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C4 GRASS INVASIONS IN EUROPEAN GRASSLANDS - CASE STUDIES ON THE EFFECTS OF INVASION ON THE VEGETATION AND SEED BANKS IN SAND GRASSLANDS

Thesis for the Degree of Doctor of Philosophy (PhD)

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Debrecen, 2025

Hereby I declare that I prepared this thesis within the Doctoral Council of Natural Sciences and Engineering, Doctoral School of ***Juhász-Nagy Pál****, University of Debrecen in order to obtain a PhD Degree in Natural Sciences at Debrecen University. The results published in the thesis are not reported in any other PhD theses.*

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Hereby I confirm that ***Patricia Elizabeth Díaz Cando*** *conducted his studies with my supervision within the* ***Functional and restoration ecology*** *Doctoral Program of* ***Juhász-Nagy Pál Doctoral School*** *between 2021 and 2024. The independent studies and research work of the candidate significantly contributed to the results published in the thesis.*

I also declare that the results published in the thesis are not reported in any other theses.

I support the acceptance of the thesis.

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General Introduction

Grasslands are among the most diverse and ecologically significant ecosystems, covering 40% of the Earth's terrestrial area (Gibson & Newman, 2019). They host unique flora, fauna, and provide vital ecosystem services like carbon storage, soil stabilization, and water regulation, and support several agriculture and pastoral activities (Gibson & Newman, 2019; Kovacsics-Vári et al., 2023). Nevertheless, these ecosystems are increasingly threatened by the invasion of alien plant species, which disrupts native biodiversity, alter ecosystem functions, and challenge conservation efforts. Grasslands, characterized by open landscapes dominated by herbaceous vegetation (Burai, et al., 2015), are particularly vulnerable due to their susceptibility to disturbances such as grazing (Blair, Nipper & Briggs 2014; Kovacsics-Vári et al., 2023), land conversion, and climate change (Hopkins, & Del Prado 2007). Such disturbances create establishment gaps (= safe sites) that alien plants can exploit, often outcompeting native species.

Plants utilize different photosynthetic pathways to optimize carbon fixation under varying environmental conditions. The three main types of photosynthetic are C3, C4 and CAM, each with distinct physiological characteristics (Niu et al., 2008; Pau et al., 2013; Kumar et al., 2017). C3 photosynthesis, used by most plants, relies on the enzyme RuBisCO for carbon fixation but is inefficient under high temperatures and intense light due to photorespiration (Kumar et al., 2017). In contrast, C4 plants have developed a more efficient mechanism, where carbon fixation occurs in specialized bundle sheath cells, minimizing photorespiration and enhancing productivity under warm, dry conditions and high light exposure

(Bouchenak-Khelladi et al., 2009; Edwards & Smith, 2010; Kumar et al., 2017). This adaptation gives C4 plants a competitive advantage in tropical and subtropical grasslands, where they dominate over C3 species (Berasategui et al., 2023).

Generally, the distribution of C3 and C4 species follows a distinct climatic pattern. C3 plants are more abundant in cooler, temperate, and high-latitude regions, where lower temperatures and moderate light conditions favour their efficiency (Sage, 2000). C4 species, in contrast, dominate warmer and drier regions, including the tropical and subtropical grasslands of Africa, Australia, and the Americas, where their higher water-use efficiency and ability to tolerate heat stress provide a survival advantage (Johnston, 1996; Sage et al., 1999; Finch, 2012; Osborne et al., 2014). In grasslands, the balance between C3 and C4 species is shaped by temperature, precipitation, and atmospheric CO_2 levels, with rising temperatures and increasing drought conditions favouring C4 dominance (Sage & Florentine, 2019).

This ecological distinction is particularly relevant when considering plant invasions in grasslands, where alien C4 grasses often have an ecological edge over native C3 species. Their ability to thrive under high temperatures and variable precipitation conditions allows them to rapidly colonize and transform grassland ecosystems (Chuine et al., 2012; Witwicki et al., 2016; Boretti & Florentine, 2019). These traits contribute to the success of invasive species, particularly in regions undergoing climate shifts, where rising temperatures and altered precipitation patterns increasingly favour C4-dominant species over native C3 plants (Theoharides & Duckes, 2007; Havrilla et al., 2023).

Alien plant invasions are a global ecological phenomenon, where introduced species establish, spread and disrupt local ecosystems beyond their native range (Kueffer, 2017). Invasive alien plants in grasslands pose a wide range of challenges. They can reduce species richness, displacing native grasses and herbs by monopolizing resources like light, water, and nutrients (Castro-Díez et al., 2016). Furthermore, they modify ecosystem functions such as fire regimes, the cycling of nutrients, and soil microbial communities, with cascading effects on native plant and animal populations (Capdevila-Argüelles & Zilletti, 2008; Finch et al., 2021; Lopes et al., 2023). Among invasive plants, grasses, especially those utilizing the C4 photosynthetic pathway, are particularly problematic in grasslands. C4 grasses possess physiological traits that provide them with a competitive advantage in environments characterized by high temperatures, intense light, and limited water availability, allowing them to dominate and change ecosystems functions in invaded areas (Chuine et al., 2012; Kumar et al., 2017; Boretti & Florentine, 2019).

Globally, invasive C4 grasses such as *Sporobolus* spp., *Cenchrus* spp., or *Andropogon* spp., have demonstrated the ability to spread rapidly across grasslands, displacing native vegetation and homogenizing plant communities (Edvardsen et al., 2010). Their success is driven by features like prolific seed production, efficient dispersal mechanisms, and resilience to environmental stressors (Reed et al., 2005; Padilla et al., 2013; Linder et al., 2018). In Europe, the increasing presence of alien C4 grasses represents a growing ecological concern, as these species interact with native flora and fauna in complex and often unpredictable ways (Collins & Jones, 1986; Mateu, 1992; Pyankov et al., 2010).

Climate change also interplays with other invasion factors, like changes in land use and disturbances (Finch, 201; Freeley, et al. 2020; Singh et al., 2023). The amplification of disturbances like wildfires, floods, and storms creates opportunities for invasive plants to establish. Many invasive C4 grasses exhibit remarkable resilience in post-disturbance landscapes, particularly in fire-prone or heavily grazed areas (Burgiel & Muir, 2010; Grenz & Clements, 2023). Their efficient water-use strategies, rapid regrowth, and high seed production enable them to quickly exploit newly available spaces created by land degradation, deforestation, or changes in agricultural practices. This ecological plasticity allows C4 invasive grasses to outcompete native C3 species, which may struggle to recover after extreme climatic events (Chuine et al., 2012; Kumar et al., 2017). Rising atmospheric CO_2 emissions associated with climate change also influence plant invasions (Amare, 2016). While elevated CO_2 generally benefits C3 plants (another photosynthetic group), C4 grasses maintain their competitive edge in high-temperature and low-nutrient environments (Bernacki, 2012). Moreover, increased CO_2 may enhance the seed production and dispersal abilities of invasive plants, promoting their spread, particularly for C4 grasses (Hager et al., 2020; Zhao et al., 2022). Some studies suggest that C4 grasses may maintain their competitive advantage in resource-limited and high-temperature environments despite benefiting less than C3 species from CO_2 enrichment (Sage & Kubien, 2003; Kumar et al., 2017; Boretti & Florentine, 2019). Climate change and human-induced land use changes, such as agriculture, overgrazing and urban expansion, create conditions that facilitate plant invasions. These disturbances alter habitat functions and resource availability, often giving invasive species a competitive edge over native vegetation (Finch, 2012; Finch et al., 2021).

Addressing these dual threats of alien plant invasions and climate change requires integrated approaches that consider both species-specific and ecosystem-level dynamics. Effective management of invasive species continues to be most successful through mitigation, early identification and rapid action (Burgiel & Muir, 2010; Wan et al., 2024). For established invasions, adaptive management plans informed by climate projections are essential. Restoration efforts must integrate ecological knowledge of invasive species, how they interact with local vegetation, and changes in the environmental conditions caused by climate change (Livingstone et al., 2023; Adelah et al. 2024).

The present thesis focuses on the invasion ecology of alien C4 grasses in European grasslands in general and has also a specific focus on the recent spread of *Sporobolus cryptandrus* in sandy areas of Hungary.

Sporobolus cryptandrus, commonly known as sand dropseed, is a perennial C4 grass native to North America. It grows typically in arid grasslands, sandy soils, and disturbed environments (Shiflet 1994; Clements et al., 2007). It has shown invasive tendencies in several regions outside its native range, including parts of Europe, where it spreads rapidly in nutrient-poor, drought-susceptible environments (Simon & Jacob, 1999; Király & Hohla, 2015; Sutton, 2021). Its successful establishment and growth are facilitated by its high seed production, resistance to drought, and capacity to adapt to disturbed habitats (Clements et al., 2007).

The study explores both the species-specific mechanism underlying the invasion of *S. cryptandrus*, such as its dispersal strategies, competitions, and adaptation to resource-poor habitats and its broader ecological consequences. The study provides information on how invasive C4 grasses affect plant community composition, biodiversity, and ecosystem stability by connecting species-level processes to ecosystem-scale effects.

Predicting the long-term effects of biological invasions in European grasslands requires an understanding of these dynamics, especially in relation to increasing environmental constraints.

Aims of the study

The thesis consists of four chapters, each based on research conducted by the author. The research examines various aspects of invasion biology, including a detailed investigation of the biological traits of *Sporobolus cryptandrus* and an assessment of the ecological impacts resulting from its spread.

The research presented in this dissertation has the results in multiple scientific publications. The first chapter is based on a review on C4 grass invasions in Europe, which has been accepted and is currently in production for publication in Journal of Vegetation Science (Impact factor: 2.2), where the candidate is the first author (Díaz at el., 2025). Two other studies on *Sporobolus cryptandrus* invasion, where the candidate is a co-author, were published in Global Ecology and Conservation (Impact factor: 3.5) (Török et al., 2021) and Land Degradation and Development (Impact factor: 3.6) (Török et al., 2024). Based on the results of the fourth chapter a manuscript is currently being developed and will be submitted soon. The research questions and hypotheses related to the chapters are summarized below:

In chapter 1, our aim was to explore the distribution patterns of alien C4 grass species across European regions and countries by reviewing published literature and online available databases. Specifically, we focused (1) on recording data on the present distribution, number of species, and the species density (per country) of detected alien C4 grass species within Europe; (2) to compare European regions and countries regarding the alien statuses of C4 grass species (casual, naturalised, and invasive); (3) to identify the most widespread and high-risk alien C4 grass species; (4) to identify the native climatic zones and the habitat preferences of each alien C4 grass species in European countries; and (5) to evaluate how the distribution of the identified species changes over time. Through these efforts, our goal was to offer valuable insights for the understanding of current invasion patterns of alien C4 grasses in Europe. This research forms a necessary starting point for subsequent studies aimed at comprehensively addressing and managing the impact of C4 grass invasions in Europe.

In the study introduced in chapter 2, we focused to clarify the current distribution, ecological impacts, and invasion potential of *Sporobolus cryptandrus* in Hungary, focusing on its effects on native sand grasslands. In particular, the aims of the study were: (i) to explore the species' range, with particular attention to Eurasian, where the species is spreading; (ii) to identify the habitat preferences in Central Europe; (iii) to characterize the seedbank formation and germination ability, and to study (iv) the effect of increased cover of the species on the vegetation composition.

In the study presented in chapter 3, we aimed at to study how the invasion of *S. cryptandrus* influences the density and species richness of the soil seed bank of dry sand grasslands in Central Europe. We assessed the vertical distribution and density of the soil seed bank in the newly established populations of the invasive grass species *S. cryptandrus*. Our hypotheses were the following: (i) As the cover of *S. cryptandrus* increases, the density and diversity of other species in the soil seed bank decrease. (ii) The density of *S. cryptandrus* seeds in the soil seed bank is highly affected by its own vegetation cover: with higher cover leading to a higher density of its seeds. (iii) The density and diversity of the soil seed bank declines with increases in depth sampling, and this density decline is influenced by the coverage of *S. cryptandrus*.

To further investigate *Sporobolus cryptandrus*, chapter four analyses whether its litter affects native vegetation through physical litter effect or allelopathy. We investigated the germination and seedling establishment of nine native sand grassland species and *S. cryptandrus* under three conditions: no litter addition, addition of native species litter, or addition of *Sporobolus cryptandrus* litter. We hypothesized that (i) litter addition negatively affects seedling germination and establishment compared to the no litter treatment; (ii) *Sporobolus* litter has a stronger negative effect on the germination and early establishment of the tested species compared to native grass litter; and that (iii) the effect of litter type is species-specific. Addressing these hypotheses provides information for designing a more effective control of this invasive grass species and contributes to a better understanding of how to manage invaded grasslands more effectively.

Materials and methods

Compilation of literature data (Chapter 1)

For the review in chapter 1, we used a standard literature review methodology to identify relevant publications and to compile an accurate and up-to-date list of alien C4 grass species present in Europe. The main sources for the literature search were Google Scholar and ISI Web of Science. To find the most relevant studies and sources, we used all the possible combinations of the following three keyword groups: (1) alien status (alien, non-native, introduced, neophyte, casual, naturalised, potentially invasive, and invasive), (2) C4 grass species (C4 grass, Poaceae, or grass), and (3) the names of the 39 European countries and two islands treated separately (see below). Boolean operators (AND, OR) were used to further refine search results. The resulting search terms looked like: ‘alien’ OR ‘introduced’ OR ‘neophyte’ OR ‘casual’ OR ‘naturalised’ OR ‘potentially invasive’ OR ‘invasive’ AND ‘C4 grass’ OR ‘Poaceae’ OR ‘grass’ AND ‘COUNTRY NAME’.

To extract more specific information (distribution range, native climate) about the identified alien C4 grasses, we used further databases: EURO+MED PlantBase, the European Distributed Institute of Taxonomy (Euro+Med, 2023); Royal Botanical Garden Kew's Plants of the World Online (POWO, 2023); CABI Compendium Invasive Species (CABI, 2023), GLONAF - Global Naturalized Alien Flora (GLONAF, 2023); PADAPT - Pannonian Database of Plant Traits (Sonkoly et al., 2023); and GBIF - Global Biodiversity Information Facility (GBIF, 2023); the last database was used to verify scientific names and unify synonyms.

The species were categorized in three statuses: casual, naturalised or invasive based on Richardson et al. (2000), using database reviews and literature to assess establishment and spreading patterns. Alien statuses were assigned consistently across countries and regions based on the most severe status recorded. In cases where the literature did not explicitly define the category, the species was evaluated based on its growth, establishment, spreading patterns and its degree of presence in the new area, and assigned status based either on these characteristics and definitions provided by Richardson et al. (2000).

Data was collected for all 39 European countries, and separately for the Canary Islands and Corsica. Although the islands are politically affiliated with Spain or France, respectively, their geographical location and climate is markedly different compared to the mainland territories to which they administratively belong. Then, countries were grouped into distinct regions within Europe: Northern Europe, Southern Europe, Western Europe or Eastern Europe based on the United Nations (UN) geoscheme created by the UN Statistics Division (United Nations Geoscheme 2024).

Species' native distributions were classified as temperate, subtropical, or tropical origins using POWO 2023. Habitat preferences were extracted from literature and habitat classes using the EUNIS Habitat Classification focused only on inland and terrestrial habitats, defining eight main habitat groups at EUNIS Level 1, taking into account the sublevels of these categories as proposed by Chytrý et al. (2020). The habitat categorization used for the current list of species follows the main habitat groups of the classification as: (1) Coastal habitats (dunes, shingle, rock/cliffs); (2) Wetlands (fens, mires and bogs); (3) Grasslands and areas predominantly covered by forbs, mosses or lichens (arid, moderate and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); (4) Heaths, scrublands and tundra (high-altitude, boreal scrublands, temperate brushlands and Mediterranean scrublands, moorlands); (5) Forests and other wooded land (broad-leaved and conifer forests and plantations; trees rows, small man-made forests, deforested area, successional forest and managed woodland); (6) Inland areas with few to no vegetation (rock/cliffs, scree, caves); (7a) Actively or recently cultivated lands, nurseries and residential gardens (including croplands, vegetable gardens, fallows fields, and recently abandoned farmland); (7b) Artificial grasslands and herbaceous-dominated environments (such as managed grasslands, artificial grasslands like athletic fields and turfgrass areas, trampled grasslands with annuals, as well annual anthropogenic herbaceous vegetation); (8) Man-made constructions, industrial and other artificial landscapes (buildings of settlements, transport networks, industrial sites, waste deposits). Note that the quality of the habitat information found for the species was highly variable, and we have no habitat information for many newly established species.

