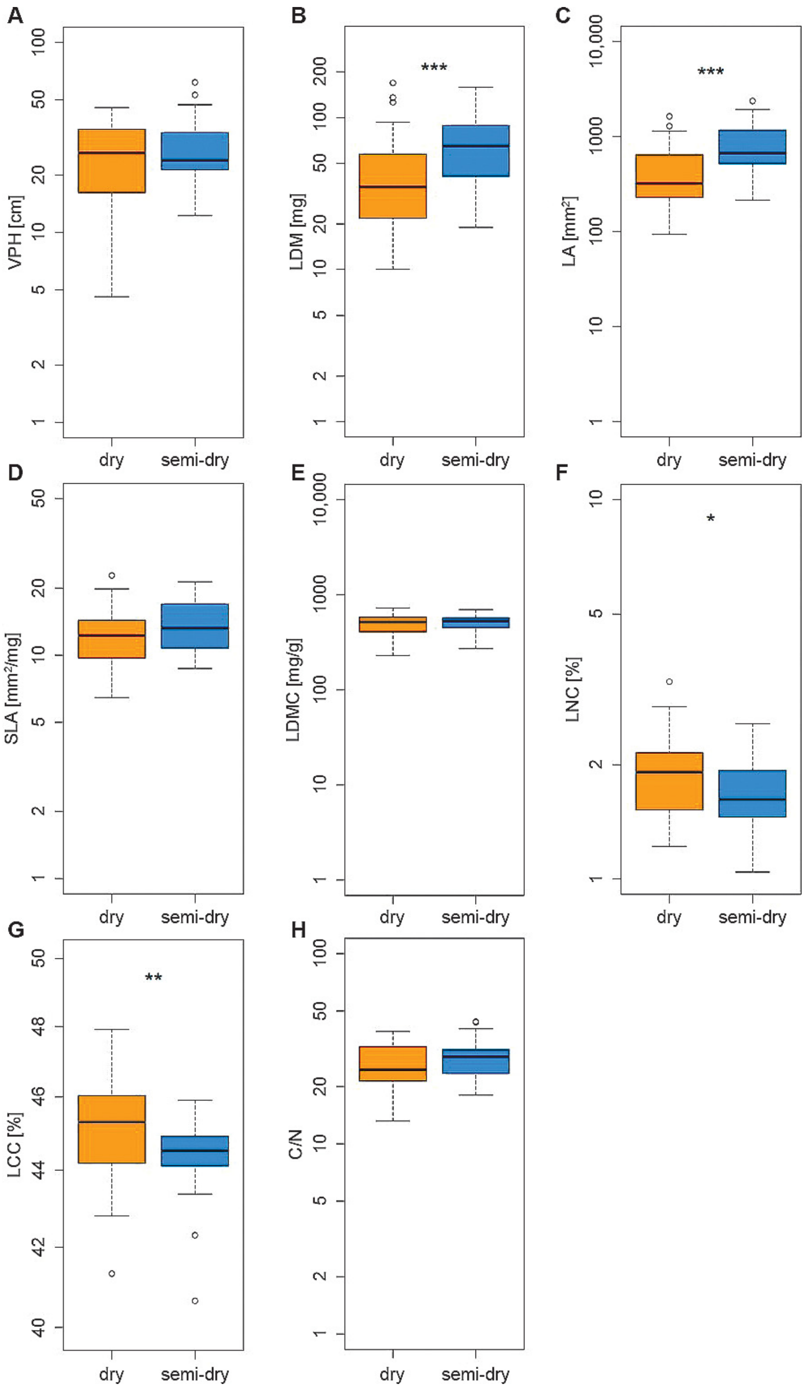


Fig. 2. Community weighted mean (CWM) for each functional trait (for abbreviations see Table 1) between dry and semidry grasslands: (A) VPH; (B) LDM; (C) LA; (D) SLA; (E) LDMC; (F) LNC; (G) LCC; (H) C/N. Results of the t-test: * $0.01 \leq P < 0.05$, ** $0.001 \leq P < 0.1$, *** $P < 0.001$.

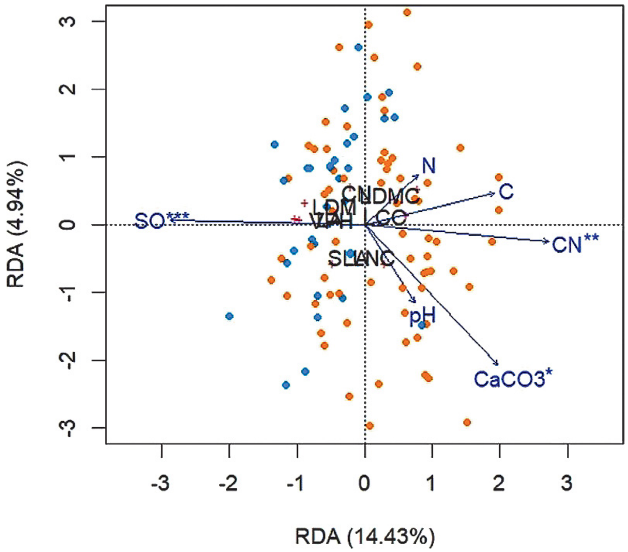


Fig. 3. Redundancy analysis (RDA) of soil factors on the community weighted mean (CWM) within the dry (orange symbols) and semidry (blue symbols) grasslands (in a total of 101 relevés). Soil factors (SO – soil depth, pH – pH-value, $CaCO_3$ – $CaCO_3$ content, N – nitrogen content, C – carbon content, CN – C/N ratio) are shown as vector arrows (dark blue colour) and functional traits (VPH, LDM, LA, SLA, LDMC, LNC, LCC, C/N; for abbreviations see Table 1) are represented as centroids. Soil factors which are significantly correlated with the axes of the RDA after forward selection are indicated as follows: $*0.01 \leq P < 0.05$, $**0.001 \leq P < 0.1$, $***P < 0.001$. The proportions of declared variability are given on the axes. The whole model was significant (9,999 permutations, $P < 0.001$).

Influence of soil factors on functional traits of dry and semidry grasslands

Only ~20% of the declared variability could be explained by soil factors on the first two axes of the RDA, while SO, $CaCO_3$ content and the C/N ratio of the soil were significantly correlated (Fig. 3). Most of the CWMs had a low variability with respect to soil factors, and there were no differences between dry and semidry grasslands.

