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ORIGINAL PAPER

Establishment of most grassland species was not more suppressed by invasive *Sporobolus cryptandrus* litter than by native grass litter

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Abstract *Sporobolus cryptandrus*, a North American C4 grass, has recently invaded European sandy grasslands, particularly in Central Europe (Hungary), where it threatens native plant communities. As allelopathy has been documented for other *Sporobolus* species, we tested whether litter from *S. cryptandrus* has a different effect on the germination and seedling emergence of native grassland species compared to native grass litter. We examined nine native grassland species and *S. cryptandrus* under three treatments: no litter (control), native litter and *S. cryptandrus* litter. We hypothesized the followings: (i) Litter addition can hinder germination compared to no-litter control because litter imposes physicochemical barriers. (ii) Following the Novel Weapons Hypothesis, *Sporobolus* litter may exert a stronger negative effect on native species than native grass litter. (iii) Litter effects are likely species-specific due to interspecific differences in traits and sensitivity to microenvironmental

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changes. Litter presence did not have a consistent negative effect across species, *Sporobolus* litter negatively affected germination only in *Bromus tectorum*. For most other species, the effects of native and *Sporobolus* litter were highly similar, suggesting that *Sporobolus* litter did not introduce physicochemical characteristics sufficiently different from native litter to produce distinct effects on native species. However, the suppression of *B. tectorum* germination by *Sporobolus* litter may indicate potential allelopathic effects. These findings suggest species-specific litter effects and highlight that *Sporobolus* litter could offer novel insights for managing *B. tectorum*, a problematic invader in North America. Future research should explore the long-term effects of *Sporobolus* litter in guiding restoration actions and invasive species management.

Keywords Grasslands · Cheatgrass · Litter effect · Plant invasion · Prairie · *Sporobolus cryptandrus*

Introduction

Plant litter is widely recognized to be among the key drivers of ecosystem processes and vegetation change (Wardle et al. 1997; Meisner et al 2012; Loydi et al. 2013; Giweta 2020). It can impact plant communities in multiple ways by affecting germination, seedling establishment (Carson and Peterson 1990; Hovstad and Ohlson 2008), species composition, and aboveground biomass production (Kelemen et al. 2013). These effects operate through various mechanisms, including shading, changing soil moisture, formation of a mechanical barrier, influencing nutrient cycling, releasing bioactive chemical compounds, and altering the structure and composition of the soil biota (Weltzin et al. 2005; Letts et al. 2015; Shen et al. 2016). The effect of litter on germination and growth can be both inhibitory and facilitative, and the net effect depends on litter depth and composition, the traits of seeds and seedlings, and the environmental context (Facelli and Pickett 1991; Li et al 2014). For instance, Meisner et al. (2012) showed that the litter of nutrient-rich exotic grass species increased soil organic N, which consequently increased the biomass of exotic and native plants, indicating a positive "legacy" effect of litter. In contrast, litter may also create a negative legacy by releasing phytotoxins, which can restrict plant growth (Meisner et al. 2012). In short, litter can enhance microsite conditions (e.g., by increasing moisture or nutrient levels) or inhibit seedlings (by light suppression, mechanical barrier or allelopathic compounds) depending on the conditions (Meisner et al 2012; Zhang et al 2022). According to Weidenhamer et al. (2023), proving allelopathy is inherently difficult because plant growth is influenced by many interacting (e.g., nutrients, pathogens, herbivores, and chemical compounds). Nevertheless, allelopathy remains a plausible mechanisms by which litter can interfere with plant germination and growth (Zhang et al. 2022).

Invasive plant species often produce litter that differs from native litter in both quantity and chemical composition (Cornwell et al. 2008; Hassan et al. 2021), and these differences can modify plant community composition and ecosystem processes by altering light availability, soil microclimate, and biogeochemical dynamics through litter inputs (Prescott and Zukswert 2016). Litter quality, particularly lignin and nutrient content are among the major determinants of decomposition rate and nutrient release (Cornwell et al. 2008; Chiba De Castro et al. 2020; Souza et al. 2023). For instance, lignin or fibre may reduce decay (Meisner et al. 2012), while litter rich in nitrogen or labile carbon decomposes and releases nutrients fast (Krishna and Mohan 2017). This is recorded in some invasive species, for example, *Bromus diandrus,* an invasive species in North America, which produces a persistent and thick litter layer inhibiting the seedling establishment of both native and invasive species, with varying effects depending on species and seed size (Chen et al. 2018). The invasive grass *Microstegium vimineum* produces litter that not only suppresses the growth and establishment of the native grass *Elymus virginicus* but also increases the incidence of fungal disease on the native species. Although both species are negatively affected, the litter disproportionately suppresses *E. virginicus*, ultimately favouring *M. vimineum* in competitive