Target species: *Sporobolus cryptandrus* (Chapter 2, 3 and 4)

Characteristics of the species

Sporobolus cryptandrus is a perennial grass that is quite tolerant to drought and principally propagates by seed. This species belongs to the dropseed genus (*Sporobolus*), which contains around 160 species, with the majority being native to Africa, Australia and North America and a part of South America. (Baaijens & Veldkam, 1991; Simon & Jacob, 1999; Király & Hohla, 2015; Sutton, 2021). The *Sporobolus* genus is native to both tropical and warm temperate regions and is broadly suited to a great variation of different soil types, like loose sandy soils, compact floodplains soils or clayey saline soils (Simon & Jacob, 1999). The species *Sporobolus cryptandrus* is a bunchgrass that grows to a height of approximately 100 cm, including its inflorescences. Leaves have a collar of dense white hairs along the margins near the node, with scattered hairiness extending along the entire leaf edge. The 4-5 mm wide leaves have sharp edges but are noticeably softer than those of *Calamagrostis* (Fig. 1). The inflorescences look somehow similar to those of *Agrostis* species (Simon & Jacob, 1999), see also in Figure 1. The seed production can reach up to ten thousand seeds per plant (Brown, 1943). These small seeds (1-mm-sized) are easily dispersedspread by various agents, particularly by wind, and become sticky when wet, enhancing its dispersion. Although seeds are highly viable, a significant percentage of them have the potential to become dormant. Therefore, successful germination requires the breaking of dormancy using methods such as cold/heat stratification, moist conditions, might also need scarification of the seed coat (Holub & Jehlík, 1987; Sartor & Malone, 2010). Furthermore, the species has the ability to establish a persistent seed bank in its natural habitat (Clements et al., 2007). It has been shown that some members of the *Sporobolus* genus produce allelopathic compounds, as was demonstrated for *Sporobolus pyramidatus* (Rasmussen & Rice, 1971), thus *S. cryptandrus* might exert an allelopathic effect on the establishment of other species.

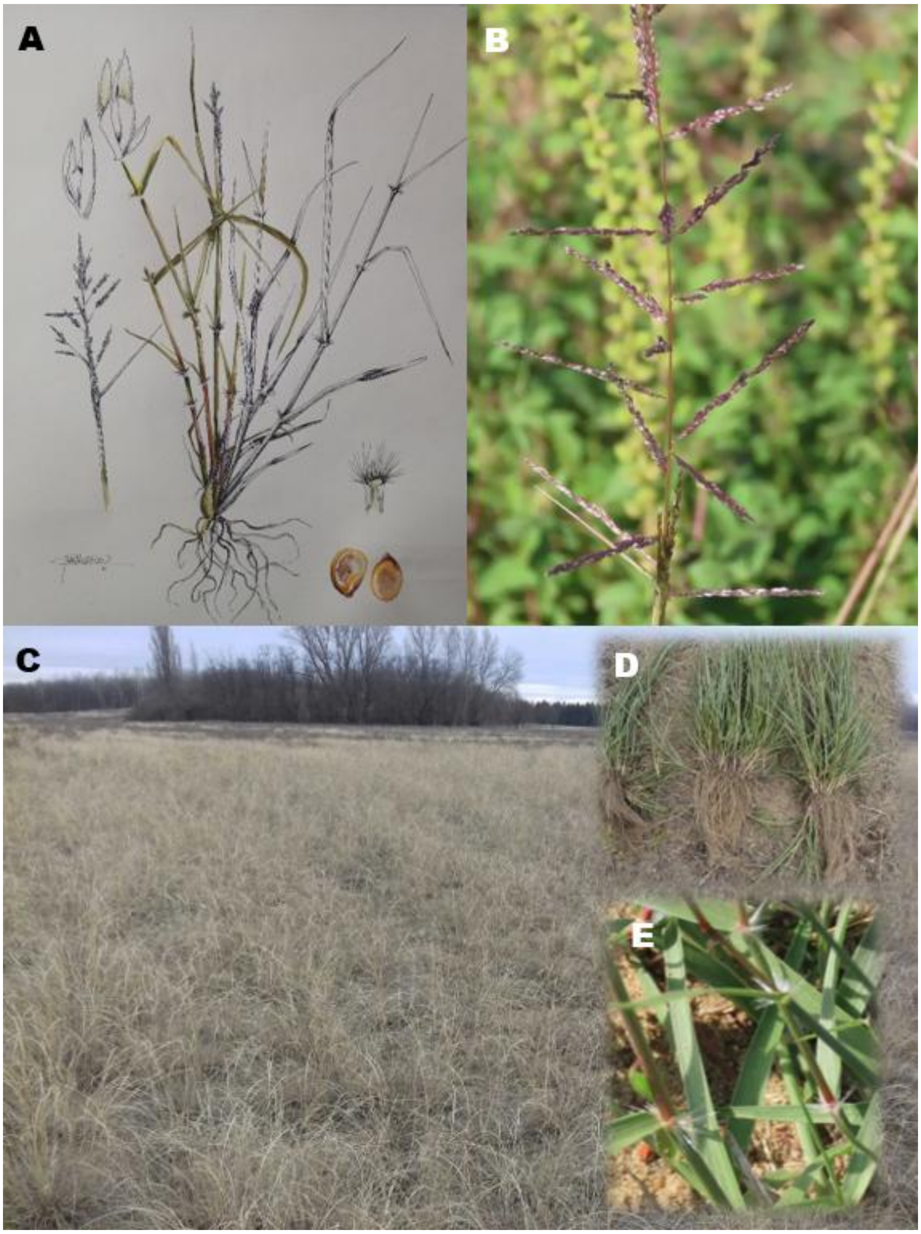


Figure. 1. *Sporobolus cryptandrus* appearance and morphological features. Annotation: A) appearance and key morphological features (drawings by L. Guallichico; B) inflorescences (photos by L. Guallichico); C) a mass invasion of *S. cryptandrus* in the Kiskunság region (picture by C. Tölgyesi); D) species root system (picture by E. Aradi); and E) nodes with leaves (photos by L. Guallichico).

Regional distribution of the species

Sporobolus cryptandrus is from north America and its distribution area extends from southern Canada to northern Mexico (Britton & Brown, 1970; Holub & Jehlík, 1987; Lackschewitz, 1991; Tilley et al., 2009; Nobis et al., 2015). The species prefers habitats in chaparral communities, deserts of sagebrush and short-grass prairies. It thrives in sandy, disturbed areas and is highly drought-tolerant (Clements et al., 2007; Albertson & Weaver 1944; Shiflet 1994). The colloquial name in English is sand dropseed for growing in sandy soils and its characteristic seed dispersal method. Due to its competitive nature, it can successfully colonize and dominate various habitats, even in arid environments.

Sporobolus cryptandrus has been documented in various regions beyond its native range including Argentina, Australia, Japan, New Zealand, Tasmania, and additional regions such as part of Europe and North America (Edgar & Connor, 2000, Curto, 2012, Randall et. al., 2017). The species was previously found in a number of isolated locations throughout Eurasia, namely Austria, Eurasia, France, Germany, Italy, Netherlands, Russia, Slovakia, Spain, Switzerland, Ukraine, and the United Kingdom (Ryves, 1988; Murr 1902; Romani et al., 2015; Sani et al., 2015; Sparrius et al., 2019; Thellung, 1919; Dflor, 2021; NMBC, 2021). As with *Sporobolus neglectus* and *Sporobolus vaginiflorus*, the current distribution of Sporobolus cryptandrus is primarily confined to the European Mediterranean and regions of Eastern Central and Eastern Europe characterized by a semi-arid or at least moderately continental climate. The species has only been occasionally recorded in more humid areas of Central and Western Europe, where its establishment remains rare (Fig.2).

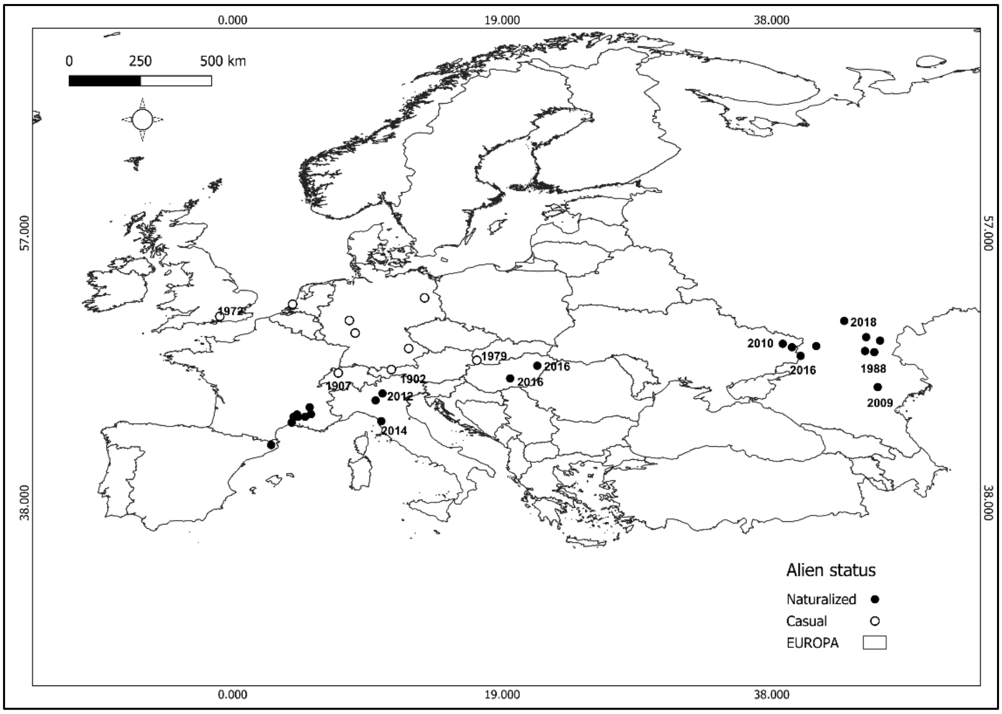


Figure 2. Eurasian distribution of *Sporobolus cryptandrus*. Black symbols represent naturalised communities, and white ones are casual occurrences.

The naturalisation of the species was first recorded by Holub & Jehlík, 1987 in a riverbank near Bratislava, Slovakia. Subsequently, it has spread extensively in steppe ecosystems of Ukraine and Western Russia (Alekseev et al., 1996; Kuvaev, 2014; Demina et al., 2016, and 2018; Gouz & Timoshenkova, 2017; Maltsev & Sagalaev, 2018). In Hungary *S. cryptandrus* was first recorded in 1927 in Győr city, northwest Hungary (Polgár, 1933), however, no further confirmation of the data has been obtained in the past. Since 2016, *Sporobolus cryptandrus* has been registered in two sandy regions in Hungary: The Nyírség region near Debrecen, characterized by acidic sand and Kiskunság region, near Kiskunhalas, where the sand is calcareous (Török & Aradi, 2017, Erdős et al., 2018, Molnár et al., 2020). A high abundance of *Sporobolus cryptandrus* in the vegetation decreases both the taxonomical and the functional diversity of the habitat, and these effects are significantly stronger in European sites compared to its native range. In both native range and introduced ranges, *Sporobolus* influences the functional composition of the vegetation by decreasing specific leaf area, increasing plant height, causing increasing abundance of wind-pollinated species to the detriment of insect-pollinated species, and increasing abundance of annuals to the compared to perennials. Some of these changes affect biomass and floral resources and reduce ecosystem provisions for higher trophic levels (Hábenczyus et al., 2022; Kröel-Dulay et al., 2024).

Study sites (Chapter 2 and 3)

The study of *S. cryptandrus* in Hungary started after its initial discovery in the Nyírség (Debrecen) and Kiskunság regions (Kiskunhalas North, Kiskunhalas East, Kecskemét Airport and Kecskemét Katonatelep) reported by Török & Aradi in 2017.

Debrecen is at the eastern edge of Hortobágy puszta (steppe) and on the southwest extremity of the sandy plain of the Nyírség area. Kiskunság Region is found in central Hungary, between the river Danube and Tisza, although it is part of the larger Great Hungarian Plain (Alföld). It is primarily formed by a mosaic of small areas like floodplains, loess plains and sand dunes (Kertész et al., 2011; Mezősi, 2017). The Nyírség (Debrecen) and Kiskunság regions share a continental climate, though the Kiskunság region is slightly dryer and warmer. In Nyírség, the yearly average annual temperature ranges 9.4–9.8°C and the yearly rainfall is between 530 and 680 mm (Dövényi, 2010). In the Kiskunság region (Fig. 3), the yearly average temperature is 10.4°C and receives between 500 and 550 mm of annual rainfall, based on data before 2000 (Kovács-Láng et al., 2000).

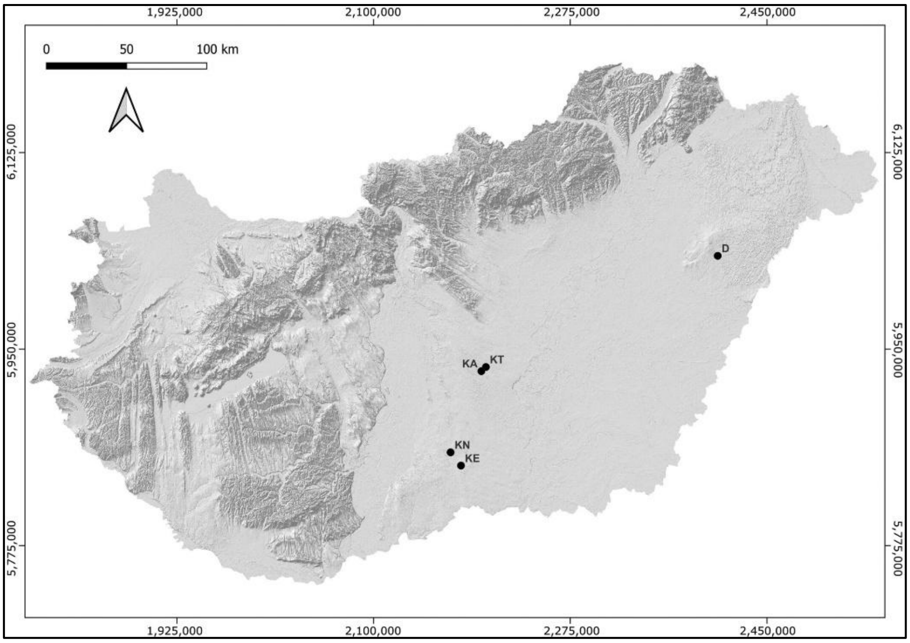


Figure 3. The sampled *Sporobolus cryptandrus* sites in Hungary, Central Europe. The dots show the study sites within the country, abbreviated as: D, Debrecen; KA, Kecskemét Airport; KE, Kiskunhalas East; KN, Kiskunhalas North; KT, Kecskemét Katonatelep.

Vegetation survey (Chapter 2 and 3)

A detailed study was conducted in Hungary, focusing on the *Sporobolus cryptandrus* distribution in two regions, Nyírség and Kiskunság. The surveys were performed in various grassland areas, degraded lands, and old fields with assistance from national park rangers, botanists and university students. In Debrecen city, the focus of the search for the localities of the species was along roads, tramlines, and public parks. In Kiskunság region, the search was initiated in areas around the first localities found like open areas near to small villages and along dirt roads. When the species was found, it was needed to estimate the population extension, a well as the type and level of habitat degradations. In order to determine the range of the invasion, more research was conducted within a 300-meter radius of the initial site.

Table 1. Location of sample sites in Central and Eastern Hungary and their soil characteristics. Table based on Török et al. (2021) and (2024).