In general, ANCOVA revealed only weak effects of the soil factors on the CWM values of dry and semidry grasslands and few significant differences in their interactions (Supplementary Table S3, Fig. 4–8, Supplementary Fig. S2–S4). Thus, no significant differences were found in the interaction between SO, soil N, soil C content, and the grassland types regarding their CWMs (Supplementary Table S3). VPH, LDM and LA showed a significant increase with increasing SO (Fig. 4A, Supplementary Fig. S2A, S3A). Moreover, VPH and leaf C/N ratio of the grassland type decreased significantly with increasing $CaCO_3$ content (Fig. 4C, 8C). We found a significant interaction between pH and grassland type on SLA (Supplementary Table S3), whereby the slope was negative in dry grasslands and positive in semidry grasslands (Fig. 5B). However, there were particularly significant differences in the interactions between $CaCO_3$ content and grassland type on the response variables LDM, LA, SLA and LDMC (Supplementary Table S3). With increasing $CaCO_3$ content, LDM and LA decreased in dry grasslands, although significantly different slopes between the two grassland types were found (Supplementary Fig. S2C, S3C). Instead, SLA showed different patterns with increasing $CaCO_3$ content,

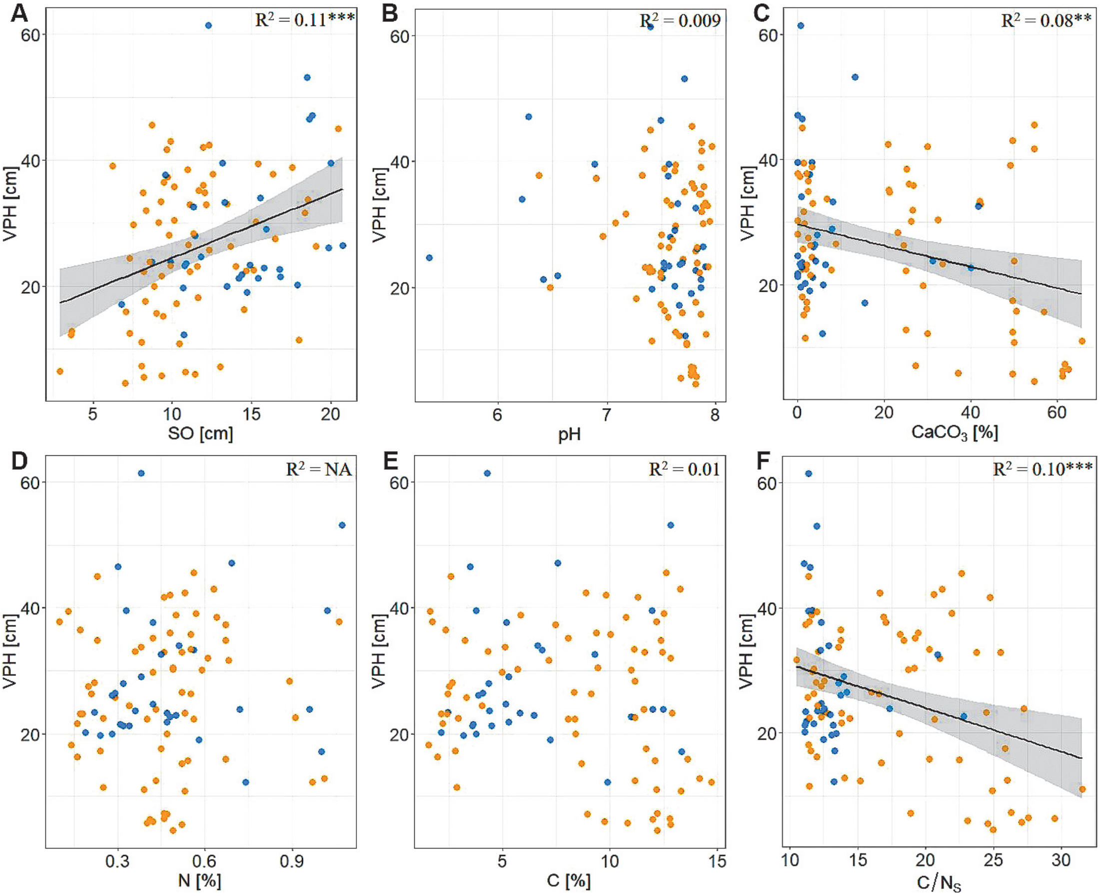


Fig. 4. Relationships between the community weighted mean of the vegetative plant height (VPH) of dry (orange colour) and semidry grasslands (blue colour) to soil factors: (A) SO – soil depth; (B) pH – pH-value; (C) $CaCO_3$ – $CaCO_3$ content; (D) N – nitrogen content; (E) C – carbon content; (F) C/N_s – soil C/N ratio. Adjusted R^2 and significance are given (**0.001 ≤ P < 0.1, ***P < 0.001, NA – not available). Visualization based on the results of the ANCOVAs (cf. Supplementary Table S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

with a negative slope in dry grasslands but a positive slope in semidry grasslands (Fig. 5C). There were significant effects on LDM, LA, SLA, LNC and LCC of the grassland type regarding soil N content, whereas a significant difference in the interaction between soil C/N ratio and grassland type was found for LDMC (Supplementary Table S3). Regarding LDMC, the slope was positive in dry grasslands and negative in semidry grasslands with increasing $CaCO_3$ content and soil C/N ratio (Fig. 6C, 6F).

Functional traits and intraspecific trait variability of xerothermic grasses

In general, we found significant differences between the five grasses in terms of their functional traits and intraspecific trait variability (Fig. 9). *Bromus erectus* and *Stipa capillata*

