Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands

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Abstract

Question: Explaining the biomass–species richness relationship is key to understanding vegetation dynamics. Several possible mechanisms have been suggested, but complex analysis of plant strategies, major biomass and species richness components along a long productivity gradient is still lacking. We provide a detailed analysis of the relationship between major biomass components (total above-ground biomass, green biomass and litter), plant strategies and species richness along a long gradient of alkali and loess grasslands in a steppe landscape in Central Europe.

Location: Hortobágy, Great Hungarian Plain, East Hungary.

Methods: Above-ground biomass of characteristic alkali and loess grassland stands was sampled along a gradient of increasing productivity. In each grassland stand, a 25-m^2 sample site was randomly selected. Within each site, ten above-ground biomass samples (20 × 20 cm) were collected randomly in June 2009, at the peak of biomass production. We classified all species into mixed C-S-R strategy types. To obtain correlations between various biomass and species richness data, Spearman rank correlation was used. The relationship between plant strategies and species composition were displayed with a DCA ordination.

Results: The frequently detected humped-back relationship was valid for the relation of total biomass and species richness. With increasing amount of total biomass, we detected an increasing proportion of competitors, and a decreasing proportion of stress tolerators in green biomass. A low proportion of ruderals was detected at both low and high biomass levels. Species richness was affected positively by litter at low litter scores, but there was a negative litter effect from much lower scores than detected previously (from 400 g·m^{-2}). There was a positive relationship between green biomass production and species richness.

Conclusions: The study revealed that at the initial part of a productivity gradient, stress is likely responsible for low species richness. Our results show that litter can shape changes in species richness along the whole biomass gradient, thus the litter effect is one of the major mechanisms structuring grassland diversity.

Introduction

Diversity of grasslands has decreased dramatically worldwide during the last century (Bakker & Berendse 1999). On one hand, substantial changes in land use have generally led to higher biomass production and lower species richness through the increased use of mineral fertilizers and pesticides in semi-natural grasslands (Fischer & Stöcklin 1997; Bischoff et al. 2005). On the other hand, the large-scale cessation of grassland management has facilitated the accumulation of litter and woody encroachment (Billeter et al. 2007), both decreasing grassland biodiversity. Thus, for the effective conservation of grassland biodiversity, it is vital to understand mechanisms shaping biomass production in relation to species richness in grasslands (Guo 2007).

The relationship between species richness and biomass is a major focus of recent scientific interest (Lamb 2008; Whittaker 2010; Adler et al. 2011). Several types of total above-ground biomass–species richness relationships have been reported, e.g. positive, negative, humped-back and U-shaped, but in some cases no clear relationship was detected (Mittelbach et al. 2001; Gillman & Wright 2006; Fridley et al. 2012). In previous studies it was found that the type of the relationship depended on the extent (Mittelbach et al. 2001; Gillman & Wright 2006) and location of the studied area (Cornwell & Grubb 2003), the degree of fragmentation (Dolt et al. 2005), the studied community types (Cornwell & Grubb 2003; Fridley et al. 2012) or successional stages (Guo 2003) and plot size (Oksanen 1996).

At the landscape scale (within 20–200 km, according to Mittelbach et al. 2001), the humped-back curve between species richness and productivity is the most common observed relationship (Mittelbach et al. 2001) if the studied communities represent a relatively long productivity gradient (Oba et al. 2001; Fridley et al. 2012). The humped-back relationship, proposed by Grime (1973), predicts that the maximum species richness is at intermediate levels of biomass. For the ascending and descending parts of the curve, several explanations are available. The ascending part of the humped-back curve is generally explained by (1) decreasing rate of stress (Grime 1973), (2) increasing abundance of plant individuals in the vegetation (Oksanen 1996; Forbes et al. 2001), (3) increasing amount and heterogeneity of mineral nutrients (Tilman & Pacala 1993) and (4) increasing litter and water availability (Xiong & Nilsson 1999). The descending part might be shaped by the (1) increasing rate of competition (Grime 1973), (2) increasing plant size (Oksanen 1996), (3) decreasing patchiness and microsite availability (Tilman & Pacala 1993), and (4) accumulation of a thick litter layer (Facelli & Pickett 1991).