Site properties	**Study sites**				
	Debrecen	**Kiskunhalas North**	**Kecskemét Katonatelep**	**Kecskemét Airport**	**Kiskunhalas East**
Coordinates	47.55422 N 21.61537 E	46.48243 N 19.47987 E	46.95044 N 19.76217 E	46.92774 N 19.72590 E	46.40935 N 19.56305 E
Subjected habitat type	Degraded urban sand grassland	Natural sand steppe surrounded with pine plantations	Meadow steppes managed by grazing	Sandy old-field (>30 years abandoned)	Sandy forest steppe
Soil characteristics					
Physical soil type	Loam/clay loam	Sand/sandy loam	Loam/clay-loam	Sandy loam/loam	sandy loam/loam
pH	5.99–6.42	6.67–7.24	6.98–7.35	7.46–7.48	7.31–7.53
CaCO3 (m/m%)	0.10–0.21	1.19–2.59	0.10–2.45	1.19–3.57	1.82–3.26
(NO_2-NO_3, mg/kg)	1.25–8.38	2.15–3.25	1.32–5.35	1.30–2.32	1.25–3.78
Nitrogen					
(P_2O_5, mg/kg)	246–523	29–60	65–179	41–104	23–54
Phosphorous					
(K_2O, mg/kg)	244–430	40–87	132–192	114–123	42–68
Potassium					
Humus (m/m%)	2.33–4.44	0.87–1.95	1.79–2.96	1.61–2.38	0.52–1.89

In Debrecen and in the Kiskunság, detailed vegetation sampling was conducted at selected sites (Table1). Each site was chosen to represent varying cover levels of *Sporobolus cryptandrus.* Within each site, 1-m^2-sized plots were established, and these plots were categorized into four cover categories based on the percentages of *Sporobolus* cover: no cover (0%), low cover (1–25%), moderate cover (26–50%), and high cover (51–75%). In the study described in chapter 2, 40 plots per site were surveyed, whereas in chapter 3. 200 plots per site were surveyed. In each plot, the percentage cover of all vascular plant species was recorded to assess vegetation composition and the influence of *S. cryptandrus* on plant community dynamics

In addition, topsoil samples (0 – 5 cm depth) were collected from 40 randomly selected locations at each site, close to vegetation plots, for soil analyses. The analyses were carried out in an accredited laboratory (SYNLAB, Mosonmagyaróvár, Hungary) following standard procedures based on Hungarian regulations: MSZ-08–0205:1978 for the evaluation of specific chemical properties of the soil by laboratory tests and MSZ-08–0206–2:1978 for determination of physical and hydro-physical characteristics of soils (Table 1).

Soil seed bank sampling (Chapter 2 and 3)

The methodologies for soil seed bank sampling in Chapter 2 and 3 were closely aligned, following the same method and criteria with the *Sporobolus* cover. However, the studies were designed to address different research questions related to soil seed bank and vegetation dynamics. The key differences between the two studies were the sampling time and the study area. Below, the methods are clearly delineated for each chapter, with a initial description of the common methodology framework followed by the chapter specific details.

For both studies, soil seed bank composition was analysed through the collection of soil cores, which were subsequently processed using the thin-layer seedling emergence method (Ter Heerdt et al., 1996). Sample processing followed a bulk reduction method, in which soil samples were washed through two sieves with different mesh sizes (2.8 mm and 0.2 mm) to separate organic and inorganic matter, allowing only the soil containing seeds to pass through. The concentrated samples were then spread in a thin layer on the surface of pots filled with steam-sterilized potting soil. These pots were placed in a greenhouse in the Botanical Garden of the University of Debrecen under natural environmental conditions, regularly watered, and monitored for seedling emergence. Any emerging seedlings were counted and either removed or transplanted for later identification.

In chapter 2, soil samples were taken around the last week of August 2020 (seed ripening period) from plots with varying levels of *Sporobolus* cover. In each group, 10 soil cores (10 cm depth × 2 cm Ø) were collected and divided into four vertical segments (0-2.5 cm, 2.5-5 cm, 5-7.5 cm and 7.5-10 cm). The germination experiment ran for 11 weeks from August 28 to November 15, 2020. Throughout this period, seedling emergence was monitored regularly under controlled greenhouse conditions.

In Chapter 3, sampling was conducted in March to early April 2022 across five sites, where 10 soil cores (10 cm depth × Ø 2 cm, 126 cm^3 each) were collected from 1 m × 1m-sized plots, stratified into four *S. cryptandrus* cover categories. This experiment lasted for 32 weeks, from early April to mid-November 2022. Unlike the first study, the germination process included an 8-week watering break (late June–August) to simulate natural summer drought (Török et al. 2018; Valkó et al. 2021)., a condition that may aid in breaking seed dormancy (Baskin & Baskin, 1998; Finch-Savage & Leubner-Metzger, 2006). No seedlings emerged during this period of drought, but after irrigation was reinstated, germination continued until mid-November, when conditions became unfavourable for further growth.

At the end of both experiments, all seedlings were identified at the highest possible taxonomic level. To ease the identification of *Sporobolus cryptandrus* seedlings and to distinguish these from that of C3 native grasses at early stage, a preliminary germination experiment was performed, which enabled the count and removal of their seedlings from the flowerpots (Török et al., 2021). Some graminoids such as *Carex stenophylla* and *Carex liparicarpos* were pooled, as were the case for *Typha latifolia* and *Typha angustifolia*. Certain dicots were also grouped: *Arenaria leptoclados* was pooled with *A. serpyllifolia, Artemisia scoparia with A. campestris,* and *Polygonum aviculare* with *P. arenarium*. In Chapter 2, there were 38 graminoid seedlings recognized at the family level (Poaceae); they were mostly likely *Poa angustifolia* seedlings or *Lolium perenne.*

Germination experiment (Chapter 2)

To investigate how seed burial depth and litter layer influence the germination success of *Sporobolus cryptandrus,* an experiment was performed in a greenhouse. A full-factorial design (9 treatments × 5 replications) was used with a total of 45 pots (8 x 8 cm in size) to determine the impacts of varying seed burial depth (seeds covered by 0, 0.5, and 1 cm of soil) and varying litter cover amounts (0, 150, and 300 g/m^2) following the experimental setup of Sonkoly et al. (2020). The thickness of both soil and litter cover were adjusted based on a modified version of Sonkoly et al. (2020) design. *S. cryptandrus* seeds, harvested in 2019, were dry-stored at room temperature

(20–25ºC) conditions at the seed collection in the Department of Ecology, University of Debrecen. Altogether 45 pots filled with steam-sterilized potting soil with 25 *Sporobolus* seeds spread uniformly over the area of each pot were used for the experiment, resulting in a total of 1125 seeds. The seeds were covered with *Festuca rupicola* litter and the same sterilized potting soil. Germination was monitored over a ten-week period, starting from March 26 to May 27, 2020. At the end of the experiment, seedlings were counted and then removed. Only the seedlings which emerged above the soil and litter covering were treated as successfully germinated and thus counted. The survival rates were calculated based on the number of individuals that perished over the course of the experiment.

Litter experiment (Chapter 4)

For the experiment, 10 species were selected, nine were native to sand grasslands and one was the invasive species *Sporobolus cryptandrus* (Table 2). The species were studied in a controlled greenhouse experiment: where seedling germination and establishment under different types of litter was recorded. The species were selected after a preliminary seed viability test.

The species' seeds were collected during the summer of 2021 in natural stands in the Great Hungarian Plain, eastern Hungary. Then, they were cleaned, and stored in a dark, dry, environment at room temperature (max. 21°C) until their use. Additionally, different treatments were applied, using different litter type. *Sporobolus cryptandrus* leaves (this treatment is referred as '*Sporobolus litter*' hereafter.), *Festuca vaginata* and *Corynephorus canescens* leaves (this treatment is referred as 'native litter' hereafter.) were collected between June and September 2021 from semi-natural grasslands. The two latter species were included mixed in the native litter because these are dominant grasses of the studied sand grasslands. The litter was dried and then stored at room temperature (max. 21°C) in a dark environment. Additionally, to be able to interpret the impact of plant litter on the germination of species, a 'no litter' control treatment was set up as well, i.e. pots with seeds but without added litter on the soil.

Table 2. Characteristics of the ten studied species, according to PADAPT (Sonkoly et al., 2023). TWS: Thousand seed weight

Species	**Origin**	**TSW**	**Local habitat in Hungary**
Sporobolus cryptandrus	North America	0.090	Grasslands, open areas, sandy soils
Arenaria leptoclados	Europe	0.020	Sandy or rocky habitats
Bromus tectorum	Europe, Asia	3.696	Disturbed areas (pastures, along roadsides)
Crepis rhoeadifolia	Europe, Asia	0.295	Meadows, open woodlands, and disturbed areas
Erysimum diffusum	Central Europe, Asia	0.187	Rocky slopes, grasslands, and open woodlands
Festuca pseudovina	Central Europe, Asia	0.263	Grasslands, meadows, and open woodlands
Festuca vaginata	Central Europe	0.647	Grassy habitats, including meadows and open woodlands.
Jasione montana	Europe, Africa	0.016	Grasslands, heathlands, and rocky slopes.
Plantago indica	Europe, Africa	0.805	Disturbed areas, along roadsides, and in grasslands.
Petrorhagia prolifera	Europe, Africa	0.278	Rocky habitats

In a greenhouse experiment, the impacts of different litter type on the germination and seedling growth of the ten species were tested either *Sporobolus* litter oor native litter wasspread to cover the seeds (2.43 g per pot, this corresponds to 300 g/m^2, see Sonkoly et al., 2020) and 'no litter' treatment was applied for control. Plastic pots (9×9 cm) were filled with about 300 g of steam sterilized potting soil and 25 seeds were set on the soil's top uniformly, thereafter we applied litter covering as described above. The experimental design consisted of 150 pots in total (10 species × 3 treatments × 5 replications). To ensure optimal germination conditions, the pots were placed in a greenhouse and watered every day with tap water. To avoid positional effects, the pots were randomly rearranged at regular intervals. The germination experiment ran from April 29, 2022, until May 26, 2022, for five weeks. Each seedling was counted and removed at the end of the germination process. We measured the shoot length of seven randomly chosen seedlings per pot and weighed their aboveground dry biomass using scale with an accuracy of 0.0001 g. We counted only those seedlings that were able to break through the litter layer.

Statistical analysis

Chapter 1: Data synthesis and analysis

The dataset only contained a single species count for each habitat group; thus, the data could not be analysed statistically. As a result, the study used descriptive statistics, and the best method for presenting the findings was data visualization. Nomenclature challenges were addressed by standardizing scientific names and synonyms across multiple databases, with the species list aligned to GBIF (2023).

For each region and country, we calculated the total number of alien species and their invasion status (casual, naturalised, invasive). In addition, to account for differences in country size, we calculated species density by dividing the number of the alien species by country’s area (expressed as species perkm^2). Species origins were analysed using simplified climatic zones (temperate, subtropical, tropical). Linear regression was performed to analyse the relationship among species statuses, assessing if the numbers of casual and naturalised species were related to the number of invasives species in the four European regions. These trends provided insight into alien species establishment and transition dynamics. Analyses were conducted in R using dplyr for data handling and ggplot2 for visualization. Chi-squared tests were used to check if species distributions by invasion status and climatic origin differed across regions.

The distribution of each species across Europe was determined by counting the number of countries where it was found. Additionally, species were ranked based on their invasion status, considering their geographic spread and alien status. To assess invasion risk, each species was assigned a score in every country where it was introduced, based on its alien status: casual = 1, naturalised = 2, invasive = 3. The total risk score for each species was calculated by summing up these values across all countries in Europe. across regions. In this way, we identified the most widely distributed species and the high-risk species at both the continental scale and within the four European regions separately.

Community similarity and temporal trends were analysed using a Detrended Correspondence Analysis (DCA). The DCA was conducted to assess regional similarities in alien C4 grass species pools based on their worst status in each country. DCA visualized species-pool variation across Europe in two-dimensional space using CANOCO 5.

Finally, historical trends the number of C4 alien grass species in Europe were analysed by comparing three published species lists (Collins & Jones, 1986; Mateu, 1992; Pyankov et al., 2010) with the current dataset to detect changes in alien C4 grass species over time. Due to limitations in our data and the small sample size, we were unable to conduct statistical analysis. Instead, we provided a qualitative description of the trends.

Chapter 2 and 3: Vegetation and soil seed bank dynamics

To analyse vegetation and soil seed bank dynamics under different *Sporobolus* covers, various statistical tests were used which focused on the analyses of species diversity, evenness and community composition.

To illustrate the general plant community species richness (S), Shannon diversity (H), and Pielou's evenness (E) were calculated for vegetation and soil seed banks, excluding *Sporobolus cryptandrus*. Generalized linear mixed models (GLMMs) were applied to study the effects of *S. cryptandrus* cover and other factors, including sample depth, on diversity metrics, seed bank density, and proportional representation of different species within the seed bank and vegetation. Site identity was considered a random factor in these studies. Species richness, Shannon diversity, evenness, total seed density, and *S. cryptandrus* seed density were included as dependent variables.

In chapter 2 we used two-way ANOVAs to study the influence of factors such as litter cover and soil burial depth on seedling emergence and survival rates in vegetation, while Chapter 3 we used two-way ANOVAs to compare the diversity and density of soil seedbanks of different sites. PCA ordinations (chapter 2) examined vegetation composition with respect to *S. cryptandrus* cover, while DCA ordinations (chapter 3) compared soil seed bank composition and the overlap between vegetation and seed banks using germinated seedling counts and presence-absence data. Sørensen's index was used to measure the similarity between the composition of seed banks and vegetation (Sørensen, 1948). Data analyses were conducted using R, SPSS 26.0 (IBM Corp., 2019), and CANOCO software (ter Braak & Šmilauer, 2002: for PCA; Šmilauer & Lepš, 2014: for DCA).

Chapter 4: Effects of litter treatments on seedling emergence and growth

For this study, One-way ANOVAs and Tukey's test for post hoc comparisons were used to examine the effects of treatments (*Sporobolus* litter, native litter, and no litter) on the emergence and the early growth of seedlings of nine native sand grasslands species and *Sporobolus cryptandrus*. The dependent variables were germination rate, seedling length, and seedling dry weight, while independent variables were litter treatment and included three categories: ‘no litter’, ‘native litter’, and ‘*Sporobolus* litter’.

Shapiro test and histograms were used to assess whether the model residual followed a normal distribution. Homoscedasticity of variance was checked using Q-Q plots. In case the case did not fit the assumption; logarithmic or square root transformation was applied for the data. The non-parametric Kruskal-Wallis test and Dunn's test with Bonferroni correction for post hoc comparisons were employed when this did not sufficiently improve model fit.

Initially, the effect of litter treatment was analysed across all studied species. For these combined analyses, germination rate, seedling length, and seedling dry weight were standardized by expressing each variable as a percentage of the corresponding value in the control treatment (no litter’) for each species. This standardization eliminated the potential confounding influence of species identity. Consequently, germination rate, seedling length, and dry weight after litter treatment were analysed for each of the studied species separately.

Chapter 1

Expanding borders: the invasion potential of C4 grass in European grasslands under changing climatic conditions

Introduction

The presence of invasive species and climate change poses a serious risk to global ecosystems, affecting both their natural process and the human systems that depend on them (Bradley et al., 2010; Burgiel & Muir, 2010; Singh et al., 2023). Due to changes in the temperature, humidity levels and the frequency of disturbances, climate change accelerates the invasion and spread of plant species (Vilà et al., 2007; Thuiller et al., 2008; Finch et al., 2021. These alterations establish proper environment for the invasive species to thrive while simultaneously putting additional pressure on the native ecosystems. Knowledge of the nature and extent of the impacts of climate change on invasive plants, particularly in relation to different invasion stages, is essential in the formulation of management strategies (Blackburn et al., 2011).