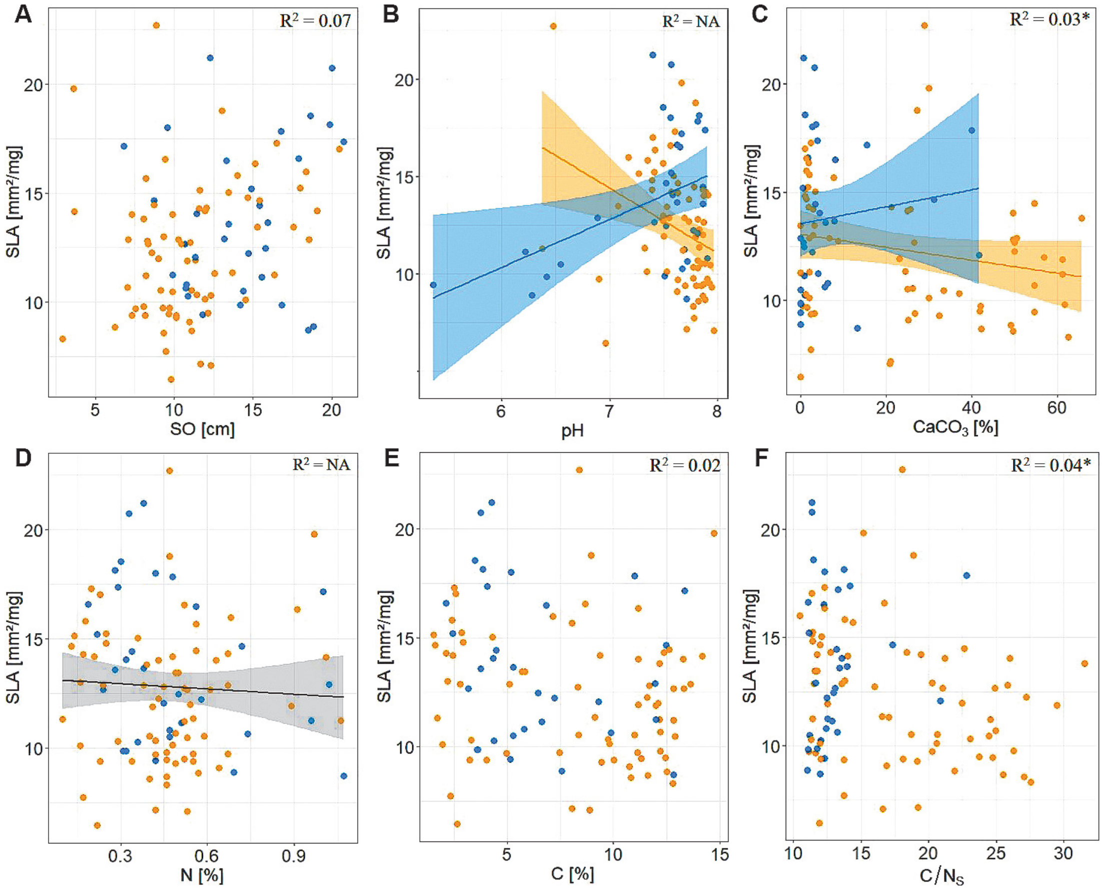


Fig. 5. Relationships between the community weighted mean of the specific leaf area (SLA) of dry (orange colour) and semidry grasslands (blue colour) to soil factors: (A) SO; (B) pH; (C) $CaCO_3$; (D) N; (E) C; (F) C/N_s (for abbreviations see Fig. 4). Adjusted R^2 and significance are given ($*0.01 \leq P < 0.05$, NA – not available). Visualization based on the results of the ANCOVAs (cf. Supplementary Table S3) as follows: significant interaction effect: two regression lines with 95% confidence level; significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

had the highest and *Brachypodium pinnatum* the lowest VPH (Fig. 9A). In contrast, *B. pinnatum* had the highest, whereas *B. erectus* and *S. capillata* the lowest CV_{VPH} (Fig. 9B). LDM was highest in *Helictotrichon pratense* and LA in *B. erectus* and *B. pinnatum*, while both traits were lowest in *Festuca rupicola* (Fig. 9C, 9E). Nevertheless, no significant differences were found between the five grasses regarding CV_{LDM} and CV_{LA} (Fig. 9D, 9F). The highest SLA was recorded for *B. pinnatum*, whereas *S. capillata* had the lowest SLA, which was not significantly different from *H. pratense* (Fig. 9G). For CV_{SLA}, only significant differences between *B. erectus* and *B. pinnatum* were observed (Fig. 9H). *Bromus erectus* and *H. pratense* had the lowest LDMC values (Fig. 9I). LNC was highest in *B. erectus*, *B. pinnatum* and *S. capillata* and lowest in *F. rupicola* and *H. pratense* (Fig. 9K). The CV_{LDMC} and CV_{LNC} of *S. capillata* were significantly different from *B. erectus* and

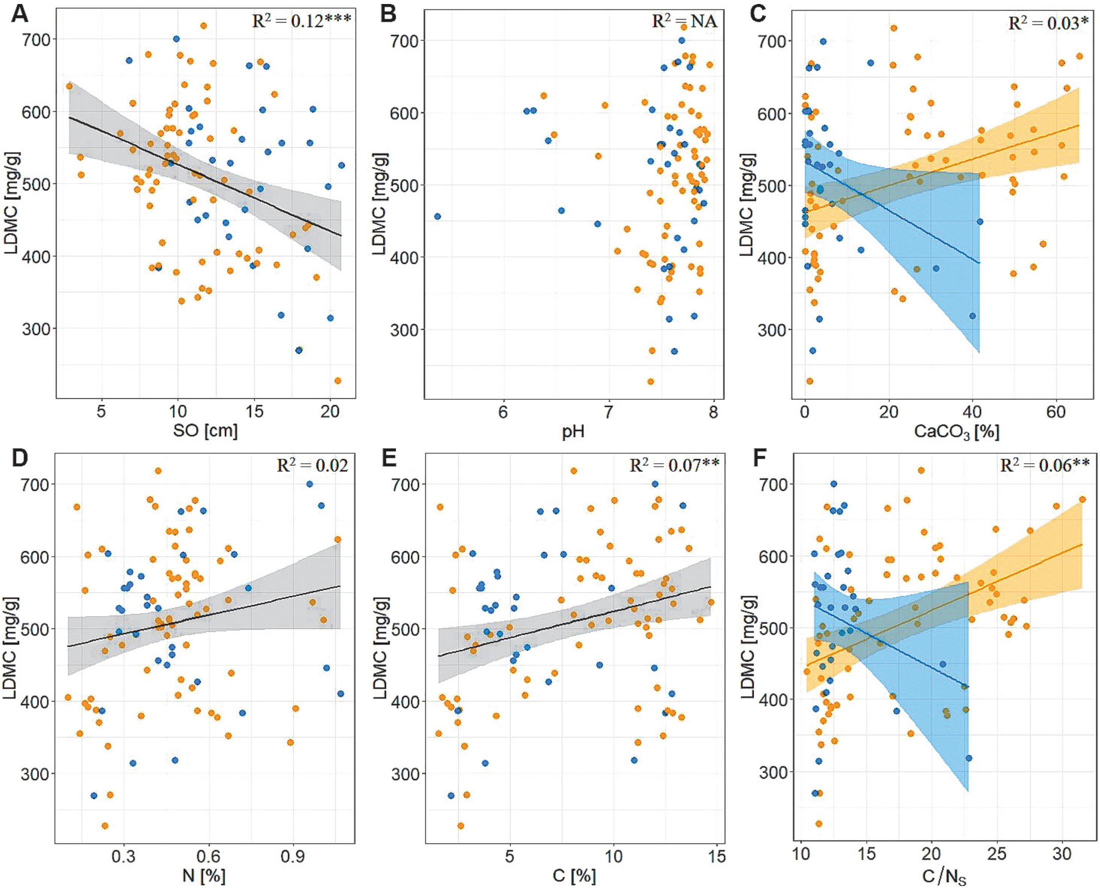


Fig. 6. Relationships between the community weighted mean of the leaf dry matter content (LDMC) of dry (orange colour) and semidry grasslands (blue colour) to soil factors: (A) SO; (B) pH; (C) $CaCO_3$; (D) N; (E) C; (F) C/N_s (abbreviations cf. Fig. 4). Adjusted R^2 and significance are given ($*0.01 \leq P < 0.05$, $**0.001 \leq P < 0.1$, $***P < 0.001$, NA – not available). Visualization based on the results of the ANCOVAs (cf. Supplementary Table S3) as follows: significant interaction effect: two regression lines with 95% confidence level; significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