Several mechanisms are suggested to explain the relationship between biomass and species richness; however, separate analysis of biomass components and plant strategies along a long productivity gradient in grasslands is still lacking. We provide a detailed analysis of the relationship between major biomass components (total above-ground biomass, green biomass and litter), plant strategies and species richness in eight types of characteristic alkali and loess grasslands in an alkali landscape in Hortobágy, Hungary. We set the following study hypotheses: (1) Humped-back hypothesis: total biomass affects species richness along a gradient of increase in biomass following a hump-shaped curve. (2) C-S-R hypothesis: competitiveness increases while stress-tolerance and ruderality decreases with increasing amount of total biomass. (3) Litter effect hypothesis: litter affects species richness positively at low amounts of litter and negatively at high amounts of litter.

Methods

Study area and sampling

The study areas are located in an alkali landscape in Hortobágy National Park, East Hungary. The climate of the region is moderately continental; mean annual temperature is 9.5 °C, while mean annual precipitation is 550 mm, with high yearly variations. The vegetation of the region is characterized by extent alkali and fragmented loess grasslands traditionally managed by grazing or mowing. These grasslands generally form a heterogeneous landscape mosaic structure in accordance with the uneven pattern of soil salinity and water content. Characteristic alkali and loess grasslands along a long gradient of increasing productivity were sampled in the region near to the towns of Egyek, Tiszafüred, Hortobágy and Balmazújváros, within a 30-km radius (GPS coordinates for the centre: 47°35′N, 21°04′E). Total above-ground biomass in three independent stands of eight characteristic grassland types was collected (total above-ground biomass = 'green biomass' and 'litter'; which latter contained both the litter layer and standing litter, not separated). For some further grassland characteristics, see Table 1. In each grassland stand, a 25-m^2 sample site was randomly selected. Within each site, ten above-ground biomass samples (20 × 20 cm) were collected randomly in June 2009, at the peak of biomass production. We used small plot size, which was proven to be appropriate to recognize the impact of local environmental factors (Grime 1997). Samples were dried (65 °C, 24 h), then sorted to vascular plant species and litter. Dry weights were measured with 0.01 g accuracy.

Data analysis

We classified all species into 19 mixed C-S-R strategy groups (see table 6 in Hodgson et al. 1999; and for the C-S-R strategy types Grime 1979) using the classification reported in Hodgson et al. (1999). This classification uses seven predictor variables (canopy height, dry matter content, flowering period, flowering start, lateral spread, leaf dry weight, specific leaf area), which are easily measureable plant traits. For the detailed classifications and species lists see Appendix S1. For the classification, we used a species list freely available on the Internet (http://people. exeter.ac.uk/rh203/allocating_csr.html), compiled using the classification method of Hodgson et al. (1999). For those species that were not included in this list, we calculated the C-S-R coordinates using the method of Hodgson et al. (1999) with a freely available Excel macro (http:// people.exeter.ac.uk/rh203/allocating_csr.html). The result of the classification was a mixed C-S-R category determined by three coordinates (C-, S- and R-coordinate) for

each species. The score of each coordinate is an integer from −2 to +2 (−2; −1; 0; +1; +2). We calculated the weighted mean of all three coordinates for each grassland stand; for this calculation, for weights we used the proportions of each species for green biomass.

To obtain correlations between various biomass and species richness data, Spearman rank correlation was used (Zar 1999). To compare biomass and species richness of different grasslands one-way ANOVA and Tukey test on nested design data were calculated (Zar 1999). To analyse the relationship of total biomass and species richness, we fitted a Gaussian curve (Rietkerk et al. 2000) using the graphical program package OriginPro (OriginLab Corp., Northampton, MA, US). The relationship between competitiveness, stress tolerance, ruderality (expressed as green-biomass-weighted means of C-, S- and R-coordinates, respectively) and species composition (presence–absence data set) was displayed using DCA ordination calculated with CANOCO (Microcomputer Power, Ithaca, NY, US). Gradient lengths were 5.536 and 2.385, while cumulative species variances were 21.5 and 28.3 for the first and second axis, respectively. Plant nomenclature follows Simon (2000).