Current scientific literature also describes multiple effects of climate change on invasive plant species (Blackburn et al., 2011). Invasive species possess certain characteristics that could enable them to succeed such as great plasticity and higher productivity under changing conditions, which give them a competitive advantage over native species (Robinson et al., 2020; Gentili et al., 2021). Nevertheless, determining potential pathways of invasive plants and their effects under conditions of multiple climate change processes is difficult, and most studies focus on the regional scale for invader dynamics. According to IPCC Sixth Assessment Report (2023) the temperature of Europe is expected to rise significantly. Northern Europe is expected to have higher temperatures in winter, while Southern Europe will suffer intensified heat and drought in summer. Changes in precipitation patterns, and along with the expansion of invasive species into Northern regions, are expected to become more exacerbated by mid-century. These climatic shifts may further promote the spread of invasive plants, particularly those originating from regions with similar environmental conditions (Cao Pinna et al., 2021; European Environment Agency, 2021; IPCC, 2023). This climatic alteration will enhance the establishment of invasive alien species, including C4 grasses that prefer arid conditions (Boretti & Florentine, 2019; Kumar et al., 2017; Chuine et al., 2012). C4 grasses are increasingly arriving as alien species with a changing implication for agriculture and ecosystem (Collins & Jones, 1986; Pyankov et al., 2010; Kalusová et al., 2024). These species are mainly from tropical and subtropical regions and are well adapted to dry and hot environments. In short term, C3 plants perform better at high CO_2 concentrations; however, this advantage is not sustainable, as their efficiency declines over time compared with the more efficient C4 plants, which benefit from their specialized carbon mechanism (Sage & Kubien, 2003). While some species, including *Sorghum halepense, Paspalum distichum,* and *Eleusine indica* are frequently found as agricultural weeds, others, such as *Sporobolus cryptandrus,* are native to certain regions but have become invasive like in the Hungarian grasslands. Their herbicide resistance also poses challenges for management (Fernando et al., 2016).

Results

Current distribution and species richness

Overall, the study revealed 133 species of alien C4 grass species in Europe with different distribution patterns from region to region as well as from country to country. For more details see Appendix 1.1. Considering the species' richness, Western Europe host 103 alien C4 grasses, followed by Southern Europe with 96 species. The number of species was considerably lower in Northern (69 species) and Eastern Europe (81 species) (Fig 1.1).

The species density of C4 alien grass species per 1000 km^2 showed some regional trends, having the highest densities in Western and Southern Europe. In Southern Europe, Kosovo had the highest density of C4 grass (1.47 species/1000 km^2), followed by Montenegro (1.23 species/1000 km^2) and Slovenia (1.18 species) (Fig. 1.2). Nonetheless, there are also southern countries with low densities, like Spain (0.14) or Portugal (0.43), or even intermediate densities, as Albania (0.59) and Corsica (0.89) (Fig. 1.2). Due to its extremely small size (8 species in 160 km^2), Liechtenstein has the highest observed density of alien C4 grass species among Western European nations. High numbers of C4 grass species were also seen in Belgium, Luxembourg, and Switzerland. In contrast, Northern and Eastern Europe presented lower species densities. In particular, Iceland and Ukraine had the lowest densities at 0.01 and 0.007 species per 1000 km^2, respectively (Fig. 1.2).

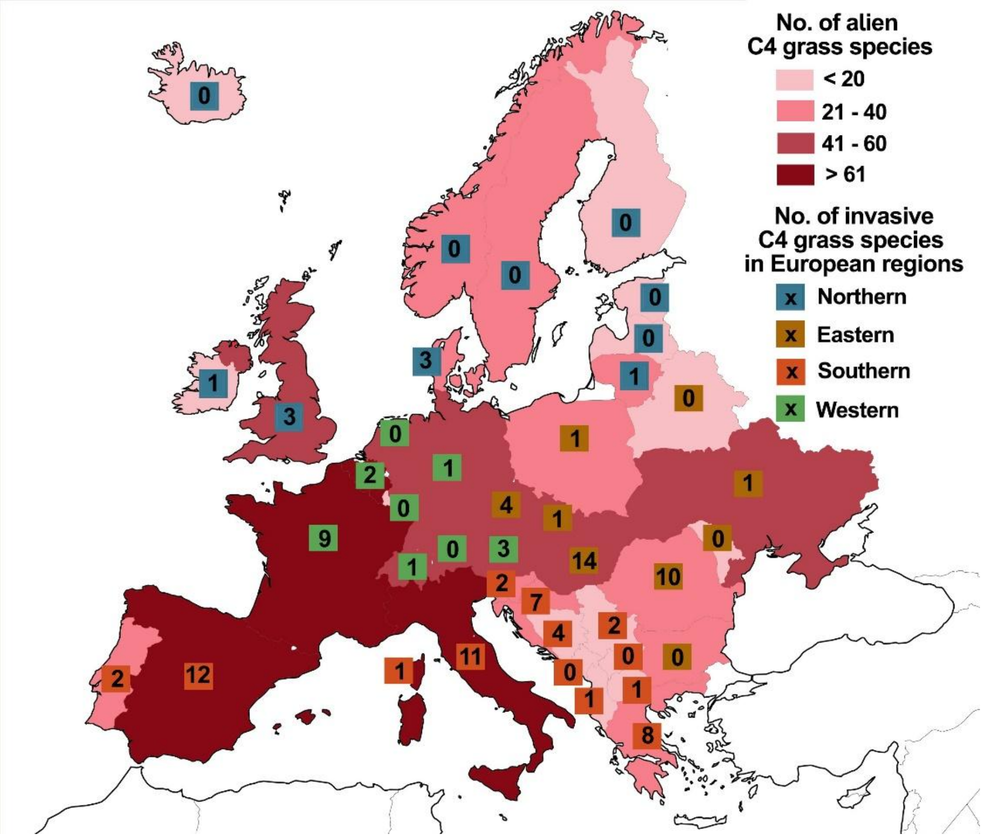


Figure 1.1. Species richness of all alien and invasive C4 grass species by country in European regions. Alien species numbers are represented by shade red, whereas colored squares show the number of invasive alien species. The color of squares indicates the region the countries belong to: Northern (blue), Eastern (brown), Southern (orange) or Western Europe (green). The Canary Islands with one invasive species out of three alien species are not shown in the map.

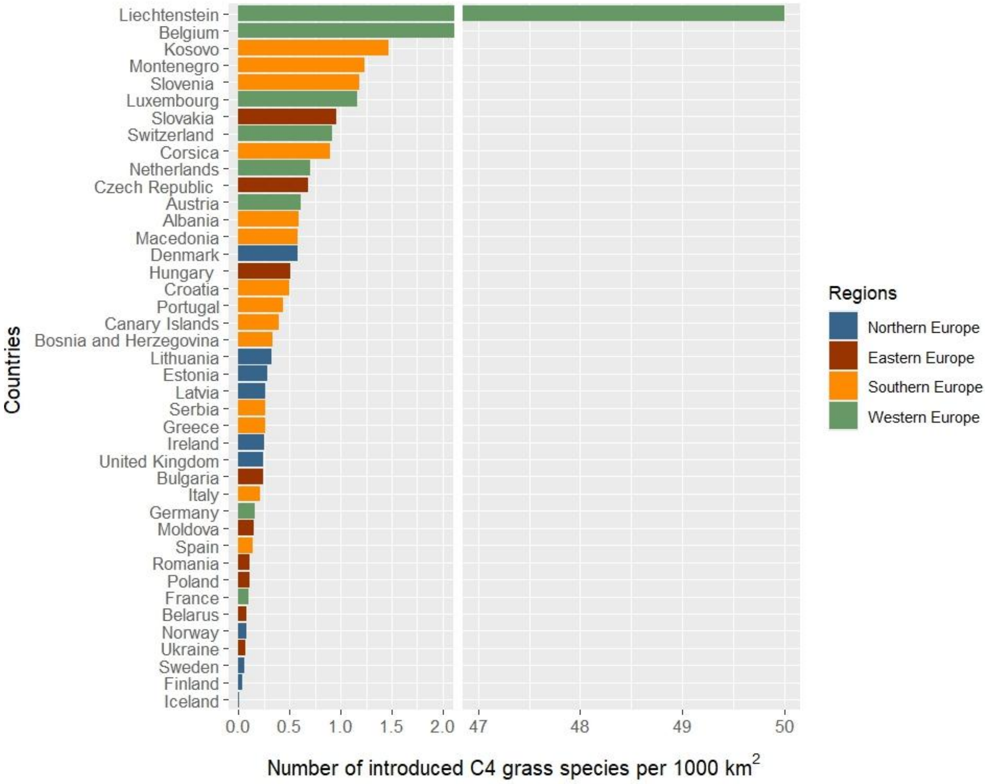


Figure 1.2. Species density across European countries and regions (number of species per 1,000 km²).

Alien status across region

The study classified C4 grass species into three categories: casual, naturalised, and invasive. Most of the identified species were sorted as casual in Northern Europe (53 species), while naturalised (55 spp.). and invasive (21 spp.) statuses were more prevalent in Southern Europe (Fig 1.3A). Invasive species, such as *Sorghum halepense* or *Sporobolus indicus*, were found to characterize agricultural and semi-natural habitats in Mediterranean countries. For further information check Appendix 1.2. We also found in Western Europe a considerable number of casual species; however, only 12 invasive species have been recorded. Eastern Europe has an intermediate position and contains moderate levels of casual, naturalised and invasive species (Fig. 1.3A). Besides, the chi-square test was significant ($\chi2=46.703$, $p<0.001$), indicating that the distribution of species with different invasion status differs significantly among regions (Fig. 1.3A).

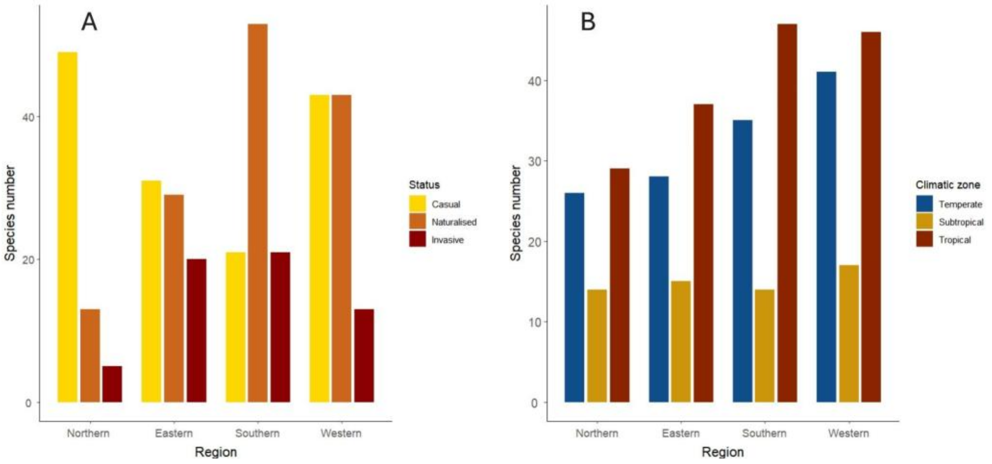


Figure 1.3. The number of C4 grass species categorized by their alien status (casual, naturalised, and invasive; A) and their climatic origin (tropical, subtropical, and temperate; B) across four different European regions.

The variation of the statuses of the alien C4 grass species was high across region. The number of invasive species was highest for Hungary which has 14 species then followed by Spain, Italy and France which has 12, 11 and 9 species respectively (Fig.1.1). The highest number of naturalised species was recorded Western European countries: France accounted for 33 species while some southern European countries, like Spain and Italy had 40 and 30 species respectively.

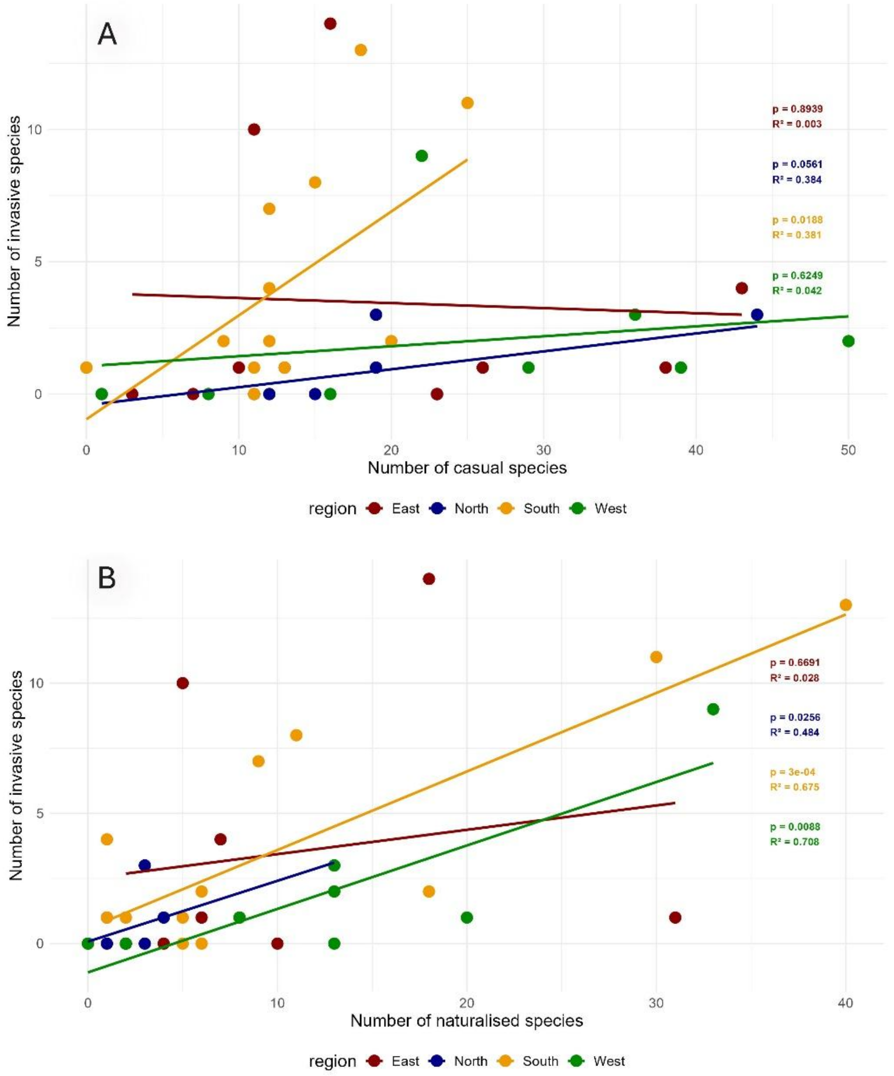


Figure 1.4. The relationship among the number of casual and invasive species (A), and the number of naturalised and invasive species (B) across four European regions: Northern, Eastern, Southern, and Western Europe. Significant relations are indicated with corresponding p-values, derived from linear regression models. Panel A shows the linear relation between the number of casual and invasive species, while Panel B presents the linear relation between the number of naturalised and invasive species. The color of the points represents regions, the points themselves represent individual countries, and a linear regression line is fitted for each region to illustrate the relationship. The R^2 values for each regression model are indicated in the figure.

Casual species had a considerable number in some of the countries like Belgium (50 species), United Kingdom (44 species) or the Czech Republic (43 species). For instance, some countries that currently displayed few occurrences of alien species such as Moldova, Iceland and Luxembourg among others, do not have records indicating the presence of invasive C4 grass species at all (Fig. 1.1). For more details check Appendix 1.1. Notably, 39 C4 grass species were known to have different statuses in different regions, or in different countries in the same region.

Significant regional differences were found in the relationship between the number of invasive, naturalised, and casual C4 grass species throughout the four European regions. Invasive C4 grass species are more prevalent in Southern and Western Europe, which are also rich in naturalised alien species. There was a significant relationship between naturalised and invasive species in the Southern (p<0.001) and Western (p=0.008), and North (p=0.025), but no significant relation in Eastern Europe (p=0.669) (Fig. 1.4B). For the relationship between casual and invasive species, a significant positive relationship was observed in Southern Europe ($p = 0.018$) and marginal significant relationship was found in the North (p=0.056). However, no significant relationship was detected in the Eastern and Western Europe ($p = 0.894$, $p = 0.624$, respectively) (Fig. 1.4A).

Native climatic zones and habitat preferences.

The number of C4 grass species with different origins (tropical, subtropical, temperate) showed similar patterns in all four major regions of Europe, with slightly more species originating from tropical regions than from temperate regions, whereas a significantly less species originates from subtropical regions (Fig 1.3B). Besides, a chi-square test ($\chi 2=1.662$, $p=0.948$) presented no significant differences in the regional distribution of the species with varying climatic origins (Figure 1.3B).