F. rupicola (Fig. 9J, 9L). The highest LCC values were recorded for *S. capillata* and the lowest for *B. erectus* and *H. pratense* (Fig. 9M). The CV_{LCC} was higher for *F. rupicola* than for *B. erectus* and *S. capillata* (Fig. 9N). All species differed from each other in their C/N, with *F. rupicola* having the highest and *B. erectus* the lowest C/N ratio (Fig. 9O). The $CV_{C/N}$ values for *F. rupicola* were higher than for *H. pratense* and *S. capillata*, but there were also significant differences between *S. capillata* and *B. erectus*, and between *B. pinnatum* and *H. pratense* (Fig. 9P).

The trait values for VPH, LDM, LA, LDMC and C/N of *B. erectus* were significantly higher in semidry grasslands than in dry grasslands (Supplementary Fig. S5A, S5C, S5E, S5I, S5O), while the trait values for LNC and LCC were significantly higher in dry grasslands than in semidry grasslands (Supplementary Fig. S5K, S5M). No significant differ-

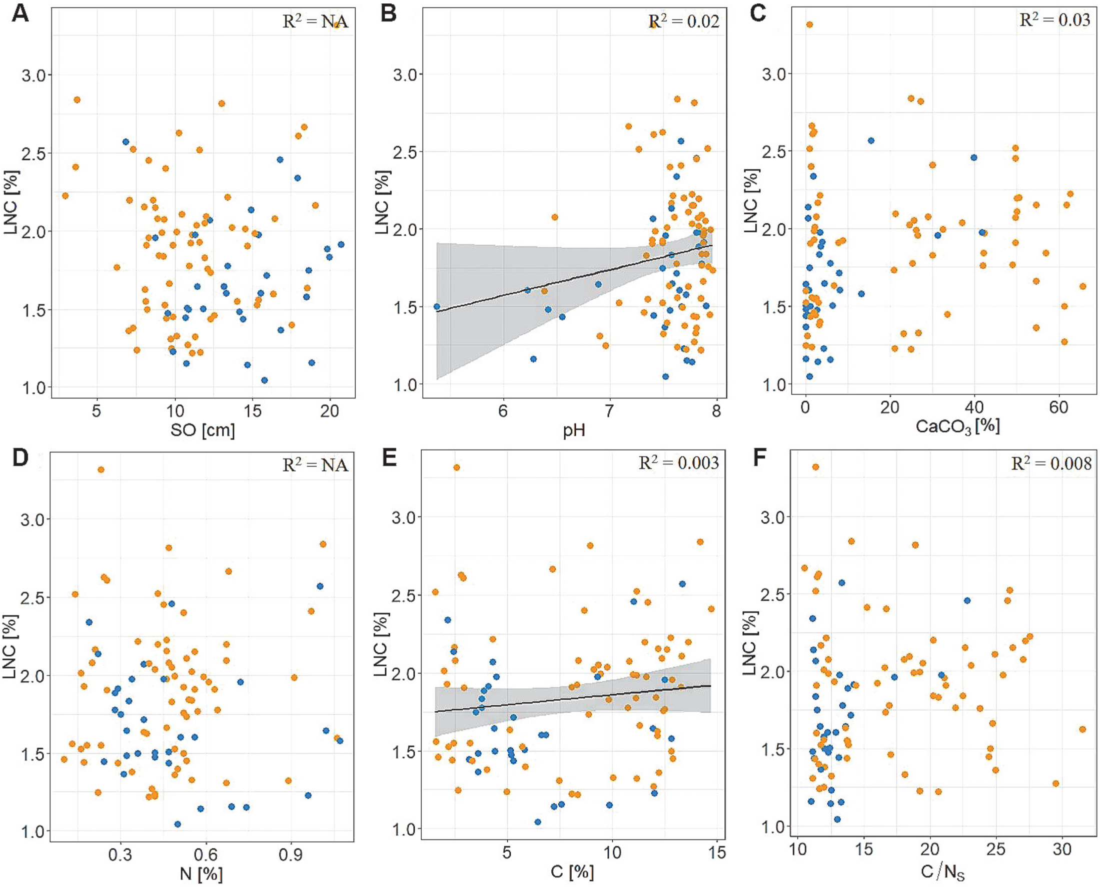


Fig. 7. Relationships between the community weighted mean of the leaf nitrogen concentration (LNC) of dry (orange colour) and semidry grasslands (blue colour) to soil factors: (A) SO; (B) pH; (C) $CaCO_3$; (D) N; (E) C; (F) C/N_s (for abbreviations see Fig. 4). Adjusted R^2 is given (NA – not available). Visualization based on the results of the ANCOVAs (cf. Supplementary Table S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

ences were found for SLA (Supplementary Fig. S5G). Regarding CV, there were no significant differences between the two grassland types.

Discussion

In this study, we found (i) only a small differentiation in functional trait composition between dry and semidry grasslands. (ii) Soil factors had only minor effects on the trait composition of both grassland types, although soil depth, C/N ratio and $CaCO_3$ content had the highest influence on this composition. (iii) The five dominant xerothermic grasses differed in their vegetative plant height and leaf traits, but contrary to our question, (iv) all grasses showed a relatively similar ITV, so we can conclude that *B. erectus* was not more adapted to changing environmental conditions.