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interactions (Benitez et al. 2022). Therefore, litter quality may differ between exotic and native species, potentially influencing the rate and composition of nutrient and compound release from litter into the soil as legacy (Drenovsky and Batten 2007; Godoy et al. 2010; Castro-Díez et al. 2012; Vujanović et al. 2022). Likewise, Berg and McClaugherty (2020) noted that humus formation and carbon and other nutrient cycles depend on litter decomposition rate and thus changes in litter inputs by invasive species may have widespread effects on the ecosystem. For example, Meisner et al. (2012) found increased soil inorganic N under exotic grass litter than under native grass litter, probably due to higher initial nutrient contents. On the other hand, exotic litter can include special secondary compounds (novel allelochemicals) which suppress native plants (Callaway and Ridenour 2004). Thus, the effect of invasive litter will depend on the net effect of these processes: improving fertility and microclimate versus exerting physical or chemical stress (Scharfy et al. 2011; Yelenik and Levine 2011).

The success of some exotic invasive plant species may be partly explained by the possession of so-called "novel weapons". According to the Novel Weapons Hypothesis proposed by Callaway and Ridenour (2004), invasive plants can release biochemical compounds that native species have not encountered previously, giving the invaders a competitive advantage. Whitin this context, in the introduced range, litter from exotic plants may chemically interfere with germination, plant growth and microbial communities (Farrer and Goldberg 2009; Souza et al. 2023). However, previous studies emphasize the fact that litter effects may be species-specific and context-dependent (Medina-Villar et al. 2017; de las Heras et al. 2020).

Recently, a new invader C4 grass, the sand dropseed (*Sporobolus cryptandrus)*, native to North America, has become an important concern in some European countries, particularly in Hungary, where it invades disturbed and semi-natural dry grasslands by outcompeting native species (Török et al. 2021, 2024; Kröel-Dulay et al. 2024). While allelopathy has been documented for other species in the same genus, such as *S. pyramidatus (*Rasmussen and Rice 1971), its potential role in the case of *S. cryptandrus* has remained unexplored so far.

In this study, we aimed to analyse whether the litter of *S. cryptandrus* affects the germination and early establishment of native sand grasslands more negatively than the litter of native grasses. We studied the germination and seedling establishment of nine native sand grassland species of Central Europe and *S. cryptandrus* under three conditions: no litter addition, addition of native species' litter, or addition of *S. cryptandrus* litter. Since our experiment does not distinguish between physical and chemical effects, we refer only to overall litter effects. Based on previous results, we hypothesised the followings: (i) Litter addition may reduce germination and seedling establishment compared to the 'no-litter' treatment through shading, mechanical impediment, and litter-derived compounds. (ii) *Sporobolus* litter may exert stronger negative effects on germination and early establishment than native grass litter, consistent with the Novel Weapons Hypothesis and differences in litter chemistry (Callaway and Ridenour 2004). (iii) Litter effects are likely species-specific due to interspecific differences in seed traits and sensitivity to litter-induced microenvironmental changes. Addressing these hypotheses can clarify how invasive grass litter may reinforce invasion and inform more effective strategies to control this invasive grass species and guide the proper management of invaded grasslands.

Materials and methods

Prior to the litter experiment, we performed a preliminary germination test under both ambient room conditions and controlled climate chamber conditions. Germination percentage was recorded after 15 days. The average germination rate of the nine native grassland species was 72%, while *S. cryptandrus* showed 76% germination under room temperature and 65% under climate chamber conditions, indicating high viability across all tested species. Because both tests indicated high viability (> 60%), we considered seed viability sufficient for the experiment.

The effect of different litter types on the emergence of sand grassland species and early seedling growth were studied using the seeds of 10 species: nine grassland species native to Central Europe and one invasive species, *S. cryptandrus*. The species were selected to represent a relatively broad range of functional traits and seed masses (Table 1). The species' seeds were collected from natural populations located in the Great Hungarian Plain in Eastern Hungary, Central Europe during the summer of 2021. The

Table 1 List of the ten 10 studied species, including their native distribution (POWO 2025), thousand-seed weight (TSW) in grams (Sonkoly et al. 2023), and habitat types where they occur (Török et al. 2021; Pladias 2025)