Results

Species richness and biomass

In total 114 species (22 graminoids and 92 forbs) were detected in the biomass samples. The highest species richness was found in *Bromus* loess grasslands (mean 15.1 species in 0.04 m^2), while the lowest species richness was typical in *Alopecurus* meadows (mean 2.4 species in 0.04 m^2). The highest total biomass scores were found in *Alopecurus* meadows (mean 2316 g·m^{-2}), while the lowest were in *Puccinellia* open alkali grasslands (mean 113 g·m^{-2}; see Table 2). The relationship between total biomass and species richness showed a humped-back curve (Gaussian curve fit, $R^2 = 0.79$; Fig. 1). The highest species richness was 750 g·m^{-2} total biomass score. The scores for open and short alkali grasslands were in the initial part of the

Table 1. Characteristics of the studied grasslands.

Community name	Abbr.	Humidity/Water regime	Alkalinity	Characteristic species
Puccinellia open alkali grassland	PUG	dry/astatic*	very high	*Puccinellia limosa, Hordeum hystrix, Spergularia rubra, Lepidium ruderale*
Achillea short alkali grasslands	ACG	dry/stable	high	*Festuca pseudovina, Cynodon dactylon, Achillea setacea, Podospermum canum*
Artemisia short alkali grasslands	ARG	dry/stable	high	*Festuca pseudovina, Carex stenophylla, Artemisia santonicum, Lotus corniculatus*
Juncus short alkali grasslands	JUG	mesic/astatic**	high	*Juncus compressus, Hordeum hystrix, Bupleurum tenuissimum, Lotus corniculatus*
Festuca loess grasslands	FLG	dry/stable	low	*Festuca rupicola, Salvia nemorosa, Filipendula vulgaris, Fragaria viridis*
Bromus loess grasslands	BLG	dry/stable	low	*Bromus inermis, Poa angustifolia, Festuca rupicola, Salvia nemorosa*
Stipa loess grasslands	SLG	dry/stable	low	*Festuca rupicola, Stipa capillata, Thymus glabrescens, Galium verum*
Alopecurus meadows	ALM	mesic/stable	low	*Alopecurus pratensis, Agropyron repens, Juncus compressus, Eleocharis palustris*

*Rapid seasonal changes in soil water regime, in early springtime they are usually wet, and become dry during the spring.
**Water-covered in spring, and are then dry till summer.

Table 2. Biomass scores (g·m^{-2}; mean ± SE) and species numbers (mean ± SE) of the studied grasslands. Species number scores are calculated for the biomass sample size (0.04 m^2).

	Total biomass	Litter	Green biomass	Species number
PUG	112.5 ± 30.2[a]	39.7 ± 14.6[a]	72.9 ± 17.7[a]	4.3 ± 0.5[b]
ACG	155.9 ± 19.1[a]	76.2 ± 14.4[a]	79.6 ± 6.3[a]	4.9 ± 0.4[b]
ARG	197.0 ± 6.4[ab]	82.6 ± 6.5[ab]	114.4 ± 12.4[a]	4.3 ± 0.1[b]
JUG	352.1 ± 42.0[bc]	208.6 ± 38.5[b]	143.5 ± 3.7[a]	5.6 ± 0.3[b]
FLG	378.2 ± 7.3[c]	210.5 ± 8.6[b]	167.7 ± 4.5[a]	13.2 ± 0.8[d]
BLG	832.0 ± 74.2[d]	160.8 ± 56.4[ab]	671.2 ± 20.4[c]	15.1 ± 1.6[e]
SLG	1117.8 ± 52.3[e]	516.0 ± 77.1[c]	601.8 ± 25.2[c]	8.6 ± 0.6[c]
ALM	2315.7 ± 18.8[f]	1856.4 ± 108.1[d]	459.3 ± 91.4[b]	2.4 ± 0.1[a]