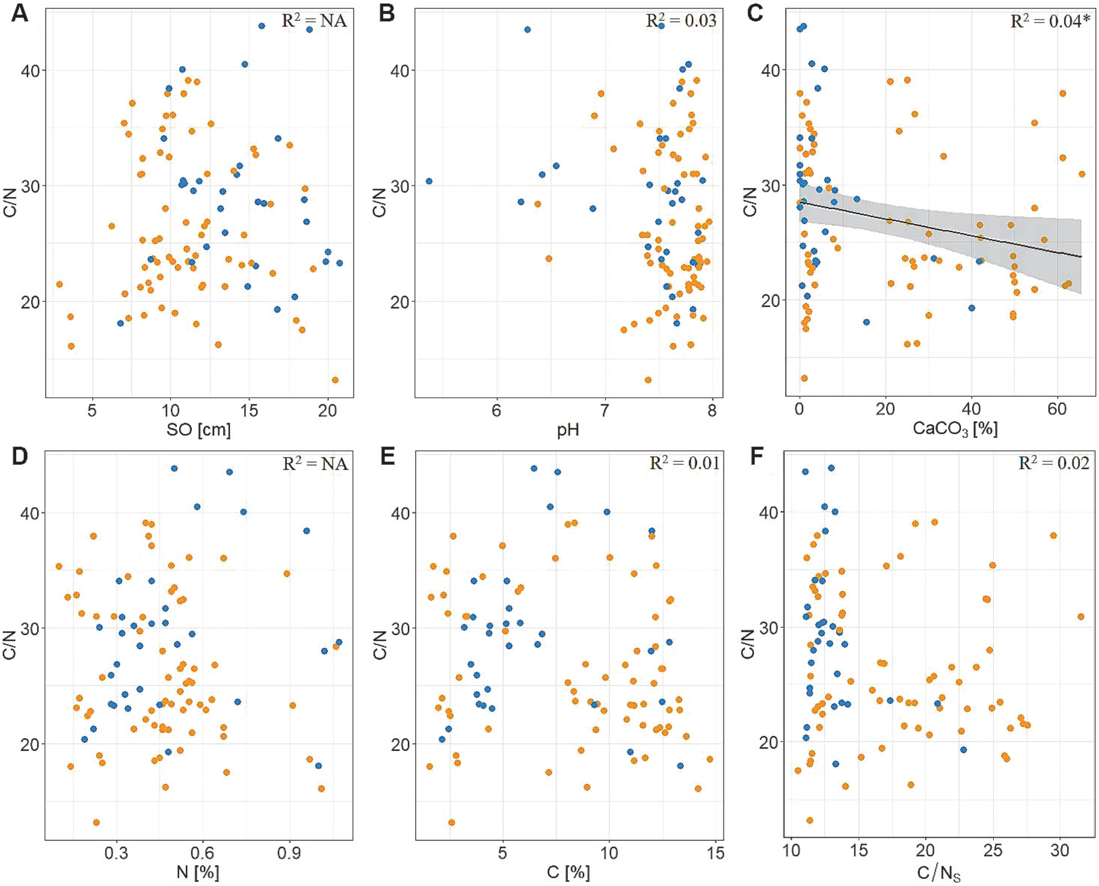
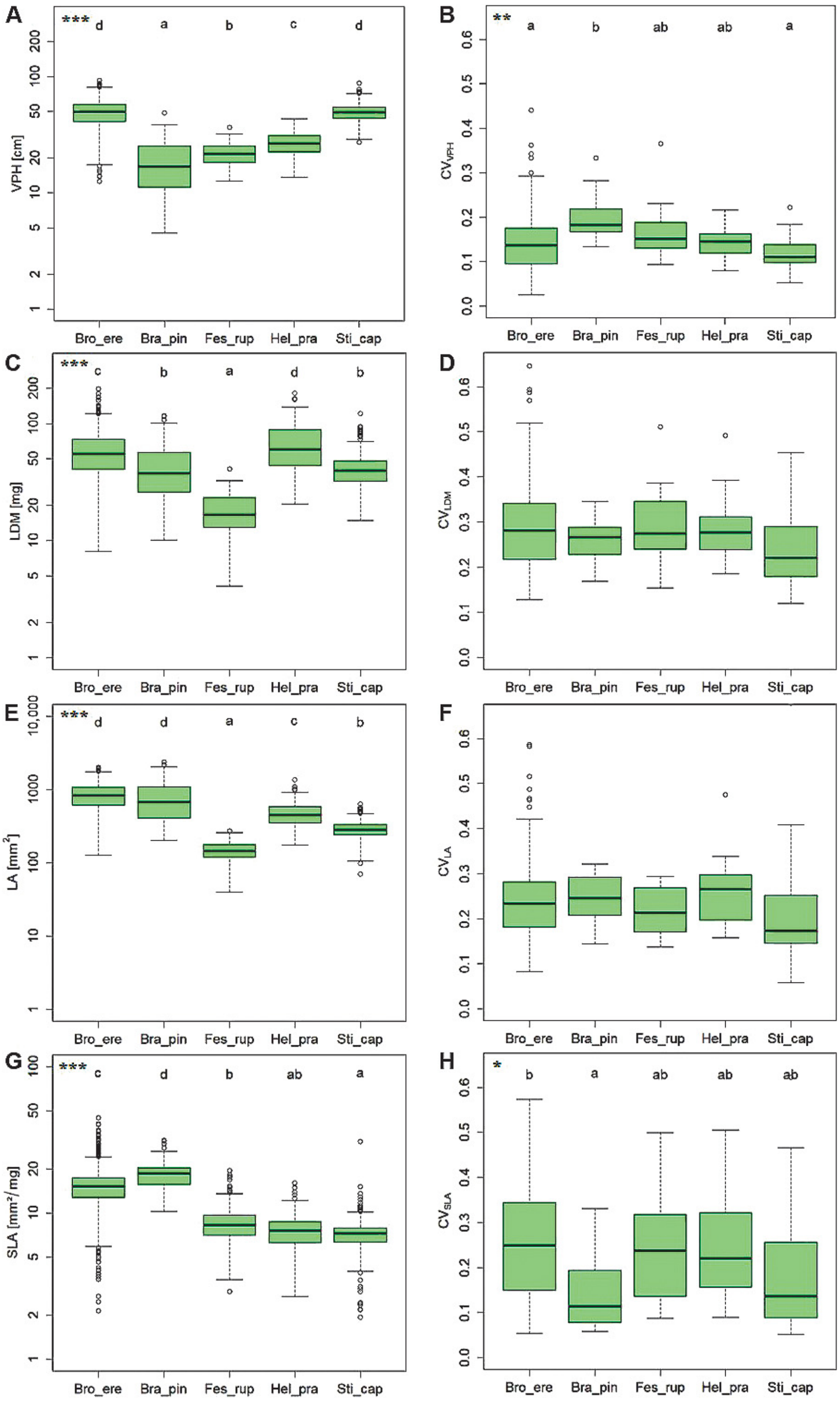