From the list of 133 identified alien C4 grass species in Europe, this study included habitat preference data for 95 of the species. Most of the alien C4 grass species studied were found in only a few types of habitats. About 24% of the species lived in just one type of habitat, 30% were found in two types, and 27% were present in three types. Only 19% of the species were more adaptable, living in many different kinds of habitats. Among these, *Ehrharta erecta* stood out as the most ecologically variable species, thriving in seven different types of habitats. For more details see Appendix 1.2. Of these 95 species, 51 were recorded from human-made and disturbed grasslands and herbaceous communities including trampled grasslands, roadsides, ruderal vegetation and lawns. There were 48 species found in constructed and built-up areas, or industrial and other artificial habitats. Many of these species are agricultural weeds found in cultivated areas (Fig.1.5). Consequently, a significantly smaller number of species was reported in natural or seminatural environments. These species most frequently colonised grasslands (39 species). Other habitats include wetlands (18 species), and forests (16 species), which are invaded by less C4 grass species than grasslands (Fig. 1.5).

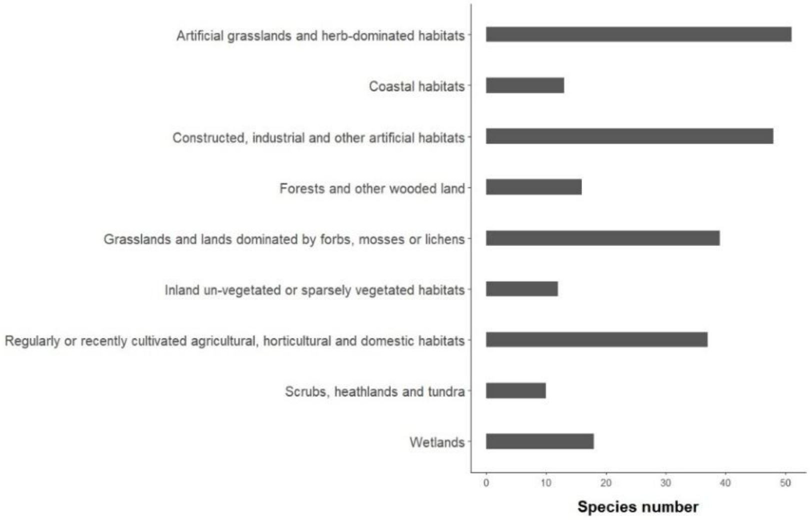


Figure 1.5. The number of alien C4 grass species in each of nine inland and terrestrial EUNIS habitat types in Europe. Most of the species were found in several kinds of habitats.

Most widespread and high-risk species

Among the alien C4 grasses, several species were identified as both widespread and potential risk species. For example, *Sorghum halepense* and *Paspalum distichum* were described as posing high-risk species because their ability to spread rapidly, threaten natural habitats and negatively impact agriculture. These species are not only widely distributed but also demonstrated moderate to very high levels of resistance to controlled herbicides thus making control even more challenging (Fernando et al., 2016).

It was found that 40 of the 133 species in the database, which is approximately 30% of the entire list, have a distribution range that covers all four European regions. We identified 14 species with a total rank sum of 35 or above and they are regarded as highly risky due to their broad distribution and and high incidence of invasiveness. The identified species in the order of total rank sums are as follows*: Eleusine indica, Panicum capillare, Sorghum* *halepense, Panicum miliaceum, Panicum dichotomiflorum, Setaria italica, Cynodon dactylon, Setaria faberi, Setaria verticillata, Zea mays, Paspalum distichum, Digiatria ciliaris, Echinochloa crus-galli, and Sorghum bicolor.* More information about this trend can be found in Appendix 1.3.

Additional attention should be paid to species that have a limited distribution but occasionally classified as invasive, as they have the potential to become invasive in further countries in the future. For instance, *Andropogon virginicus* has been declared to be invasive in France and *Sporobolus pyramidalis* in Slovakia although these two plant species are present only in these two countries.

The species pool of alien C4 grass species of Southern Europe was distinct from that of other regions. Several species in this region like *Paspalum distichum, Paspalum dilatatum, Cenchrus longisetus* and *Sporobolus elongatus*, are widespread. However, in the North and West, these species may be completely absent, occur only as casual or naturalised records. For a more detailed description of the species-pool, check Appendix 1.4.

Temporal distribution patterns

The assessment of temporal dynamics identified the trend of a relatively recent introduction and increasing establishment of alien C4 grass species. This trend is probably connected with rising temperature, altered precipitation patterns and increased human activity facilitating dispersal. It is interesting to see that the rate of new introductions was highest in the Mediterranean countries as other studies had expected an increase in invasibility with climate change. The newly compiled list was compared with three lists of European C4 grass species from articles published in 1986, 1992 and 2010. Based on this comparison, there is noticeable increase in the introduction of the alien C4 grass species over the last decade (Fig. 1.6). Based on this analysis, four distinct groups were identified: **Old introductions:** Species observed in Europe before 1986 consisting of 30 species of grasses, weeds which include *Cenchrus ciliaris, Echinochloa crus-galli, Sporobolus indicus,* and *Sorghum halepense*. **New introductions:** Species not reported by Collins and Jones (1986) but recordedby Mateu (1992) and/or Pyankov et al. (2010), in total 10 species, for example *Cenchrus longispinus, Miscanthus sinensis,* and *Paspalum urvillei.*

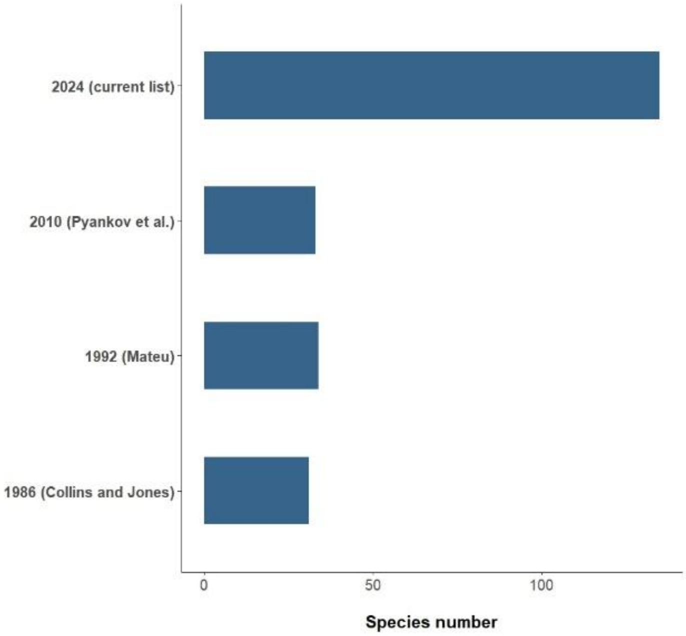


Figure 1.6. Temporal changes in the number of C4 alien grass species in Europe according to three published lists and the current study.

Recent introductions: Species which have not been mentioned in the above-mentioned lists but have been included in the present list, 70 species in total, such as *Andropogon virginicus, Chloris barbata* and *Ehrharta calycina*. **Range-expanding species:** Species formerly classified as native to Europe but have invaded new European countries, represented by 25 species including *Tragus racemosus, Eriochloa villosa,* and *Sporobolus alterniflorus.*

Discussion

The C4 carbon fixing mechanism developed in hot regions, as supported by the presence of C4 plant in tropical regions. This is further evidenced by the positive correlation found in the data of Griffith et al. (2015), and the results of Watcharamongkol et al. (2018). Generally, C4 grasses do not have physiological constraints on their ability to invade temperate or cooler climates, however, geographical and ecological restrictions once prevented their expansion (Watcharamongkol et al., 2018). Current climate warming and globalization have favored invasions of different climates, leading to an increase in both the number and diversity of alien C4 grass species invading Europe. Therefore, the results of this work describe an overall increase and high variations in the spatial distribution and mechanisms of alien C4 grass species invasion across the European continent. Western Europe has the greatest number of alien species with a total of 103 but Southern Europe is even more heavily affected by naturalised species, 55 of which have also proved to be invasive, indicating a high level of invasion pressure. In contrast, low densities of invasive species are recorded in Northern Europe, where most of the casual species can be found. Positive associations between naturalised and invasive species in Southern and Western Europe suggest that both climatic and human activities play a role in faciliting invasions. An analysis of temporal trends demonstrated that increases in invasive species over the last ten years were predominantly more pronounced in anthropogenic environments, highlighting the significant role of human-driven in their spread.

Current distribution and species richness

Alien C4 grasses showed a hotspot in southwestern Europe. These are influenced by the climate, trade history, wealth, country size, and research traditions (Pyšek et al., 2022a). For example, Spain, Italy, France, and Belgium host many species due several key factors like: mild climates (Mediterranean and oceanic climates), providing suitable conditions for C4 species establishment; historical hubs, exchanging and introduction of alien plants through trade and migration (Celesti-Grapov et al., 2009); historical links with overseas territories, horticultural practices, and ornamental plant trade (Arianoutsou et al., 2021), along with interest in C4 grasses for bioenergy purposes (Lewandowski et al., 2003); large land areas; and strong botanical research efforts also contribute to higher number of alien species records (Celesti-Grapow et al., 2016; Kalusová et al., 2024). These combined factors explain why some countries harbour more alien species than others.

In light of the fact that C4 species have limited capacity to successfully adapt to the cold climate of the areas such as continental, polar or alpine because they cannot tolerate a long period of cold (Watcharamongkol et al., 2018), there is a surprising number of casual alien C4 species in Northern Europe (53 species). This may be due to the influence of the North Atlantic Current which makes the climates of Norway, Sweden, Denmark and Great Britain relatively temperate compared to other regions at similar latitudes (Jóhannesson et al., 1995). These two climate parameters are favourable because coastal climates are less harsh during the winter season (Hulme, 2017; Clements & DiTommaso, 2022). The total number of alien C4 grass species is given at 69 for Northern Europe, which is significantly lower than the numbers for Western (103), Southern (96), and Eastern Europe (81); nevertheless, Northern Europe accounts for 53 casual species, implying that factors other than climate, such as human activity or habitat availability, may play a more significant role in their distribution.

Alien status across region

In the context of plant invasions, significant changes have been observed in the distribution and establishment of alien species across Europe. In the past, southern European countries identified more naturalised alien plants than northern countries (Weber, 1997). However, new trends show a change in this; most of naturalised species are currently recorded in Northern Europe (Pyšek et al., 2022a). A similar trend is observed with C4 grasses. The proportion of naturalised species is relatively high in Southern Europe compared to Northern Europe, because Southern Europe is at a more advanced stage of the invasion process than Northern Europe, and alien C4 grasses in Northern Europe are considerably more likely to have a casual status than species in Southern Europe. Western and Eastern Europe also fall into intermediate position, number of casuals here is approximately same as number of naturalised species. Lambdon et al. (2008) suggest that this pattern may be due to residence time and climate change. Western and Southern European regions with long histories of species introduction and trade have enabled the naturalization and invasion of C4 grasses over several decades. Populations in other regions have shorter average residence times and historically less favourable climates. In this respect, our data extend the study of Pyšek et al.

(2022b), who observed a weak but significant positive relationship between the numbers of naturalised and invasive species in Europe. Likewise, for alien C4 grasses, there was a similar correlation across Southern and Western Europe while casual species' numbers did not predict invasive richness most likely because of different traits needed for their first colonization and then for subsequent spread (Theoharides and Dukes 2007, Catford et al 2019).

Native climatic zones and habitat preferences

A majority of the alien species in Europe originate from temperate Asia and the Americas, especially North America because of high climate matching and previous trading networks (Pyšek et al., 2022a; Kalusová et al., 2024). In particular, climate matching is confirmed to be very important for the processes of colonization and naturalization of the alien species. Notably, most of the C4 grasses occur naturally in the tropical regions of the world, but they also occur in the wild in European countries as a result of human activities that reduce climatic barriers. For instance, exotic ornamental plants from tropical regions like *Miscanthus sinensis* (Dougherty et al., 2014), *Stenotaphrum secundatum* (Englmaier & Wilhalm, 2018) and *Eragrostis spectabilis* (Qing et al., 2013), which are currently grown in Europe have been reported as species escaping cultivation (Rigó et al., 2023). Alien C4 grasses mainly occur in disturbed or ruderal environments, particularly during the early phase of their colonization (Collins & Jones, 1986; With, 2002). Earlier literature suggest that these species are only partly effective at colonizing natural or semi-natural habitats in temperate climates. Studies from Minnesota, USA (Tilman, 1997) and southern New Zealand (White et al., 2001) indicate that they are mainly found in areas with trampled soil. Several alien C4 grass species in Europe also mostly occur in disturbed habitats, such as *Eragrostis minor, Eleusine* *indica* and *Cynodon dactylon* (Čarni & Mucina, 1998). These findings imply that C4 grasses have high disturbance tolerance but may have lower competitive abilities (White et al., 2001).

However, recent studies indicate that extreme climatic conditions, such as heatwaves reduce the competitive ability of native C3 grasses, which favors the colonization of C4 grasses (Churchill et al., 2022). As the experimental research shows, changes in the amount of moisture in the soil and productivity in the course of the season, associated with warming, also improve competitiveness of C4 plants in the seminatural communities (Lemoine & Budny, 2022). In stressed conditions, C3 grasses may be outcompeted by C4 species, leading to shifts in species distribution and interactions (de Deus Vidal et al., 2021). Seasonal segregation, where C3 species predominate during cooler seasons, and C4 species thrive in hot summer (Niu et al., 2008; Pau et al., 2013), could also favor C4 species in the long term, due to more frequent droughts in the spring and autumn period (Witwicki et al., 2016; Havrilla et al., 2023).

Most widespread and high-risk species

Several invasive alien plant species have emerged as agricultural weeds across Europe over the past few decades (Follak & Essl, 2013). From these, the commonly occurring species in our database was *Panicum* spp., *Setaria* spp., *Eleusine indica, Sorghum halepense*. These species exhibit varied invasion histories: some Archaeophytes including *Panicum miliaceum*, *Setaria italica* and *Sorghum bicolor* were intentionally brought to cultivation several centuries or millennia ago (Pyšek et al., 2022b), whereas neophytes like *Eleusine indica, Sorghum halepense*, or *Panicum capillare* have been present in Europe for less than 200 years; accidental or deliberate introduction in this case (Pyšek et al., 2022b). Such factors contributing to the spread of both archaeophytes and neophytes include herbicide resistance (Loddo et al., 2020; Vazquez-Garcia et al., 2020), changes in agricultural practices such as huge increase in maize farming, evolutionary adaptation of these weed species (Clements & DiTommaso, 2011; Paterson et al., 2020) and climate change. Some invasive species like *Sorghum halepense* can threaten crop productivity (Follak & Essl, 2013). Unfortunately, humans contribute to their spread by accidentally dispersing these species with contaminated seeds, which enables these species to colonize new areas even more rapidly. An study by Wang & Wan (2020) listed the ten worst weeds globally (with seven C4 grass species among them: *Cynodon dactylon, Echinochloa colona, E. crus-galli, Eleusine indica, Imperata cylindrica, Panicum maximum, Sorghum halepense*) and found that all of these species inhabit both cultivated and non-cultivated regions around the globe and outcompeting the other crops in terms of adaptability to habitats.

Temporal distribution patterns

The list of alien C4 species introduced to Europe has expanded significantly compared to the former lists of alien C4 grass species introduced to Europe (Collins & Jones, 1986; Mateu, 1992; Pyankov et al., 2010). Our study registered 71 new additions to the list and 25 species found native to areas of Europe but now listed as aliens in other countries in the continent. New online facilities in data sharing and the checklists compiling plant details have made species documentation and identification easier and more accurate (Groom et al., 2017). Furthermore, comprehensive field surveys and database analyses helped document rarely encountered plants such as *Sporobolus cryptandrus*. This species forms monocultures in Hungary (Török et al., 2021) and has been present in Slovakia's natural habitats since 1987 (Holub & Jehlík, 1987).

The increase in the list of C4 grasses is also attributed to improved knowledge on the C4 photosynthetic pathway, systematic phylogenetic study and taxonomic changes (Osborne et al., 2014). However, we can reasonably assume that the direct and indirect effects of climate change are also propelling this increase. Expanding native species in Europe require careful consideration, as their spread can be driven either by human activities—such as habitat modifications or introductions beyond their historical range—or by climate change (Essl et al., 2019). Species introduced due to human influence are classified as alien and should be managed accordingly, whereas those moving naturally due to climate change are considered ecological refugees and may require conservation efforts to support their survival.