Species	Family	Origin	Life form	Growth form	TSW	Local habitats in Central Europe
Sporobolus cryptandrus	Poaceae	North America	Perennial	Grass	0.090	Dry grasslands and other open areas, on sandy to rocky soils
Arenaria leptoclados	Caryophyllaceae	Europe, Asia	Annual	Forb	0.020	Sandy and rocky habitats
Bromus tectorum	Poaceae	Europe, Asia	Annual	Grass	3.696	Disturbed areas (pastures, along roadsides)
Crepis rhoeadifolia	Asteraceae	Europe, Asia	Annual	Forb	0.295	Meadows, open woodlands, and disturbed areas
Erysimum diffusum	Brassicaceae	Central Europe, Asia	Short-lived perennial	Forb	0.187	Rocky slopes, various grasslands, and open woodlands
Festuca pseudovina	Poaceae	Central Europe, Asia	Perennial	Grass	0.263	Dry grasslands, meadows, and open woodlands
Festuca vaginata	Poaceae	Central Europe	Perennial	Grass	0.647	Dry grasslands, meadows, and open woodlands
Jasione montana	Campanulaceae	Europe, Africa	Short-lived perennial	Forb	0.016	Grasslands, heathlands, and rocky slopes
Plantago indica	Plantaginaceae	Europe, Africa	Annual	Forb	0.805	Disturbed areas, along roadsides, and in grasslands
Petrorhagia prolifera	Caryophyllaceae	Europe, Africa	Annual	Forb	0.278	Sandy and rocky habitats

Tait data were collected from published source (LEDA Traitbase: Kleyer et al. 2008)

seeds were cleaned, and stored in a dry, dark environment at room temperature (max. 21 °C) until their use.

Many inhibitory compounds, such as soluble phenolic compounds are released in the earliest phases of litter decomposition (Jäderlund et al. 1996, de las Heras et al. 2020) and litter can lose its allelopathic effect early during decomposition (see e.g., Jäderlund et al. 1996; Bonanomi et al. 2006, 2011; Al Harun et al. 2015). Therefore, in accordance with previous experiments studying the potential allelopathic effects of litter (e.g., Chen et al. 2018; Li et al. 2025; Muturi et al. 2017), we used standing litter instead of already decomposing litter. The standing litter (dead plant material still attached to the upright stems) was collected from June to September of 2021 from semi-natural grasslands, using secateurs. The standing litter was collected from three species: the invasive *S. cryptandrus* and from two native species: *Festuca vaginata* and *Corynephorus canescens.* The litter was air-dried at room temperature and stored in a dark and dry environment until the experiment.

In a greenhouse experiment, plastic pots (9 cm×9 cm×9 cm) were filled with steam-sterilized potting soil, and 25 seeds from one of the ten species were evenly placed on the soil surface in each pot. The seeds were either (1) left uncovered (*no litter* treatment); (2) covered with 2.43 g (corresponding to 300 g/m^2, see Sonkoly et al. 2020) of a 1:1 mixture of *F. vaginata* and *C. canescens* litter (*native litter* treatment), or (3) covered with 2.43 g of dry litter of *S. cryptandrus* (*Sporobolus litter* treatment). The native litter treatment was a mixture of *F. vaginata* and *C. canescens* litter because these native species are co-occurring and co-dominant grass species of sand grasslands and are responsible for most of the accumulated litter in these habitats. The experimental design consisted of 150 pots in total (10 species × 3 treatments × 5 replications). The pots were arranged randomly in a greenhouse (and frequently re-arranged) and watered daily or every other day with tap water to maintain soil moisture conditions comparable to typical conditions occurring in the field during the spring. The germination experiment started on 25th April 2022 (mid spring), and seed germination and seedling emergence were monitored for five weeks. This duration was chosen based on previous studies that show most seedlings emerge within 7–14 days under greenhouse conditions (Török et al. 2021) and are well established within 4–6 weeks (Török et al. 2024; UMCES 2025). On 26th May 2022 (late spring) all seedlings were counted and removed. The length of seven randomly selected seedlings per pot was measured and the total aboveground dry biomass of seedlings in each pot was weighed with an accuracy of 0.0001 g. Only seedlings that successfully emerged above the litter layer were considered.

Statistical analyses

We used three measured variables as response variables which characterised early seedling performance: germination rate, seedling length, and dry weight per seedling (see Online Resource 1). The response variables are interrelated and moderately or strongly correlated with each other; therefore, we first applied a multivariate approach. We used multivariate analysis of variance (MANOVA) to test the effect of litter type, species, and their interaction on the multivariate response. Germination rate data were arc-sine transformed and seedling length and seedling dry weight data were log transformed to improve multivariate normality. Pillai's trace was used for generating an F test, because it is robust to moderate violations of multivariate normality. After a significant MANOVA, we carried out follow-up univariate analyses by analysing each response variable separately using two-way ANOVAs with litter type, species, and their interaction as fixed effects. Response variables were transformed as appropriate to meet ANOVA assumptions (arcsine-square-root for germination, log-transformation for seedling length and dry weight). Residual plots for normality and homogeneity of variance were checked to verify model assumptions. Following significant litter × species interactions, pairwise contrasts (pairwise differences between the litter types within each species) were calculated using the *emmeans* (estimated marginal means) package in R, with the Tukey method for *p*-value adjustments. Pairwise comparisons were performed on the transformed scale, but non-transformed values are shown on plots for clarity and easier interpretation. All analyses were conducted in R version 4.3.2 (R Core Team 2023).