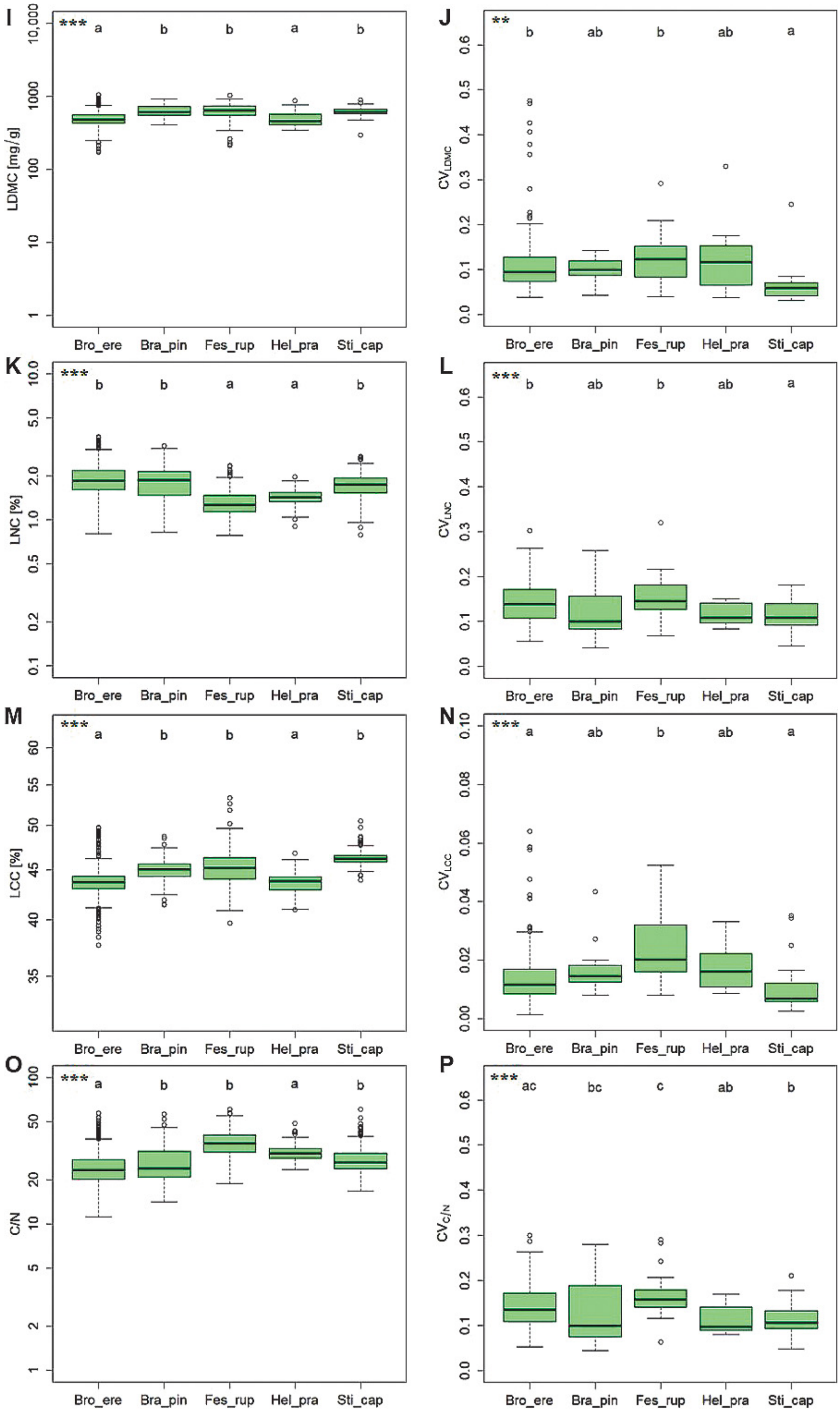
Fig. 8. Relationships between the community weighted mean of the leaf C/N ratio (C/N) of dry (orange colour) and semidry grasslands (blue colour) to soil factors: A) SO; (B) pH; (C) $CaCO_3$; (D) N; (E) C; (F) C/N_s (for abbreviations see Fig. 4). Adjusted R^2 and significance is given ($*0.01 \leq P < 0.05$, NA – not available). Visualization based on the results of the ANCOVAs (cf. Supplementary Table S3) as follows: significant main effect, but no interaction effect: one regression line with 95% confidence level; no significant main effect and interaction effect: without regression line.

Functional comparison of dry and semidry grasslands

We have found a slight differentiation in functional trait composition between dry and semidry grasslands. The semidry grasslands had significantly higher LDM and LA than the dry grasslands, likely indicating higher relative growth rates of the species (Garnier et al. 2016). Indeed, based on PCA, we detected a gradient between taller semidry grassland

Fig. 9. Functional traits and their coefficient of variation (CV) of the five dominant grasses (Bro_ere – *Bromus erectus*, Bra_pin – *Brachypodium pinnatum*, Fes_rup – *Festuca rupicola*, Hel_pra – *Helictotrichon pratense*, Sti_cap – *Stipa capillata*): A) VPH, B) CV_{VPH}, C) LDM, D) CV_{LDM}, E) LA, F) CV_{LA}, G) SLA, H) CV_{SLA}, I) LDMC, J) CV_{LDMC}, K) LNC, L) CV_{LNC}, M) LCC, N) CV_{LCC}, O) C/N, P) $CV_{C/N}$ (for abbreviations see Table 1). Results of the one-way ANOVA ($*0.01 \leq P < 0.05$, $**0.001 \leq P < 0.01$, $***P < 0.001$) and calculated Tukey's post-hoc test (different letters indicate significant differences at $P < 0.05$). See next 2 pages.


A
*** d a b c d
VPH [cm]
1 2 5 10 20 50 100 200
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
B
** a b ab ab a
CV_{VPH}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
C
*** c b a d b
LDM [mg]
1 2 5 10 20 50 100 200
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
D
CV_{LDM}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
E
*** d d a c b
LA [mm^2]
1 10 100 1000 10,000
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
F
CV_{LA}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
G
*** c d b ab a
SLA [mm²/mg]
1 2 5 10 20 50 100
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap
H
* b a ab ab ab
CV_{SLA}
0.0 0.1 0.2 0.3 0.4 0.5 0.6
Bro_ere Bra_pin Fes_rup Hel_pra Sti_cap