PUG, *Puccinellia* open alkali grasslands; ACG, *Achillea* short alkali grasslands; ARG, *Artemisia* short alkali grasslands; JUG, *Juncus* short alkali grasslands; FLG, *Festuca* loess grasslands; BLG, *Bromus* loess grasslands; SLG, *Stipa* loess grasslands; ALM, *Alopecurus* meadows.
Different superscripted letters indicate significant differences within each column tested using one-way ANOVA and Tukey test ($P < 0.05$).
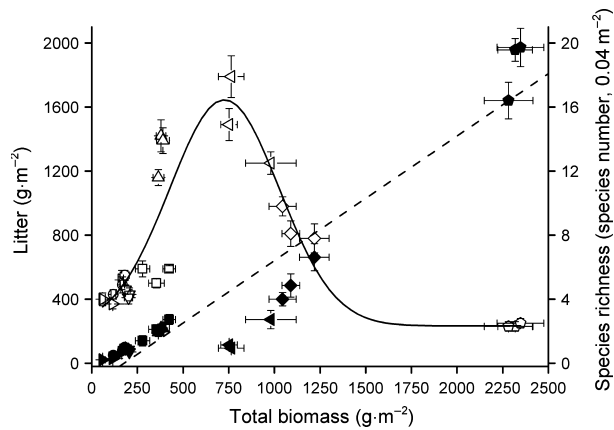
Fig. 1. The relationship between total biomass (g·m^{-2} ± SE) and the amount of litter (g·m^{-2} ± SE, filled symbols) or species richness (species number for .0.04 m^{-2} ± SE, empty symbols), respectively. Notations: *Puccinellia* open alkali grasslands -▷, ▶; *Achillea* short alkali grasslands -○, ●; *Artemisia* short alkali grasslands -▽, ▼; *Juncus* short alkali grasslands -□, ■; *Festuca* loess grasslands -△, ▲; *Bromus* loess grasslands -◁, ◀; *Stipa* loess grasslands -◇, ◆; *Alopecurus* meadows - ⬠, ⬟.

curve (low total biomass and species richness), scores of loess grasslands were in the middle (medium total biomass with high species richness), and scores of *Alopecurus* meadows were in the terminal part of the curve (high total biomass with low species richness; Fig. 1, Table 2).

The C-S-R strategies

With increasing total biomass, also increasing green-biomass-weighted mean scores of C-coordinates were found (Spearman rank correlation, $R = 0.88$, $P < 0.001$; Fig. 2a). We detected a strong negative correlation between total biomass and green-biomass-weighted means of S-coordinates (Spearman rank correlation, $R = -0.87$, $P < 0.001$; Fig. 2b). The relationship between total biomass and green-biomass-weighted means of R-coordinates followed a humped-backed curve. Thus, no single correlation was obtained (Spearman rank correlation, $R = 0.27$, $P = 0.19$; Fig. 2c). The highest green-biomass-weighted means of R-coordinates were found at peak species richness (750 g·m^{-2} total biomass score; Fig. 2c). For detailed biomass scores of mixed C-S-R strategy types in each grassland type, see Appendix S2.