The temporal analysis revealed an increased trend in the introduction and establishment of alien C4 grass species over recent decades. This trend correlated with rising temperatures, altered precipitation patterns, and increased human activity facilitating dispersal (Essl et al., 2009). Notably, the rate of new introductions was highest in Mediterranean countries, consistent with projections of enhanced invasibility under climate change scenarios.

Conclusions and outlook

This work highlights an interactive effect between climate change and biological invasions on European grasslands ecosystems. Climate change and anthropogenic activities have enabled alien C4 grasses to become predominant in disturbed and ruderal sites. Their ability to compete is evident from characteristics such as heat tolerance, ability to resist herbicides, and frost tolerance in certain species like *Miscanthus sinensis* and *Digitaria ischaemum*.

In the past 14 years, the awareness of alien C4 grass species in Europe has risen, and 133 species were recorded in 39 European countries. The highest species richness is mostly observed in areas with high anthropogenic impact as Southern and Western Europe. Climate change exacerbates the invasion process as it increases stressors that create gaps in ecosystems reducing native C3 grasses. In managing these challenges, long-term monitoring and research are crucial. Identifying temporal niche dynamics, the processes enabled by climate change and the socio-economic consequences will be important. Effective strategies are needed to conserve the grassland ecosystems of Europe, which are threatened by climate change and invasive species.

Chapter 2

Distribution, habitat, and impact of *Sporobolus cryptandrus* in Central Europe

Introduction

Invasive plants have become more widespread and abundant in the last decades, which has created substantial problems for the preservation and management of natural and semi-natural environments around the world (van Kleunen et al., 2019, Pyšek et al., 2020). Among these invasive species, transformer invasive species pose a bigger threat to ecosystems through reduction of biological diversity and altering disturbance regimes and disrupting ecosystems functions (Byers et al., 2010, Catford et al., 2011). Control and prevention of invasive plants is considered expensive when professionals do not understand their ecology, the spread of the plants or the weaknesses in ecosystems. However, species like grasses, are often a challenge to detect and recognise (Jarić et al., 2019). Their small size and similar appearance can lead to them being grouped into broad categories, making it hard to implement targeted control measures.

The Poaceae family (grasses) is among hte plant families that contribute with the highest numbers of invasive species worldwide, and they can use either the C3 or the C4 photosynthesis pathways (D'Antonio & Vitousek, 1992, Fusco et al., 2019, van Kleunen et al., 2019). The C4 grasses are well adapted to arid/warm conditions since they have low water requirements, high heat tolerance and fire tolerance which have exposed high invasion ability in arid and warm habitats (Chuine et al., 2012; Kumar et al., 2017; Boretti & Florentine, 2019). These traits have allowed their spread to areas like the Americas and Australia contributing to high rates of biotic homogenization in savannas, forest and grassland ecosystems (Williams and Brauch, 2000; Brooks et al., 2010). In Eurasia where most grasslands were previously dominated by C3 grasses, species such as *Bothriochloa ischaemum* and *Cynodon dactylon* have started to expand their range, sometimes due to climatic change (Hurka et al., 2019). Rising temperatures, changing rainfall patterns, and increased incidence of drought lead to selection for drought-tolerant nonindigenous C4 grass over C3 grass. There are several species of the *Sporobolus* genus, which have invaded Europe in the last few years. Two of them, *Sporobolus neglectus* and *Sporobolus vaginiflorus*, mostly occur in Mediterranean and dry Central European regions and do not pose a threat to natural vegetation (Hohla et al., 2015; Király & Hohla, 2015; Király, 2016; Jogan, 2017; Englmaier & Wilhalm, 2018), whereas a more aggressive *S. cryptandrus* possesses the capacity to invade various habitats that include natural and seminatural grasslands. This North American C4 grass has been seen to spread in dry grassland habitats in Hungary and other areas of Europe (Török & Aradi, 2017).

Results

Habitat preference in Hungary

More than 620 field observations of *Sporobolus cryptandrus* were recorded during the study, of which most of the population density was concentrated in the Kiskunság region, central Hungary. In addition, *Sporobolus* was observed in several habitats of disturbed urban grasslands in the city of Debrecen, which are typically mown. These urban sites were areas between individual buildings, the edge of the roads, car parks, and around the tram tracks. While populations of the species in Debrecen were found in urban localities, populations in Kiskunság region were confined to rural localities. Most populations were found in dry sandy areas, mostly in open sand grasslands that were disturbed or severely degraded. Some were found in species-poor, dry and desiccated interdune grasslands which had developed from species-rich wet interdune *Molinia*-dominated meadows. The species was discovered along artificial linear environments like firebreak, motocross and dirt roads. Also, it colonized sand sites that were ploughed within the last three decades and on the margins of young tree plantation.

Co-occurring species observed in old fields of different ages, including young old fields dominated mostly by short-lived species such as *Ambrosia artemisiifolia*, *Anthemis ruthenica, Bromus tectorum*, and older fields with dominant perennnial grasses such as *Bothriochloa ischaemum, Cynodon dactylon* and *Festuca pseudovina*. The spreading of Sporobolus cryptandrus was also enhanced by other disturbances as well, such as former overgrazing by sheep or the presence of game feeders. The species also occurs in grasslands that were burned 10 to 20 years ago and successfully regenerated since then, with the presence of sand grassland species like *Alkanna tinctoria, Dianthus serotinus, Festuca vaginata, Koeleria glauca, Stipa pennata* and

Silene otites. However, *Sporobolus cryptandrus* has become dominant where *Festuca vaginata* and *Stipa pennata* previously coexisted in drought-affected sandy grasslands. On the south facing slopes of sand dunes where *Festuca vaginata* tussocks are particularly vulnerable to drought stress *S. cryptandrus* has successfully gained dominance. In the northern Kiskunság near Kecskemét, *Sporobolus cryptandrus* was also found in dried-out stands of meadow steppe and closed interdune communities. Although, *S. cryptandrus* has not yet been recorded colonizing undisturbed natural sites directly, it is becoming evident on open, sandy grasslands, being a potential threat to vulnerable sand grassland species like *Dianthus diutinus*, an important species of European conservation interest. Notably, *S. cryptandrus* is a shade intolerant species and few populations are recorded in the shaded section of the invaded habitat.

Characteristics of the vegetation and the soil of the study locations

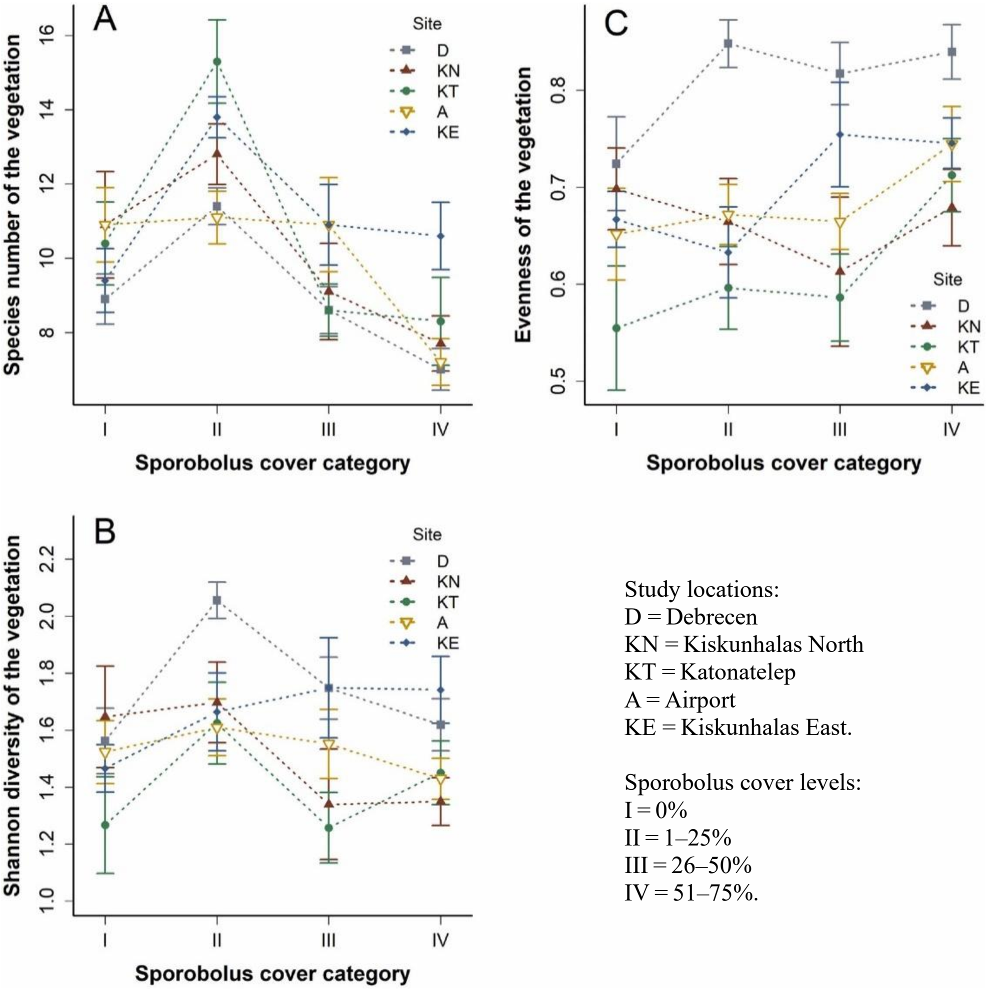
The soil samples of selected sites showed a pH between 6.16 and 7.41. The lowest pH was detected in Debrecen due to the presence of the acidic sand and high values were typical in Kiskunság because of the characteristic calcareous sand deposits. Hence, the soil texture differed across sites and was comprised between sandy and clay loam. Some of the sites had an elevated nutrient concentration, particularly in phosphorus and potassium at the Debrecen (D) and Katonatelep (KT) sites, as well as in potassium at the Airport (A) site (Refer to soil properties in Table 1). Nevertheless, based on the values obtained for the various soil parameters analysed, no clear relationship can be assumed with the cover of *S. cryptandrus.*

Studying the selected five sites, we found that both increasing Sporobolus cover, and the sampling site significantly affected most of the studied vegetation variables, with the cover of *Sporobolus* not included in the calculation. (Table 2.1).

Table 2.1. The effect of increasing Sporobolus cover on the vegetation variables (GLMM, bolded values indicate significant values, $p < 0.05$, the study location used as a fixed factor for the analyses).

	***Sporobolus* cover**	
Vegetation variables	$F_{3,196}$	p
Species richness	**18.909**	**< 0.001**
Shannon diversity	**3.663**	**0.013**
Evenness	**3.463**	**0.017**

Across all sites, species richness, Shannon diversity, and evenness were higher in sites with lower cover (category I and II) compared with higher *Sporobolus* cover levels (category III and IV) (Fig. 2.1 A-C). However, the highest species richness was observed in category 22, where *Sporobolus* is present but relatively low cover. This trend aligns with the ordination analysis (Fig 2.2), which shows that vegetation homogenization increases as *Sporobolus* cover becomes more dominant across the sites, negatively affecting nearly all other plant species (Fig. 2.2).



Study locations:
D = Debrecen
KN = Kiskunhalas North
KT = Katonatelep
A = Airport
KE = Kiskunhalas East.

Sporobolus cover levels:
I = 0%
II = 1–25%
III = 26–50%
IV = 51–75%.

Figure. 2.1. The relationship between *Sporobolus* cover categories and vegetation metrics, including species richness (A), Shannon diversity (B) and evenness (C), was analysed within study sites, excluding *Sporobolus* itself from the calculations. Error bars represent standard error.

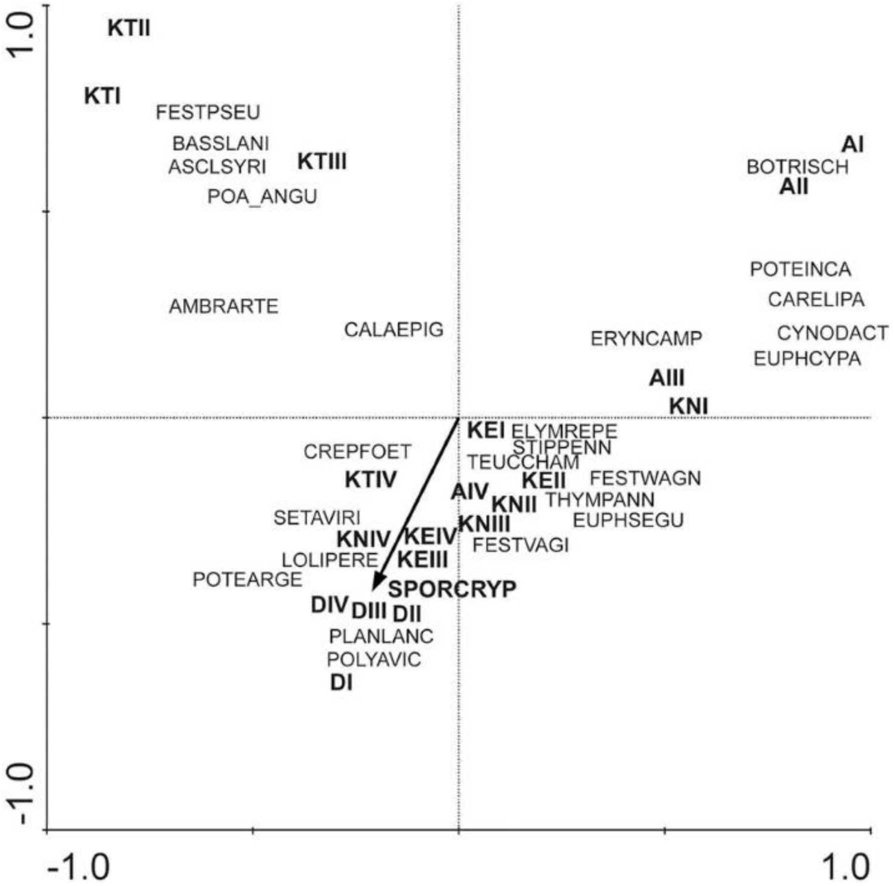
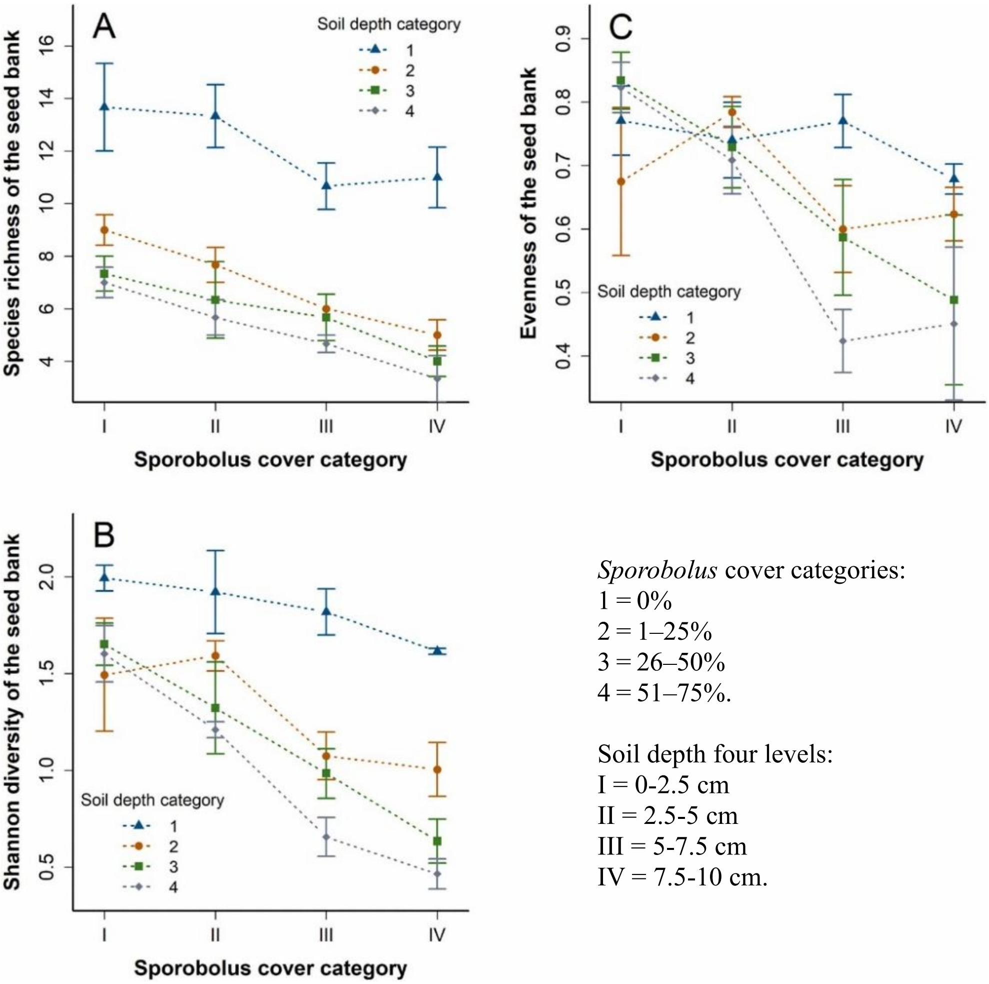


Figure 2.2. PCA triplot shows the 25 most prevalent species, with Eigenvalues of 0.289 and 0.187 for the first and second axis, respectively. The mass locality sites' vegetation composition varies in terms of *Sporobolus* cover. The species abundances are displayed in the main matrix, with the exception of *Sporobolus* (10 plots per site and pooled *Sporobolus* cover categories; four merged plots per site are included (I-IV). The cover of *Sporobolus cryptandrus* is represented by the secondary matrix (added arrow by weighted averaging). Among the locations were D for Debrecen, KN for Kiksunhalas North, KT for Katonatelep, A for Airport, and KE for Kiksunhalas East. The species names were abbreviated using the first four words of both the genus and species name, for example SPORCRYP stands for *Sporobolus cryptandrus*.