Results

MANOVA indicated significant effects of both litter type (Pillai = 0.31, $F_{(6,236)} = 7.17$, $p < 0.001$), species (Pillai = 2.64, $F_{(27,\ 357)} = 99.37$, $p < 0.001$), and their interaction (Pillai = 0.93, $F_{(54,\ 357)} = 2.98$, $p < 0.001$) on the multivariate response. Therefore, we conducted follow-up univariate ANOVAs and species-specific pairwise comparisons. The univariate ANOVAs showed that across species, litter type had a significant effect on germination rate and seedling length, but not on seedling dry weight (Table 2). Species identity and the interaction of litter type and species had a significant effect on all three response variables (Table 2, Fig. 1).

Table 2 The results of two-way ANOVAs testing the effect of litter type, species identity, and their interaction on germination rate, seedling length, and seedling dry weight

	Effect	df	F	*p*-value
Germination rate	Litter type	2, 119	3.137	*0.0470*
	Species	9, 119	49.424	*< 0.0001*
	Litter × Species	18, 119	2.023	*0.0132*
Seedling length	Litter type	2, 119	14.135	*< 0.0001*
	Species	9, 119	241.081	*< 0.0001*
	Litter × Species	18, 119	2.591	*0.0011*
Seedling dry weight	Litter type	2, 119	0.785	0.459
	Species	9, 119	203.052	*< 0.0001*
	Litter × Species	18, 119	5.287	*< 0.0001*

Significant effects are denoted with italics

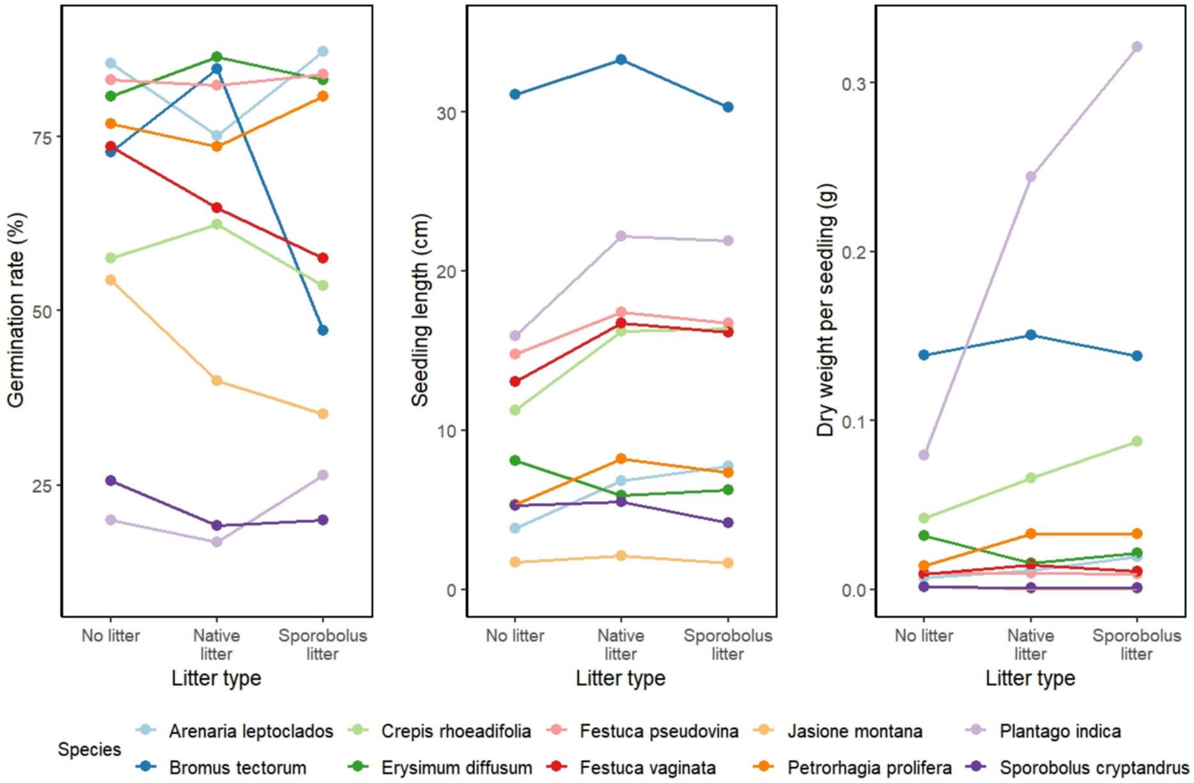

Fig. 1 Effects of litter type on early seedling performance across species. Interaction plots showing the effects of litter type on the germination rate, seedling length, and seedling dry weight of each species. Points and lines represent the observed mean values. Standard error is not plotted to avoid overcrowding the plots