I
***
a b b a b
LDMC [mg/g]
1
10
100
1000
10,000
J
**
b ab b ab a
CV$_{LDMC}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
K
***
b b a a b
LNC [%]
0.1
0.2
0.5
1.0
2.0
5.0
10.0
L
***
b ab b ab a
CV$_{LNC}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
M
***
a b b a b
LCC [%]
35
40
45
50
55
60
N
***
a ab b ab a
CV$_{LCC}$
0.00
0.02
0.04
0.06
0.08
0.10
O
***
a b b a b
C/N
1
2
5
10
20
50
100
P
***
ac bc c ab b
CV$_{C/N}$
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Bro_ere
Bra_pin
Fes_rup
Hel_pra
Sti_cap

species with larger leaves and small dry grassland species with smaller leaves. Especially small and evergreen dry grassland species with scleromorphic leaves decreased within the last two decades in western and central Europe (Diekmann et al. 2019), but we assume that such species with a smaller VPH, LDM and LA might be better equipped for dry years that have occurred multiple times in previous years (e.g. 2015, 2018, 2019). For dry grasslands in Slovenia, it was shown that threatened species richness decreased significantly with increasing VPH and SLA, whereby the influence of tall and competitive species should be considered (Pipenbaher et al. 2013). The dry grasslands had a significantly higher LNC and LCC, so they were able to accumulate more nitrogen and carbon in their tissues, which may be associated with thicker leaves to maintain stomatal transpiration under drought stress (Hultine & Marshall 2000, Siefert 2012).

Nevertheless, no differences were found in VPH, SLA, LDMC and C/N between dry and semidry grasslands. This can probably be attributed to the different management practices of these grasslands. Grazing can regulate the functional trait composition of grasslands through ITV and species turnover (Niu et al. 2016), which in our case can lead to a shift from less conservative to more conservative species (i.e. that these species tend to be less variable in their traits) as such species develop grazing-avoidance strategies (Adler et al. 2004, Zheng et al. 2015). These are particularly slow-growing, conservative perennial grasses whose traits are adapted by grazing (Wang et al. 2023). However, we measured functional traits on both grazed (and therein with different grazing intensities) and abandoned sites, suggesting that the observed effects may have overlapped. Unfortunately, as we were not primarily interested in comparing different management practices on the functional trait composition of our dry and semidry grasslands, this aspect was not investigated and would require clarification in a further study.

However, both grassland types are characterized by a large proportion of grasses, which in our study had higher VPH, LDMC and LCC than forbs. Grasses have a higher percentage of structural tissue and relative cover (Reich et al. 2003, Al Haj Khaled et al. 2005, Pichon et al. 2022). The dominant grasses (e.g. *B. erectus*) were the most abundant species in our investigated dry and semidry grasslands (cf. Meier et al. 2021: increasing cover of all grasses of ~40% within the last two decades; see also Supplementary Table S1) and we assume that the functional composition and structure of these grasslands is largely determined by these species (cf. Lepš et al. 2011), supporting the biomass ratio hypothesis (Grime 1998). Moreover, the functional traits of dominant grasses have important implications for the ecosystem function (e.g. primary production) of natural and restored grasslands (de Vries et al. 2011, Baer et al. 2016). Otherwise, due to the extreme summer droughts in 2018/2019 in Central Germany (Boergens et al. 2020, European Drought Observatory 2021), nutrient uptake by the plants was likely suppressed by water limitation (Ellenberg & Leuschner 2010, Meier et al. 2022b), so that in both dry and semidry grasslands many species could only acquire few resources via the soil and thus longer-term storage of e.g. nitrogen in the leaves might have been necessary.

Functional changes in dry and semidry grasslands caused by soil factors

The soil factors had minor effects on CWM of dry and semidry grasslands, which is in line with Meier et al. (2019), who found no effects of soil properties on the functional traits of *Stipa* grasslands in Central Germany. Conversely, Li et al. (2017) postulated that quantitative functional traits, but not functional diversity, are directly associated with soil properties and play therefore an important role in plant-soil interactions, but we could not prove this fact.

In our study, soil depth, $CaCO_3$ content and soil C/N ratio were the strongest drivers of CWM differentiation between dry and semidry grasslands and had consequently the highest influence on their functional trait variability. Regarding the $CaCO_3$ content, there was a significant decrease in LDM and LA, while the soil C/N ratio showed a similar trend (no interaction between soil factor and grassland type). Dry grassland communities are characterized by many calcareous species (Schubert et al. 2001). In the dry grasslands over lower shell limestone in the Saale-Unstrut-Triasland (Becker 1998), a significant decrease in species richness due to increasing drought and additional nitrogen deposition was detected after more than two decades (Meier et al. 2022b), but not for the regions Kyffhäuser and Porphyry outcrops (Meier et al. 2021). We therefore assume that calcareous species in particular have suffered from these extreme environmental changes in that they were only able to form a lower VPH, LDM and LA and probably stored more nitrogen and carbon in the leaves.

Furthermore, LDM and LA increased with increasing soil depth (in relation to section 'Functional comparison of dry and semidry grasslands' especially for semidry grasslands) and decreased with increasing soil N and C content, although no significant differences in the interaction between soil parameters and grassland type could be revealed. Species on sites with deeper soils can have higher relative growth rates, but despite higher soil nutrient levels, their uptake of nitrogen and carbon may be limited by stressed water availability, likely due to extreme drought events (Ellenberg & Leuschner 2010). These species will likely need to invest in the conservation and protection of their resources in the longer term as part of the leaf economics spectrum (Wright et al. 2004).

Functional comparison of xerothermic grasses

To our knowledge, our study is the first to provide a direct functional comparison across xerothermic grasses and their ITV. As in our study, *B. erectus* and *B. pinnatum,* for example, were investigated functionally, but in terms of different management practices (Targetti et al. 2013) or to show several strategy types (Fort et al. 2012), while their ITV was not considered in detail.