Seed banks

A total of 2,132 seedlings from the soil seed bank samples were germinated, belonging to 32 taxa, including 320 seedlings of *Sporobolus cryptandrus*. In addition to *Sporobolus*, some other species were also represented by a large number of seeds in the seed bank, like *Arenaria leptoclados/serpyllifolia* (508 seedlings), *Portulaca oleracea* (492 seedlings), *Potentilla argentea* (200 seedlings), *Digitaria sanguinalis* (153 seedlings) and *Cerastium semidecandrum* (104 seedlings). More than 83% of the seed bank was represented by the six taxa mentioned previously. According to the pooled seed bank data from 30 soil cores (0–10 cm layer) at each location, *Sporobolus* seed density ranged from 1,114 to 3,077 seeds/m^2. Increasing *Sporobolus* cover had a negative impact on the total seed number of other species, as well as on the seed bank diversity measures, i.e., species richness, Shannon diversity, and evenness.

Increasing Sporobolus cover negatively affected the total seedling number of other species (Fig. 2.3-2.4) as well as species richness, Shannon diversity, and evenness of the seed bank (Table 2.2, Fig. 2.3A-C). The cover of Sporobolus did not significantly influence the density of its own seed bank; we detected Sporobolus soil seed banks even in nearby reference plots where the species was absent. The soil layer significantly impacted almost all seed bank parameters, with scores decreasing as soil depth increased (Fig. 2.3-2.4). Sporobolus seedlings emerged from all studied soil layers (Fig. 2.4).



Sporobolus cover categories:
1 = 0%
2 = 1–25%
3 = 26–50%
4 = 51–75%.

Soil depth four levels:
I = 0-2.5 cm
II = 2.5-5 cm
III = 5-7.5 cm
IV = 7.5-10 cm.

Figure. 2.3. The relationship of *Sporobolus* cover categories and seed bank diversity measures: species richness (A), Shannon diversity (B) and evenness (C), excluding *Sporobolus*. The standard errors of the mean are shown by the error bars.

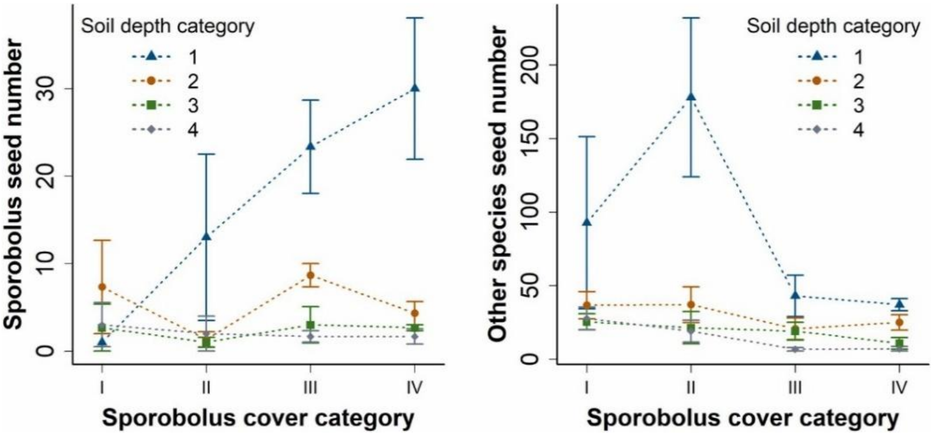


Figure. 2.4. Relationship between *Sporobolus* cover categories and *Sporobolus* seed bank (A) and the seed bank density of other species (B). *Sporobolus* cover was categorized into four levels: 0%, 1-25%, 26-50%, and 51-75%. Soil depth was also categorized into four levels: 0-2.5 cm, 2.5-5 cm, 5-7.5 cm, and 7.5-10 cm. The standard errors of the mean are shown by the error bars.

An interaction between soil layer and Sporobolus cover was detected only for seed bank density of Sporobolus and seed bank evenness (Table 2.2).

Table 2.2. *Sporobolus cryptandrus* cover effects on the subjected plots' seed bank measures. Boldface was used to indicate significant effects (two-way ANOVA).

	***Sporobolus* cover**		**Soil layer**		***Sporobolus* cover × Soil layer**	
Measures	$F_{3,47}$	p	$F_{3,47}$	p	$F_{9,47}$	p
Seedling number						
Total	2.442	0.082	**12.465**	**< 0.001**	1.503	0.189
Sporobolus	2.727	0.060	**12.845**	**< 0.001**	**2.913**	**0.012**
Other species excl. *Sporobolus*	**3.848**	**0.019**	**10.133**	**< 0.001**	2.024	0.069
Species richness	**11.626**	**< 0.001**	**50.652**	**< 0.001**	0.264	0.980
Shannon diversity	**23.346**	**< 0.001**	26.845	< 0.001	1.622	0.151
Evenness	**8.659**	**< 0.001**	2.482	0.079	1.612	0.154

Germination

In general, during the experiment, 24% of all *Sporobolus* seeds germinated. The highest germination rates of seeds were observed when the seeds were buried shallowly and without litter cover. Both germination and seedling survival were impacted by litter and soil cover, but these two variables did not interact (Table 2.3).

Table 2.3. Litter and soil cover impact on the total germination rate and seedling survival of *Sporobolus cryptandrus* (two-way ANOVA; bolded values indicate significant values, $p<0.05$).

	Litter cover		**Soil cover**		**Litter cover × soil cover**	
	$F_{2,45}$	p	$F_{2,45}$	p	$F_{4,45}$	p
Total germination	**14.139**	**< 0.001**	**9.005**	**0.001**	0.932	0.456
Seedling survival	**4.153**	**0.024**	**3.777**	**0.032**	0.612	0.657

The lowest germination rates occurred when seeds were deeply buried and covered with a high amount of litter. However, under such conditions, some seedlings did emerge and survived until the end of the experiment. In most cases, litter cover increased germination success; however, shallow burial depths were more effective than no burial.

There was great variation in seedling survival rate between treatments, even within those treatments which were most successful. The treatments with high soil/high litter cover and no soil/high litter cover had the lowest mean survival rates (Fig.2.5.).

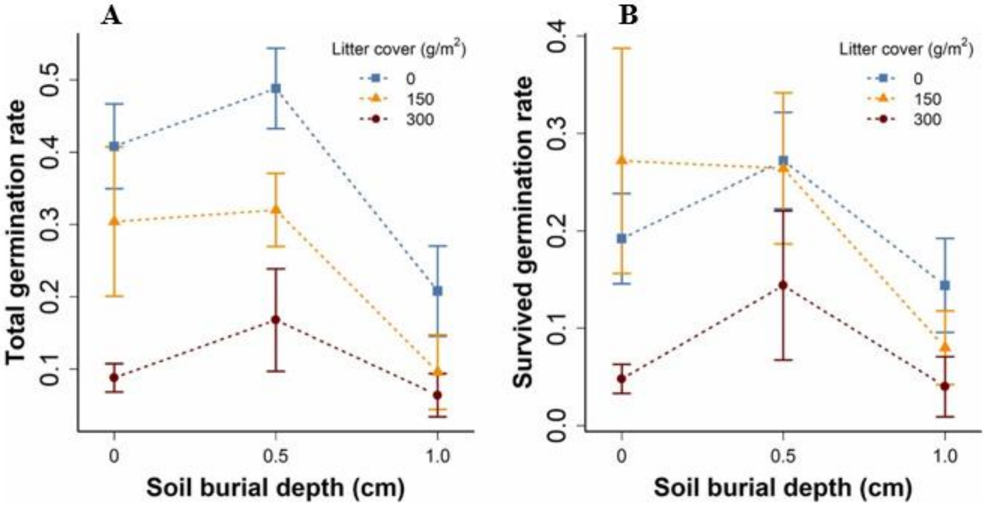


Figure. 2.5. The effect of litter and soil covering on total germination rate (A) and survival rates (B) of *Sporobolus cryptandrus* seedlings.

Discussion

Dry grasslands are generally less susceptible to plant invasion than other habitats (Chytrý et al., 2009; Guarino et al., 2021). Halophytic ecosystems, including also alkaline habitats, as well as open rocky grasslands a relatively resistant to invasions, but sand grasslands are at significantly higher risk of invasions (Botta-Dukát, 2008). Based on MÉTA database by Molnár et al. (2007), invasive species affect 50-70% of Hungary's sandy steppes and open sand grasslands, primarily trees like *Ailanthus altissima, Elaeagnus angustifolia* and *Robinia pseudoacacia* as well as clonal forbs such *Asclepias syriaca* (Botta-Dukát, 2008).

Sporobolus cryptandrus, a highly drought-tolerant species, has invaded both undisturbed sandy grasslands in the Kiskunság region and steppe grasslands in Ukraine and Russia (Demina et al., 2018). Given its tolerance to dry conditions, this species poses a growing threat to other dry grassland habitats in Europe, particularly as climate change continues to alter environmental conditions.

Impact of treatments (soil cover and litter) on the species' germination

Sporobolus cryptandrus germination decreased by litter cover and soil burial, though the two factors did not interact. Interestingly, some seedlings emerged under the highest levels of soil and litter cover. These findings are similar with those of Sonkoly et al. (2020), whose study explored how the germination of 11 invasive species was affected by soil burial, in concert with the presence of litter. Even with 2 cm of soil burial in combination with 600 g/m^2 of litter cover, most of the species were able to germinate. In addition, Sonkoly et al. (2020) also tested whether the effects depend on the size of the seeds and found that litter had a stronger effect on the germination of small-seeded species than on those with larger seeds. This is in line with this study, since for the small-seeded *S. cryptandrus*, shallow burial at 0.5 cm with no litter cover resulted in the highest germination rates. In comparison to certain other invasive grasses, the overall germination rate of *S. cryptandrus* was rather low. However, it was still within the range or they or marginally higher than previously recorded germination rates observed after heat stratification (Sartor & Malone, 2010).

Importantly, the seeds used in this study had been collected the previous year, thus indicating that the seeds of *S. cryptandrus* remain viable even after prolonged dry storage time. This underlines the potential of the species for persistence: it can withstand storage without major loss in viability.

Impact of Sporobolus on sand grasslands seed banks and local vegetation

According to this study, as the level of *Sporobolus* cover increased, the species richness and abundance of subordinated species decreased in both the vegetation and seed banks. Although the invasive grass negatively impacted diversity at higher densities, there was a weak facilitative effect detected at low cover of *Sporobolus cryptandrus*, where the establishment of other species seemed to be supported by *Sporobolus.* This is in line with Kelemen et al. (2015) who found that *Festuca pseudovina*, a dominant species in dry alkali grasslands, had comparable facilitative effects. In this case, *F. pseudovina* likely ameliorates extreme microclimatic conditions in arid environments and, therefore, generates more favourable conditions for germination and survival of other species, particularly those that are short-lived, such as *Arenaria leptoclados, Cerastium semidecandrum,* or *Portulaca oleracea,* among others. The invasive *Asclepias syriaca* from the same area has also been shown to facilitate other species (Szitár et al., 2018). However, plots with high *S. cryptandrus* cover, where competitive pressure likely outweighed any positive interactions, did not exhibit this 'nursing' effect.

The facilitation by dominant perennials like *Sporobolus* usually favours the processes of germination and initial establishment of other plant species that rely on existing vegetation for favourable microclimatic conditions and protection. However, earlier studies showed that with the increase in the facilitator density, such facilitation could become a competition between species for space and light (Liancourt et al., 2005; Le Roux et al., 2013). Thus, this interaction seems to be also density-dependent: at low densities, the facilitative effects dominate, while competitive interactions arise at higher densities, especially where dominance of the facilitator species is achieved (Kelemen et al., 2019). This is supported by the data shown here: plots with a high *Sporobolus* cover were characterized by low diversity, while low *Sporobolus* density plots exhibited increased subordinate species richness and density compared to no *S. cryptandrus* sites. But this observational study was unable to prove a direct connection between *Sporobolus* cover and seed bank and vegetation dynamics, thus further manipulative experiments are needed to clarify the issue.

We detected viable seeds of *S. cryptandrus* in the seed bank in all layers of soil, suggesting that the species can form a persistent seed bank. This agrees with previous works concentrating on North American natural prairie communities (Coffin & Lauenroth, 1989; Pérez et al., 1998; Clements et al., 2007). However, deeper soil layers had a considerably lower seed density, and with the increase in *Sporobolus* abundance in vegetation, the seed density increased considerably only in the uppermost soil layer. That might suggest that the species at the study site is still in its initial phases of invasion and had limited time for seeds to accumulate in the seed banks and penetrate deeper soil layers. The concentrations we observed are similar to those observed in the native prairie ecosystem, where Clements et al. (2007) reported high densities of *Sporobolus* seeds up to 3414 seeds/m². Nevertheless, frequent mowing in the sampled urban grassland prior to seed maturation may restrict the number of seeds produced and the consequent formation of a seed bank for this species. Although late and even second flowering is possible with *S. cryptandrus*, for which reason this factor needs further investigation once the seed banks of all sampled sites are adequately assessed.

Future research directions.

Our results suggest that *Sporobolus cryptandrus* is behaving as transformer invasive species, since its invasion posed a high threat for steppe grasslands and dry sand areas in Eurasia. To develop an effective management and suppression strategy for *Sporobolus cryptandrus*, further research is needed. Despite such data, additional studies are required focusing on several aspects related to the biological features, population dynamics, and dispersal mechanism of the species. This information will be crucial for designing targeted and effective control measures. For instance, firstly, seed bank studies across sites with different *S. cryptandrus* establishment histories are needed in order to estimate density and speed of development of a seed bank, which will help assess its long-term persistence. Secondly, more information is needed on its competitive abilities, not only aboveground but also to test if it has allelopathic effects and root competition that might give it an advantage over the native species. Thirdly, a full-factorial manipulative experiment that partially or fully eliminates *S. cryptandrus* from plots with a range of cover would yield valuable information about the role of this species in determining vegetation composition. Fourthly, genetic analyses, including phylogeographic research employing genomic methodologies, are necessary to recognize the probable origin of established/naturalized populations and understand the mechanism of its long-distance-dispersal (LDD). It is very important for being able to predict the rate of spread and population growth. Finally, effective control of this species relies on studies of natural enemies within its home range and testing the efficiency of more classic management practices like grazing and mowing. There may well be opportunities for mechanical methods, such as shading, or chemical treatments to suppress or even eliminate the species.