Due to the significant interactions, we calculated pairwise contrasts between litter types within each species. The effect of litter treatment on germination rate was only significant for *Bromus tectorum* (see Table S1 in Online Resource 2). The germination rate of *B. tectorum* was significantly lower in the *Sporobolus* litter treatment than in the no litter or the native litter treatment (see Fig. 2). The contrasts showed a significant effect of litter type on the seedling length of five species: *A. leptoclados*, *C. rhoeadifolia*, *F. vaginata*, *P. prolifera*, and *P. indica* (Fig. 3, Table S2 in Online Resource 2). Seedling length was increased in the native litter treatment compared to the no litter treatment in all these species, and seedling length did not differ between the native litter and the *Sporobolus* litter treatment for any of the species (see Fig. 3). For seedling dry weight, significant differences between litter treatments were indicated in six species: *A. leptoclados*, *C. rhoeadifolia*, *J. montana*, *P. prolifera*, *P. indica*, and *S. cryptandrus* (Fig. 4, Table S3 in Online Resource 2). Seedling dry weight in the native litter treatment was not different from the no litter treatment in *A. leptoclados*, *C. rhoeadifolia*, and *J. montana*. Both native litter and *Sporobolus* litter increased seedling dry weight in *P. prolifera* and *P. indica*, while both litter types decreased dry weight in *S. cryptandrus*. However, seedling dry weight differed between the native litter and the *Sporobolus* litter treatment only in the case of *J. montana*, where *Sporobolus* litter resulted in decreased seedling dry weight compared to both the no litter and the native litter treatment (see Fig. 4).

Discussion

Our hypothesis that litter addition reduces seed germination and establishment compared to the no-litter treatment was only partially supported. As reported in previous studies, litter can exert both positive and

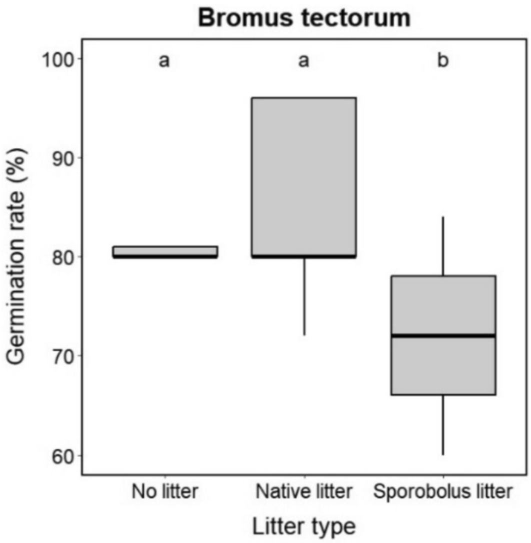

Fig. 2 Germination rate of *Bromus tectorum* across litter treatments. Boxes show the median and interquartile range of the observed values. Different letters above boxes indicate significant differences among litter treatments based on Tukey-adjusted pairwise contrasts. Species with no significant differences are not plotted, the results of all pairwise contrasts can be found in Table S1 in Online Resource 2

negative effects on plant germination and growth. In our study, litter generally had neutral to positive effects, with negative responses restricted to a small number of species. Some previous studies found that litter effects depend on both species and litter types (Donath and Eckstein 2008; Ruprecht et al. 2010). However, our results showed that compared with the no-litter treatment, both litter types (native and *Sporobolus* litter) had a significant positive effect on seedling length in several species, and we found only limited differences between the effects of litter types in most species. This may be because both types of litter come from grasses that are adapted to dry, nutrient-poor environments and tend to produce litter with similar structural characteristics, such as high C:N ratios and slower decomposition rates (Cornwell et al. 2008; Szabó et al. 2017; Seres et al. 2022). Some studies reported that using litter from distinct plant groups like forbs or sedges can have different physical or chemical effects on seedling emergence and growth compared to grass litter (Xiong and Nilsson 1999).