The studied grassland types were clearly separated based on species composition along competitiveness, stress tolerance and ruderality gradients in the DCA (Fig. 3). There was also a strong negative correlation between competitiveness and stress tolerance expressed by green-biomass-weighted means of C- and S-coordinates. The open and short alkali grasslands were characterized as having high stress tolerance and low competitiveness scores (Fig. 3). In
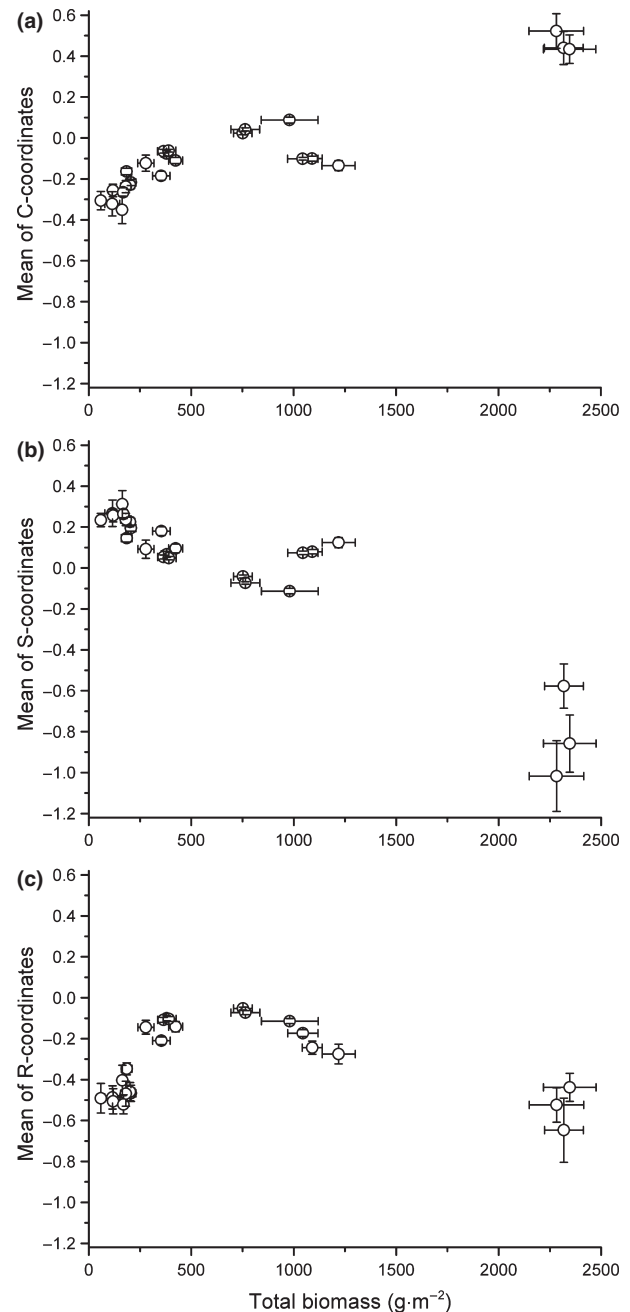

Fig. 2. The relationship between total biomass (g·m^{-2}, mean ± SE) and the green-biomass-weighted mean scores of C- **(a)**, S- **(b)**, and R-coordinates **(c)** (mean ± SE).

short alkali grasslands, the competitiveness scores were higher than in *Puccinellia* open alkali grasslands, and increased with increasing total biomass. The *Alopecurus* meadows were clearly separated from the open and short alkali grasslands in the direction of the higher scores of competitiveness. The highest scores for ruderality were detected in loess grasslands (typically in the *Bromus* loess grasslands; Fig. 3).
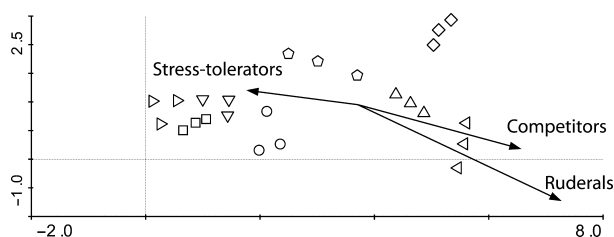
Fig. 3. Species composition (presence–absence main matrix, ten pooled biomass samples in each stand); competitiveness, stress -tolerance, and ruderality (expressed as green-biomass-weighted scores of C-, S- and R-coordinates, means of ten biomass samples per stand, added as secondary matrix using weighted averaging) displayed in a DCA. Notations: *Puccinellia* open alkali grasslands -▷ , *Achillea* short alkali grasslands -○, *Artemisia* short alkali grasslands -▽ , *Juncus* short alkali grasslands -□, *Festuca* loess grasslands - △, *Bromus* loess grasslands -◁, *Stipa* loess grasslands - ◊, *Alopecurus* meadows - ⬠.