In our functional comparison, all five dominant grasses showed species-specific responses. Generally, they are conservative species with low SLA but high LDMC, corresponding to longer leaf lives, denser leaf tissues and lower growth rates to better protect their resources from abiotic (e.g. extreme temperatures, intense sunlight, drought events) and biotic stress (e.g. herbivory) (Wright et al. 2004, Hodgson et al. 2005, Kleyer et al. 2008). For example, *B. erectus* showed high VPH, SLA and LNC, but lower LDMC, while *B. pinnatum* had the highest SLA (cf. Arredondo & Schnyder 2003 and Targetti et al. 2013 for trait values of *B. erectus* and *Brachypodium rupestre*, which have similar ecological behaviour to *B. pinnatum*). In particular, species with significantly higher VPH and SLA often grow on moister (or rather less dry) soils (Wellstein et al. 2013, Garnier et al. 2016). Such species can have a competitive advantage over species with opposite trait characteristics (Poorter et al. 2009, Lauterbach et al. 2013). Both *B. erectus* and *B. pinnatum* produced larger and heavier leaves than *F. rupicola* and *S. capillata*, which can be related to the results of Bohner et al. (2019) by showing that generally larger, broad-leaved grasses displace medium-sized, fine-leaved grasses. In fact, it was experimentally verified that *B. erectus* under nutrient addition produced more biomass and negatively affected the grasses *S. capillata* and *S. tirsa*, which could lead to the displacement of these rare species in the future (Meier et al. 2022a). As a competitive species, *B. erectus* can quickly access additional resources (Hautier et al. 2009) and is more stress-tolerant to drought and disturbance (Liancourt et al. 2005, Targetti et al. 2013), which we confirmed by their increased LNC and LCC in dry grasslands. Moreover, such species invest in vessel sclerification to maintain water uptake and transport during dry conditions (Fort et al. 2012). Nevertheless, besides *B. erectus*, *S. capillata* also showed increased VPH and LNC. Both species are deep-rooting, whereby *B. erectus* develops up to 90 cm and *S. capillata* theoretically up to 280 cm deep roots (Kutschera & Lichtenegger 1982) and can therefore assimilate resources in deeper soil layers. Their growth was probably promoted by nitrogen deposition in combination with drought, which has led to an increasing abundance of both species within the last two decades (Meier et al. 2022b). *Helictotrichon pratense* could rather be considered as a functional intermediate between the other species in our study.

Nevertheless, all grasses had low variation in their trait values (except for slightly increased CV_{SLA} values) and in contrast to our initial question (iv), *B. erectus* is not more adapted to environmental conditions in its functional traits than the other grasses as previously expected. Indeed, even the CV values for *B. erectus* between dry and semidry grasslands did not differ significantly from each other. However, SLA of all grasses showed higher CV values, which was consistent with other studies on ITV indicating that SLA is a highly variable functional trait at different spatial scales (Wellstein et al. 2013, Siefert et al. 2015, Mitchell et al. 2017). The five dominant grasses had a relatively similar ITV, thus they likely exhibit a high degree of habitat specialization and may have a relative fitness advantage at preferred sites (Sultan 2000, Sides et al. 2014). Species with low ITV occupy narrower niches, are associated with relatively homogeneous environmental conditions and play an important role in stabilizing plant communities (Umaña et al. 2015, He et al. 2018).

Conclusions

There were a few differences (LDM, LA, LNC, LCC) in the functional trait composition of dry and semidry grasslands in Central Germany. Soil properties also had only a minor influence on the trait composition of both grassland types. Therefore, we assume that the environmental gradient was too moderate to derive clear differences in the ecosystem function between these two grassland types. Rather, the functional structure of the grasslands was determined by the dominant grass species (particularly *B. erectus*), which changed the traits of the plant communities by changes in their abundance, and our results suggest that such grasslands have a relatively similar primary production (vegetative plant height as proxy).

Although a shift in abundance was already detected in the dominant grasses (Meier et al. 2021, 2022b), our results showed that there were no obvious differences in their ITV during the time of sampling, which is particularly true for *B. erectus*. In the future, this species will increase in abundance due to increasing nitrogen deposition and climate warming (Meier et al. 2022a, b), but presumably, the adaptation of its functional traits to environmental conditions is independent of the grassland type, as currently no differences between dry and semidry grasslands are detectable in its ITV.

Supplementary materials

Fig. S1. Correlation matrix of pairwise correlations of all functional traits.
Fig. S2. Relationships between the community weighted mean of the leaf dry mass of dry and semidry grasslands to soil factors.
Fig. S3. Relationships between the community weighted mean of the leaf area of dry and semidry grasslands to soil factors.
Fig. S4. Relationships between the community weighted mean of the leaf carbon concentration of dry and semidry grasslands to soil factors.
Fig. S5. Functional traits and their coefficient of variation of *Bromus erectus* within dry and semidry grasslands.
Table S1. Mean frequencies and covers of the most common species and their functional traits.
Table S2. MANOVA for directly testing the difference between all functional traits together as response variables and the grassland type as a predictor.
Table S3. ANCOVA after model simplification for testing the effect of soil factors on functional traits between dry and semidry grasslands.

Supplementary materials are available at www.preslia.cz

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Funkční přístup ke xerotermním trávníkům středního Německa: druhové vlastnosti, dominantní trávy a půdní faktory

Funkční vlastnosti určují, jakým způsobem druhy a společenstva reagují na environmentální gradienty. Ty jsou ovlivněny globální změnou, která se projevuje změnami klimatu a způsobu využívání půdy, což následně ovlivňuje půdní vlastnosti, druhovou bohatost a funkční rozmanitost v suchých nebo polosuchých travinných společenstvech. Během posledních desetiletí se v těchto společenstvech ve středním Německu zvýšila dominance travních druhů jako je *Bromus erectus*, ale faktory ovlivňující jejich vnitrodruhovou variabilitu zatím dost dobře neznáme. Cílem práce bylo jednak porovnat funkční vlastnosti suchých a polosuchých trávníků a zhodnotit, jaký vliv na ně mají vlastnosti půdy, a jednak odhalit rozdíly ve funkčních vlastnostech pěti dominantních druhů trav: *B. erectus*, *Brachypodium pinnatum*, *Festuca rupicola*, *Helictotrichon pratense* a *Stipa capillata*. Na místě vegetačních snímků jsme měřili funkční vlastnosti (VPH – vegetativní výška rostlin, LDM – sušina listu, LA – listová plocha, SLA – specifická listová plocha, LDMC – poměr sušiny v biomase, LNC – obsah dusíku v listech, LCC – obsah uhlíku v listech, poměr C/N) a analyzovali půdní faktory (hloubka půdy, hodnota pH, obsah $CaCO_3$, obsah N a C v půdě, poměr C/N v půdě). Pro každou plochu jsme vypočítali vážené průměry společenstva (CWM) všech funkčních vlastností a porovnali rozdíly mezi oběma typy trávníků. Mezi suchými a polosuchými trávníky byly zjištěny drobné rozdíly v CWM některých funkčních vlastností (LDM, LA, LNC a LCC), zatímco ostatní vlastnosti se mezi oběma typy trávníků nelišily. Půdní faktory měly malý vliv na vlastnosti druhů travních společenstev, hloubka půdy, obsah $CaCO_3$ a poměr C/N však byly potenciálně nejsilnějšími faktory pro diferenciaci. Pět studovaných druhů trav vykazovalo relativně podobnou intraspecifickou variabilitu, nezdá se proto, že by *B. erectus* byl lépe adaptován na měnící se environmentální podmínky než ostatní trávy. Obecně jsme zjistili pouze drobné změny ve funkčním složení vlastností suchých a polosuchých trávníků ve středním Německu.

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