Some studies suggest that allelopathy may play a key role in supporting alien species in invading plant communities (Callaway and Aschehoug 2000; Ruprecht et al. 2008; Loydi et al. 2015). This idea is in line with the Novel Weapons Hypothesis, which suggests that many invasive species have biochemical compounds that are evolutionarily novel and thus more inhibitory to native plants (Callaway and Ridenour 2004). According to Kalisz et al. (2021) and Zhang et al. (2020), most invasive species produce allelochemicals with the potential to negatively affect native plant performance and native plants suffer more from leachates of alien plants than from leachates of other natives. Allelopathic effects have been documented in the *Sporobolus* genus as well, where allelopathy has been demonstrated for *Sporobolus pyramidatus* (Rasmussen and Rice 1971), which suggests that allelopathic activity may be present in other related species as well. Allelopathic effects may arise not only from compounds actively produced by living plants, but also from the microbial or abiotic decomposition of litter, as observed in species like *Juglans regia* or *Eucalyptus* species (Jose and Gillespie 1998; Zhang and Fu 2010). Despite this, our study detected few significant negative effects of either native litter or *Sporobolus* litter, and these were limited to a restricted number of species. However, this may partially be the result of this experiment being designed to study the early effects of litter such as shading, modification of soil moisture, and early release of water-soluble compounds, and not to explore the long-term effects such as nutrient release and microbial interactions associated with decomposing litter. Our findings are in contrast with previous studies (e.g., Loydi et al. 2013; 2015) which found that non-native litter reduced the native species' germination rate while increased the biomass of successfully established seedlings, compared to control conditions without litter.

Regarding our second hypothesis, we expected that *Sporobolus* litter would have a stronger negative effect on the germination and early establishment of native species than the native grass litter. Our results provided a partial support: *Sporobolus* litter had a strong negative effect on *Bromus tectorum*, by suppressing its germination rate compared to its germination rate in the native litter treatment. Besides *B. tectorum*, the effects of *Sporobolus* litter on other species were similar to that of native litter, only the seedling dry weight of *Jasione montana* was significantly lower in the *Sporobolus* litter treatment than