Litter effect

With increasing total biomass, an increasing amount of litter was detected (Spearman rank correlation, $R = 0.93$, $P < 0.001$; Fig. 1). In the studied grasslands, where total biomass and the amount of litter was relatively low (total biomass yield up to 750 $g \cdot m^{-2}$, and amount of litter up to 400 $g \cdot m^{-2}$), we detected a strong positive correlation between litter and species richness (Spearman rank correlation, $R = 0.84$, $P < 0.001$). Conversely, in grasslands where total biomass and the amount of litter was high (exceeding 750 $g \cdot m^{-2}$ and 400 $g \cdot m^{-2}$, respectively), litter was negatively correlated with species richness (Spearman, $R = -0.95$, $P < 0.001$; Fig. 1). The correlation between green biomass and species richness was positive for the whole gradient (Spearman rank correlation, $R = 0.47$, $P < 0.05$).

Discussion

Total biomass and species richness

Our findings confirmed the first hypothesis: we detected a humped-back relationship between total biomass and species richness along the studied productivity gradient (Fig. 1). The total above-ground biomass scores (including litter layer) detected in this study ranged from 60 $g \cdot m^{-2}$ up to 2350 $g \cdot m^{-2}$, which is in line with some other studies that investigated a long biomass (standing crop + litter layer) gradient in grasslands (ca. 100–2600 $g \cdot m^{-2}$, Al-Mufti et al. 1977; 130–1850 $g \cdot m^{-2}$, Lamb 2008). Although wet meadows are characterized generally by higher total above-ground biomass scores (up to 2600 $g \cdot m^{-2}$, Wisheu & Keddy 1989; up to 3900 $g \cdot m^{-2}$, Gough et al. 1994); the peak of species richness was at intermediate levels of biomass in grasslands. In our study, the peak of the humped-back curve was at quite similar total biomass scores (at 750 $g \cdot m^{-2}$) to the study of Al-Mufti et al. (1977), where the humped-back relationship was first published. In our study, the peak was at higher total biomass scores than in former studies (ca. 270 $g \cdot m^{-2}$, Day et al. 1988; 100–300 $g \cdot m^{-2}$, Wisheu & Keddy 1989), but was within the typical range of productivity detected in grasslands. In our study, the peak was at 31% of the studied biomass range, while in former studies the peak was between 25.7–60.7% of the productivity range (Cornwell & Grubb 2003). There is no clear explanation for differences in the location of the peak in grasslands. Several factors might be jointly responsible for the differences, e.g. climate factors (Hawkins et al. 2003), disturbance regime (Biswas & Mallik 2010, 2011), vegetation type/gradient and some landscape properties (e.g. landscape level heterogeneity and rate of fragmentation; Dolt et al. 2005; Emanuel et al. 2011). It should also be noted that the comparison of our above-ground biomass scores with scores reported in most papers is quite difficult, because of the different sampling of the total above-ground biomass (in most studies the litter layer were not included to the total above-ground biomass).

Trends in C-S-R strategies

With increasing total biomass an increasing proportion of competitors and a decreasing proportion of stress tolerators in green biomass were found. These results partly confirm our second hypothesis. The relative proportion of competitors and stress tolerators in green biomass along the productivity gradient is probably due to different levels of stress and competition (see Liancourt et al. 2005; Michalet et al. 2002; Wang et al. 2011). Low biomass and species richness scores were detected in *Puccinellia* open alkali grasslands, which were shaped by high levels of two joint stress factors, high seasonal variability in soil moisture and high alkalinity (see Egan & Ungar 2000). Due to high levels of stress, these types of grassland were dominated by a few stress tolerators, which are usually small and slow-growing species with low biomass production (Grime 1979; Safford et al. 2001).

In the *Alopecurus* meadows, characterized by more stable mesic soil moisture conditions and low levels of alkali salts, the highest biomass was detected (Table 1). In productive habitats with low levels of stress, competition becomes more important than the effect of stress (Fraser & Keddy 2005). Thus, competitors can gain dominance, even if environmental conditions are also appropriate for stress tolerators (Bhattarai et al. 2004; Dostál et al. 2009). This latter assumption might be indicated by the presence of some stress tolerators in productive grasslands (loess grasslands and *Alopecurus* meadows) of the present study (see also Bhattarai et al. 2004; Chiarucci et al. 2004).

There appears to be a humped-back relationship between total biomass and the relative proportion of ruderals in green biomass (Fig. 2c). The share of ruderals in a given community is strongly influenced by three major conditions: (1) suitability of abiotic environment, (2) availability of microsites for establishment, and (3) propagule limitation (Grime 1979; Tilman & Pacala 1993; Thompson et al. 1997). Ruderals accounted for the highest relative proportion in green biomass in loess grasslands. These grasslands, with medium biomass and high species richness, were typical at dry habitats with low levels of alkali salts. We detected a low share of ruderals at both the initial and terminal part of the productivity gradient, which can be explained as establishment limitation caused by the high levels of stress (Grime 1979) and microsite limitation (Tilman 1993).

Litter effect

The litter effect hypothesis was supported through our results. Similar to the literature, we also found both positive and negative effects of litter on species richness (Carson & Peterson 1990; Fig. 1). We detected a positive relationship between litter and species richness at the initial part of the productivity gradient (see also Facelli & Pickett 1991; Boeken & Orenstein 2001). In stressed grasslands with relatively low biomass production, a slight increase in litter improves species richness by mitigating extremities in irradiation (Grace & Pugesek 1997) and fluctuations in temperature (Eckstein & Donath 2005), and evaporation (Facelli & Pickett 1991), resulting in a more humid microclimate (Xiong & Nilsson 1999). It was also found that litter accumulation can decrease the rate of salinization (Bakker 1985); therefore, the slightly increased amount of litter could promote germination and establishment of many plant species and mitigate the above-mentioned extremes.

We detected a negative relationship between litter and species richness at high levels of total biomass. The main reasons might be because: (1) litter can decrease solar irradiation on the soil surface (Amatangelo et al. 2008), (2) litter acts as a mechanical barrier which can hamper seed penetration into the soil (Ruprecht & Szabó 2011) and germination and establishment of certain plants through microsite limitation (Facelli & Pickett 1991; Foster 1999; Lepš 1999). (3) Litter can also have allelopathic effects (Ruprecht et al. 2010) and (4) can increase the risk of fungal infection (García-Guzmán & Benítez-Malvido 2003). (5) In addition, litter accumulation might decrease the number of flowering shoots, leading to decreased seed production and propagule limitation in the long term (Facelli & Pickett 1991; Bischoff et al. 2005). Several species groups in grasslands are clearly negatively impacted by high amounts of litter, e.g. forbs (Facelli & Pickett 1991), ruderal species (Facelli et al. 1988), annual species (Carson & Peterson 1990), plants with small seeds (Ruprecht & Szabó 2011) and small-sized species (Lepš 1999; Dolt et al. 2005). It was also found that competitor graminoids are often supported by the presence of litter, via improved re-sprouting and germination, which can lead to increased competition (Carson & Peterson 1990; Xiong & Nilsson 1999).

Several publications have attempted to quantify the amounts of litter that affect species richness either positively or negatively. Positive trends were found at low litter scores, generally up to 300 $g \cdot m^{-2}$ (Willms et al. 1986; Carson & Peterson 1990); when the amount of litter exceeded 900 $g \cdot m^{-2}$, a negative litter effect was detected (Carson & Peterson 1990; Deák et al. 2011); between 300 and 900 $g \cdot m^{-2}$ litter scores there were no correlations between litter and species richness, or contradictory findings were reported (Willms et al. 1986; Facelli & Carson 1991). Contrary to former findings, we detected a negative litter effect at lower litter scores than those previously published (from 400 $g \cdot m^{-2}$; Fig. 1).

Some authors suggest that green biomass plays a crucial role in determining species richness in grassland communities via facilitation (Michalet et al. 2006) or competition (Guo & Berry 1998; Török et al. 2011). Conversely, others suggest that accumulated litter plays a more important role in determining species richness than green biomass (see Lamb 2008). We detected a weak but positive correlation between green biomass and species richness; thus, the decrease of species richness at high biomass scores might not be caused by the increasing amount of green biomass. According to our results, litter can shape the changes of species richness along the whole biomass gradient, thus the litter effect is one of the major mechanisms structuring grassland diversity.

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Supporting information

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

Appendix S1. Classification of species into mixed C-S-R strategy types.

Appendix S2. Biomass scores of the different mixed C-S-R strategy types in the studied grasslands.