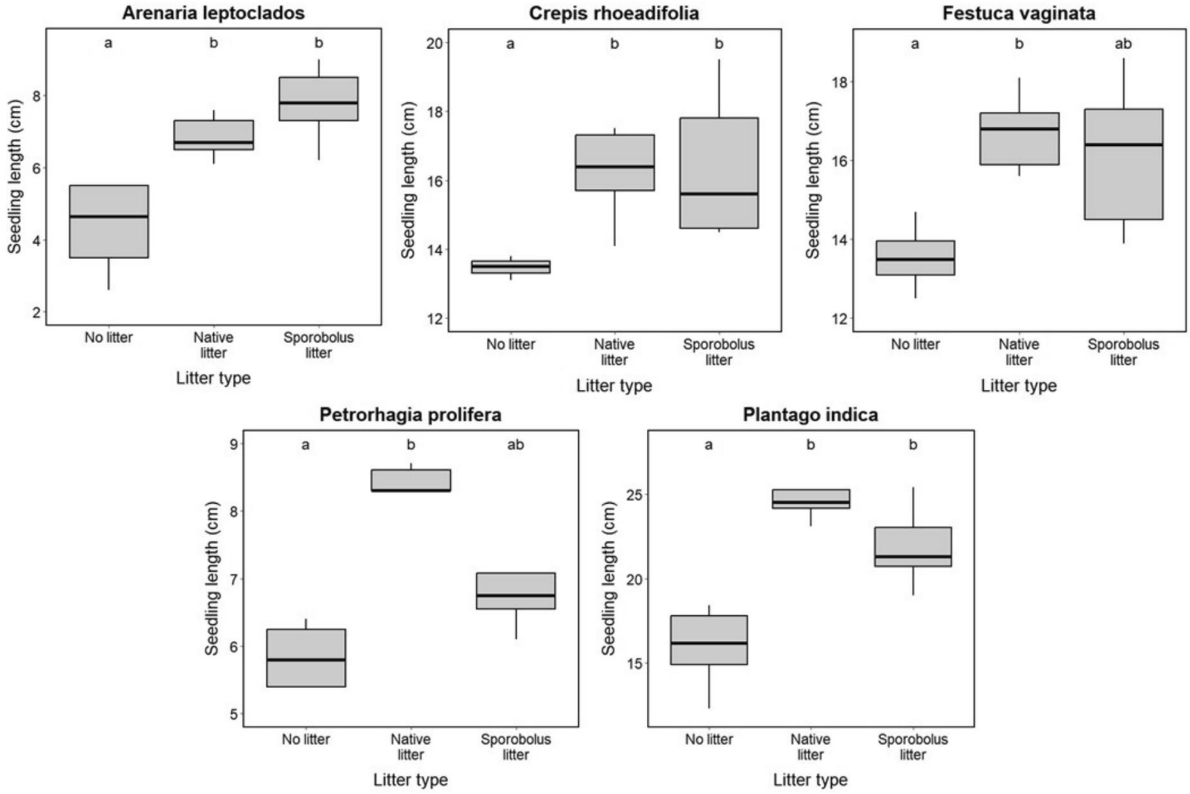

Fig. 3 Seedling length across litter treatments. Boxes show the median and interquartile range of the observed values. Different letters above boxes indicate significant differences among litter treatments based on Tukey-adjusted pairwise contrasts. Species with no significant differences are not plotted, the results of all pairwise contrasts can be found in Table S2 in Online Resource 2

in the native litter treatment. The generally similar effects of native and *Sporobolus* litter on most species indicate that litter effects were comparable across litter types, without allowing separation of physical and chemical mechanisms. However, the stronger suppression of *B. tectorum* under *Sporobolus* litter indicates a species-specific interaction, possibly involving allelochemicals, as observed for another species in the genus (*Sporobolus pyramidatus*; Rasmussen and Rice 1971). Additionally, *B. tectorum* is known to be sensitive to allelopathic effects, especially under stressed conditions like shading or nutrient competition (Machado 2007; Blank and Morgan 2012; Nesrine et al. 2012). While our study did not directly assess chemical composition, this known sensitivity may help explain the stronger response of this species compared to the other studied ones. Further research is needed to clarify the mechanisms driving these interactions, particularly the role of allelochemicals released during litter decomposition and their species-specific effects.

The third hypothesis was supported by the results: the effect of litter type was found to be highly species-specific: responses to litter were highly variable across species. Germination rate was only effected in *B. tectorum*, the only annual grass species in our study. The presence of both native and *Sporobolus* litter significantly increased the seedling length of five species (*Arenaria leptoclados*, *Crepis rhoeadifolia*, *Festuca vaginata*, *Petrorhagia prolifera*, and *Plantago indica*) and significantly increased the seedling weight of six species (*A. leptoclados*, *C. rhoeadifolia*, *J. montana*, *P. prolifera*, *P. indica*, and *S. cryptandrus*). While litter promoted seedling elongation in several species, this did not necessarily lead to an increase in seedling dry weight. Instead, elongation may be a stress response rather than an indicator of enhanced growth. Although seedlings grew taller,

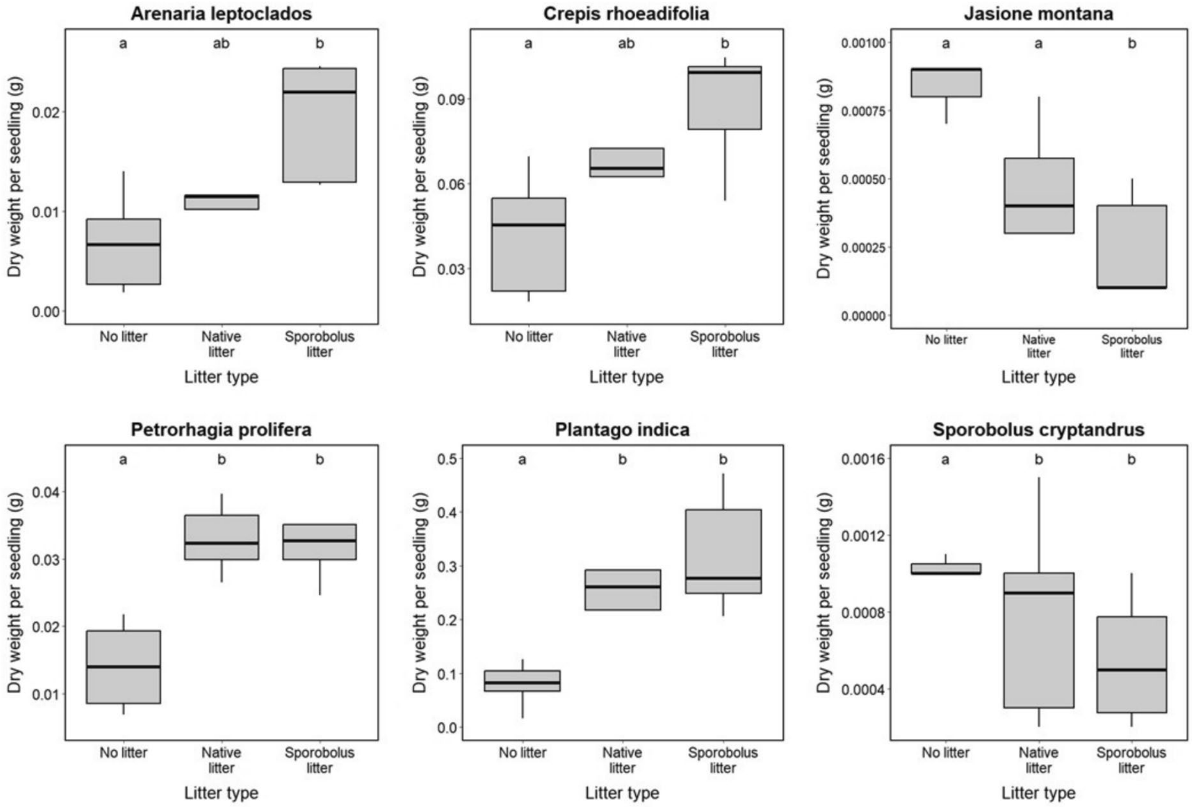

Fig. 4 Seedling dry weight across litter treatments. Boxes show the median and interquartile range of the observed values. Different letters above boxes indicate significant differences among litter treatments based on Tukey-adjusted pairwise contrasts. Species with no significant differences are not plotted, the results of all pairwise contrasts can be found in Table S3 in Online Resource 2

they may not necessarily be more robust or healthier, as suggested by their biomass (Liu et al. 2017). This trade-off between elongation and accumulating biomass is particularly relevant in short-term experiments, such as ours (lasting five weeks), where seedlings may still be in an early stage of resource allocation. For instance, *F. vaginata* displayed significant elongation under native litter compared to the no-litter treatment but did not accumulate more biomass, indicating that its response was driven by the shading of litter rather than improved conditions for growth.

Our findings suggest that the effects of litter, particularly shading and moisture retention, interact with species-specific characteristics like germination requirements, thereby creating microenvironmental conditions that differently affect species. The observed species-specific litter responses may be mediated not only by seed size but also by other seed and germination traits such as light requirements, dormancy type, seed coat permeability, and germination speed. For example, larger-seeded species may tolerate shading better, whereas smaller-seeded species might experience reduced emergence due to light limitation (Scarpa and Valio 2008; Wang et al. 2022). This aligns with previous research showing that litter can act as both a physical barrier and a protective microenvironment, depending on species traits (Ming-Zhang et al. 2003; Makkonen et al. 2013; Dias et al. 2017). However, it must be noted that the effects detected at the germination and early seedling stage do not necessarily translate into long-term demographic or community-level consequences, particularly in perennial species. Moreover, litter effects are likely to be highly context-dependent and may interact with environmental heterogeneity (e.g., soil pulses, soil variability, disturbance) which cannot be captured under greenhouse conditions. Furthermore, litter effects may shift over time as litter decomposition progresses (Bonanomi et al. 2006; de las Heras et al. 2020), potentially altering the balance between facilitative and inhibitory effects.

The differential effect of *Sporobolus* litter on *B. tectorum* has interesting implications for the interaction between native and invasive species. In North American prairies, where *S. cryptandrus* is native, these results may offer an additional possible option for managing invasive species such as *B. tectorum* (Mack 1981; Leger and Goergen 2017). Although our results only provide indirect indication for a possible allelopathic effect of *S. cryptandrus* on *B. tectorum*, our findings imply that the issue deserves additional investigation. First of all, the inhibitory effect on *B. tectorum* should be corroborated under field conditions, and the inhibitory compounds involved in the process should also be identified.

In summary, our findings show that litter influences germination, seedling emergence and early seedling growth in a strongly species-specific manner. While the effects of native and *Sporobolus* litter were broadly similar and positive for most species, *Sporobolus* litter exerted a stronger negative effect than native litter on certain species, particularly on the germination of *B. tectorum* and the seedling weight of *J. montana*. The finding that the germination and seedling length of *S. cryptandrus* itself was not affected by either native or conspecific litter may indicate high litter tolerance possibly contributing to its rapid establishment and hence competitive advantage, especially in communities with high litter accumulation.

Conclusions

Contrary to our expectations, we found that compared to native litter, the litter of *Sporobolus cryptandrus* significantly suppressed germination only in *Bromus tectorum*. Although our results do not support a general allelopathic effect, they indicate that species-specific sensitivity to *S. cryptandrus* litter may occur. The broadly similar (and in some cases positive) effects of native and *Sporobolus* litter further suggest that the litter-mediated impact of *S. cryptandrus* on native plant communities is generally limited.

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Author contributions All authors contributed to the study conception, design, and data collection. Data analyses were performed by Judit Sonkoly. The first draft of the manuscript was written by Patricia Elizabeth Díaz Cando and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data Availability All data generated or used in this study will be deposited in Figshare Digital repository upon acceptance.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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