Since the first detection of *S. cryptandrus* in Hungary, we have detected more than 620 individual sites of the species with targeted field surveys. According to Jarić et al. (2019), it clearly represents a case of cryptic invasion, and there is a strong probability of discovering this species in further dry sandy areas of Hungary and in other Central European countries as well. Based on the Hungarian data, the species is expected to spread quickly, which emphasizes the urgent need for thorough monitoring of the species outside of its existing range.

According to our literature review, so far, naturalised populations of *S. cryptandrus* have been identified in Mediterranean and Eastern Central to Eastern European regions characterized by semi-arid or moderately continental climates. However, considering climate change projections, areas with sandy substrates farther north might also become ideal for the establishment and expansion of the species, which would render ongoing monitoring and management even more critical.

Chapter 3

Impact of *Sporobolus cryptandrus* on soil seed banks in dry sand grasslands

Introduction

Over the past few decades, invasive species and climate change have become increasingly significant factors affecting ecological processes worldwide (Hulme, 2017; Ravi et al., 2022). Climate change affects phenological patterns of species, changes distributional areas, and modifies the composition of communities, often facilitating plant invasions and the emergence of novel ecosystems (Esquivel-Muelbert et al., 2019; Feeley et al., 2020; Gaertner, 2013). These changes are especially beneficial for species with the C4 photosynthetic pathway, which are well adapted for dry and warm climates as they optimize water usage, have a higher optimum temperature of CO_2 fixation and lower photorespiration rate (Johnston, 1996; Dukes & Mooney, 1999; Chuine et al., 2012). With increasing global temperatures and other climate related extreme events such as droughts and eventually wildfires (Kovats et al., 2014), C4 species are predicted to increase their range thus having negative impacts on ecosystems that are dominated C3 grasses (de Deus Vidal et al., 2021).

Due to climate change, European grasslands, which predominantly consist of C3 grasses, are quickly becoming vulnerable to the invasion of C4 species (Petermann et al., 2021; de Deus Vidal et al., 2021). Severe droughts combined with depletion of soil moisture eradicates many native grasses and opens up the niches for drought-tolerant and water- efficient C4 plants (Taylor et al., 2014). From these invaders, *Sporobolus* species, specifically *S. cryptandrus,* is spreading at an alarming rate in Central Europe. Indeed, while most other *Sporobolus* species are restricted to disturbed habitats, *S. cryptandrus* has invaded seminatural grasslands where it becomes a threat for native species and rare sand grassland plants (Török et al., 2021).

Soil seed banks have a vital role in supporting the plant community's species population and play a significant role in the establishment and persistence of species (Thompson et al., 1997; Miao et al., 2020; Török et al., 2020). Some of the negative effects presented by invasive species include characteristics such as decreased recruitment and genetic variability of native species and the formation of persistent soil seed banks that allow invasive species to persist (Gioria et al., 2014). Nevertheless, the effect of *S. cryptandrus* on soil seed banks is not yet understood, particularly in the regions where it is invasive. In its native area *S. cryptandrus* is known to produce small, abundant seeds and build-up soil seed banks (Brown, 1943; Clements et al., 2007).

Results

Structure and density of soil seed bank

We recorded 92 species apart from *Sporobolus cryptandrus* in the soil seed bank. From these, 30 species contributed more than 90% of total density of the soil seed bank. Among these species, 10 had more than 100 viable seeds; they were *Conyza. canadensis* (847 seeds), *Portulaca. oleracea* (774), *Arenaria. serpyllifolia* (700), *Cerastium. semidecandrum* (126)*, Cerastium. stenophylla* (112), and *Potentilla. argentea* (105). Overall, 19,313 seedlings emerged from the soil samples with 15,149 of them being *S. cryptandrus*. Both the overall soil seed bank densities and the *S. cryptandrus* soil seed bank densities showed significant variance (Table 3.1). The lowest density was identified in the Kiskunhalas North site, while the Debrecen site has nearly ten times higher values. The Kecskemét Katonatelep location had the highest *S. cryptandrus* soil seed bank density, with an average of 95,000 seeds per m^2 for the species at cover category 4 (Table 3.1).

The results showed that most of the soil seed bank measures were impacted by *S. cryptandrus* cover. However, *Sporobolus* cover had an impact on both the density of the soil seed bank and the percentage of *S. cryptandrus* seeds; the highest seed density values were found in areas with the highest *S. cryptandrus* cover. All tested seed bank characteristics were significantly affected by the study site. Additionally, *S. cryptandrus* density and proportion, Shannon diversity, and Pielou's evenness were also influenced by the interaction effect of the *S. cryptandrus* cover and site identity (Table 3.2).

Table 3.1. Seed bank characteristics of the studied sites. Cover categories of *Sporobolus cryptandrus*: (1) no cover; (2) cover between 1% and 25%; (3) cover between 26% and 50%; (4) cover between 51% and 75%. [a]Calculated with the exclusion of *Sporobolus cryptandrus* (Mean ± SE).

	Cover category of *Sporobolus cryptandrus*			
	1 (0%)	**2 (1% and 25%)**	**3 (26%–50%)**	**4 (51%–75%)**
Debrecen				
Seed bank density [a]	8,727 ± 3000	10,425 ± 46	8,223 ± 1960	12,228 ± 2488
Sporobolus cryptandrus seed density	318 ± 183	345 ± 148	2,387 ± 452	3,024 ± 443
Proportion of *Sporobolus* seeds (%)	5.2 ± 4.2	3.2 ± 1.3	23.3 ± 2.5	21.1 ± 5.5
Species richness [a]	17.3 ± 0.3	13.0 ± 1.7	7.7 ± 1.2	10.7 ± 1.5
Shannon diversity [a]	2.52 ± 0.08	1.52 ± 0.20	0.93 ± 0.16	1.00 ± 0.27
Pielou's evenness [a]	0.88 ± 0.02	0.59 ± 0.06	0.47 ± 0.09	0.42 ± 0.09
Kiskunhalas North				
Seed bank density [a]	716 ± 122	1,034 ± 518	1,406 ± 70	1,088 ± 299
Sporobolus cryptandrus seed density	186 ± 116	1,114 ± 301	6,446 ± 2671	9,921 ± 2128
Proportion of *Sporobolus* seeds (%)	18.8 ± 9.5	55.4 ± 16.4	78.4 ± 5.7	90.4 ± 0.8
Species richness [a]	2.3 ± 0.9	5.0 ± 0.6	5.7 ± 0.3	5.7 ± 0.9
Shannon diversity [a]	0.65 ± 0.37	1.35 ± 0.10	1.37 ± 0.07	1.47 ± 0.11
Pielou's evenness [a]	0.63 ± 0.31	0.86 ± 0.08	0.79 ± 0.02	0.86 ± 0.03

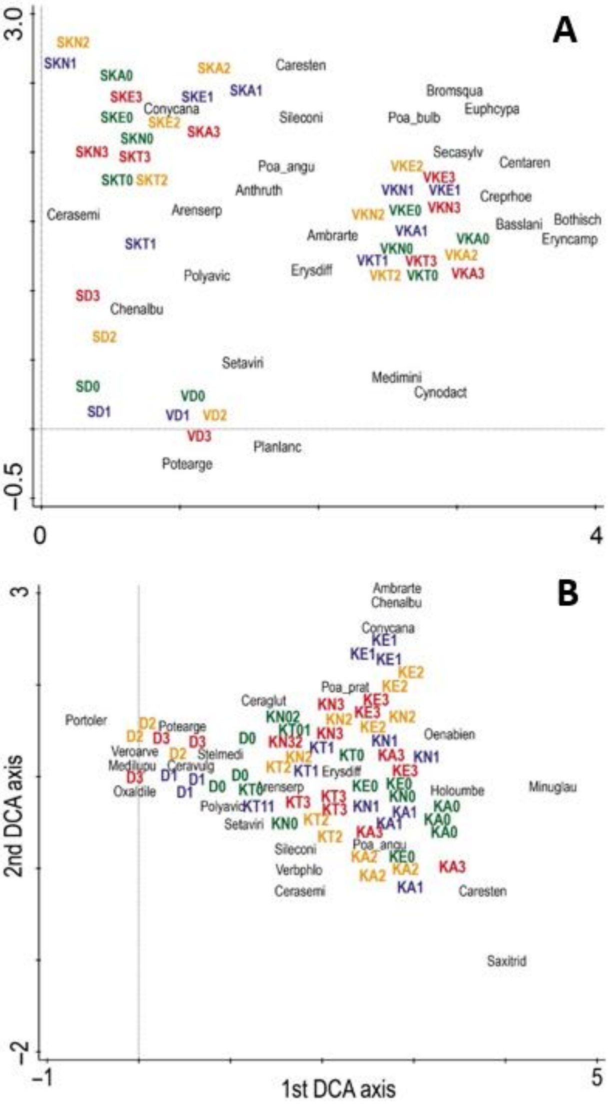
Table 3.1. continued.

	Cover category of *Sporobolus cryptandrus*			
	1 (0%)	**2 (1% and 25%)**	**3 (26%–50%)**	**4 (51%–75%)**
Kecskemét Katonatelep				
Seed bank density[a]	4,775 ± 1143	5,411 ± 1658	5,968 ± 622	3,395 ± 879
Sporobolus cryptandrus seed density	637 ± 184	33,555 ± 11,149	85,731 ± 42,584	95,413 ± 7470
Proportion of *Sporobolus cryptandrus* seeds (%)	13.8 ± 6.5	82.8 ± 6.8	90.8 ± 3.3	96.6 ± 0.78
Species richness[a]	16.0 ± 1.5	13.7 ± 3.9	12.3 ± 1.5	11.0 ± 1.5
Shannon diversity[a]	2.44 ± 0.08	1.88 ± 0.24	1.80 ± 0.14	1.90 ± 0.13
Pielou's evenness[a]	0.88 ± 0.03	0.76 ± 0.04	0.72 ± 0.06	0.80 ± 0.03
Kecskemét Airport				
Seed bank density[a]	4,669 ± 853	3,263 ± 279	3,979 ± 858	6,048 ± 4109
Sporobolus cryptandrus seed density	80 ± 46	32,786 ± 2529	60,028 ± 10,928	51,460 ± 4464
Proportion of *Sporobolus cryptandrus* seeds (%)	1.9 ± 1.0	90.9 ± 1.0	93.7 ± 1.1	90.9 ± 5.3
Species richness[a]	11.3 ± 1.5	9.3 ± 1.5	10.0 ± 1.7	9.3 ± 2.8
Shannon diversity[a]	1.81 ± 0.05	1.79 ± 0.10	1.68 ± 0.13	1.59 ± 0.07
Pielou's evenness[a]	0.76 ± 0.06	0.81 ± 0.01	0.74 ± 0.02	0.76 ± 0.06
Kiskunhalas East				
Seed bank density[a]	4,801 ± 2193	13,608 ± 4728	6,764 ± 1874	3,925 ± 2654
Sporobolus cryptandrus seed density	106 ± 27	3,183 ± 211	6,923 ± 557	8,196 ± 2087
Proportion of *Sporobolus cryptandrus* seeds (%)	3.4 ± 1.8	23.3 ± 7.5	52.2 ± 8.2	71.1 ± 15.1
Species richness[a]	14.0 ± 2.3	7.7 ± 1.5	10.0 ± 2.0	10.7 ± 4.3
Shannon diversity[a]	2.03 ± 0.17	0.66 ± 0.05	1.39 ± 0.36	1.91 ± 0.28
Pielou's evenness[a]	0.79 ± 0.09	0.34 ± 0.06	0.60 ± 0.11	0.87 ± 0.02

Table 3.2. The effect of *Sporobolus cryptandrus* cover study site, and their interaction on soil seed bank characteristics. Italics (two-way GLMs) indicate marginally significant effects ($p < 0.1$), while **bold face** ($p < 0.05$). indicate significant effects. [a] Calculated with the exclusion of *S. cryptandrus*.

Seed bank characteristics	***Sporobolus cover***		**Site**		***Sporobolus cover* × site**	
	$F_{3,40}$	*p*	$F_{4,40}$	*p*	$F_{12,40}$	*p*
Seed bank density[a]	0.836	0.482	**15.944**	**<0.001**	1.180	0.329
Sporobolus seed density	**5.444**	**0.003**	**59.278**	**<0.001**	**6.955**	**<0.001**
Proportion of *Sporobolus* seeds (%)	**8.718**	**<0.001**	**52.353**	**<0.001**	**6.316**	**<0.001**
Species richness[a]	0.242	0.866	**11.600**	**<0.001**	1.427	0.194
Shannon diversity[a]	0.628	0.601	**10.533**	**<0.001**	**6.942**	**<0.001**
Pielou's evenness[a]	0.195	0.899	**4.053**	**0.008**	**2.982**	**0.005**

The Debrecen site exhibited the highest similarity between the soil seed bank and the vegetation, with Sørensen similarity values ranging from 0.32 to 0.59. In contrast, much lower values (0.10–0.31) were typical for the other sites in the Kiskunság region. This pattern is clearly illustrated by the presence-absence DCA ordination (Fig 3.1.A). It also highlights the clear distinction between the species composition of the vegetation and the soil seed banks. Additionally, the point clouds representing the soil seed bank compositions of Debrecen sites and vegetation are both distinctly separated from those of the other four sites (Fig. 3.1.A). Furthermore, the composition of soil seed bank at the Debrecen site is clearly distinct from that of the Kecskemét Airport and Kiskunhalas North sites, while the other two sites are positioned between these three in the ordination (Fig. 3.1.B).



Figures 3.1 DCA illustrates the similarity among soil seed bank and vegetation across the studied sites based on two different datasets. A) is based on presence-absence data from both soil seed banks and vegetation, with gradient lengths for the first and second axes of 5.32 and 4.07, respectively. B) represents the similarity of seed banks using seedling counts, with gradient lengths of 3.57 and 3.01 for the first and second axes. In both figures, site codes are abbreviated as follows: the first letter indicates V for vegetation or S for soil seed bank (in Figure A only), while the second letter(s) represent the specific sites: D for Debrecen, KA for Kecskemét Airport, KE for Kiskunhalas East, KN for Kiskunhalas North, and KT for Kecskemét Katonatelep. The numbers and colors signify the cover levels of *Sporobolus cryptandrus*, with green (0) = 0%, blue (1) = 1%–25%, orange (2) = 26%–50%, and red (3) = 51%–75%. In both cases, the 30 most prominent species are labeled using abbreviations of their species names, such as Ambrarte for *Ambrosia artemisiifolia*.

The top 2.5 cm layer had the highest density of *S. cryptandrus* seeds and the total density of soil seed banks. There was significant effect of the sampling depth on most of the studied soil seed bank characteristics, but none of them were impacted by the increasing cover of *S. cryptandrus*. The model analysing *S. cryptandrus* seed density showed a significant interaction between the *S. cryptandrus* cover and sampling depth (Table 3.3).

Table 3.3. Effects of *Sporobolus cryptandrus* cover, depth of seed sampling and their interaction on soil seed bank characteristics. Italics (two-way GLMs) indicate marginally significant effects ($p < 0.1$), while **bold face** ($p < 0.05$). indicate significant effects. [a] Calculated with the exclusion of *S. cryptandrus*.

Seed bank characteristics	***Sporobolus cover***		**Sampling depth**		***Sporobolus cover* × sampling depth**	
	$F_{3,224}$	p	$F_{3,224}$	p	$F_{9,224}$	P
Seed bank density[a]	1.166	0.324	**74.465**	**<0.001**	0.403	0.933
Sporobolus seed density	0.657	0.579	**45.443**	**<0.001**	**4.481**	**<0.001**
Proportion of *S. cryptandrus* seeds (%)	1.878	0.134	**5.030**	**0.002**	0.592	0.803
Species richness[a]	0.084	0.969	**62.106**	**<0.001**	0.909	0.518
Shannon diversity[a]	0.069	0.976	**34.571**	**<0.001**	0.501	0.873
Pielou's evenness[a]	0.005	1.000	2.455	0.064	0.485	0.884

Specifically, *S. cryptandrus* seed density in the upper 2.5 cm was significantly higher in the plots having considerably more cover (3rd and 4th cover categories in comparison with the plots with less cover (Fig. 3.2). A similar trend, though less pronounced, was observed in the deeper soil layers: *S. cryptandrus* seed density was significantly higher in deep layers of the plots with a high *Sporobolus* cover than in the deep layer of plots with low cover.

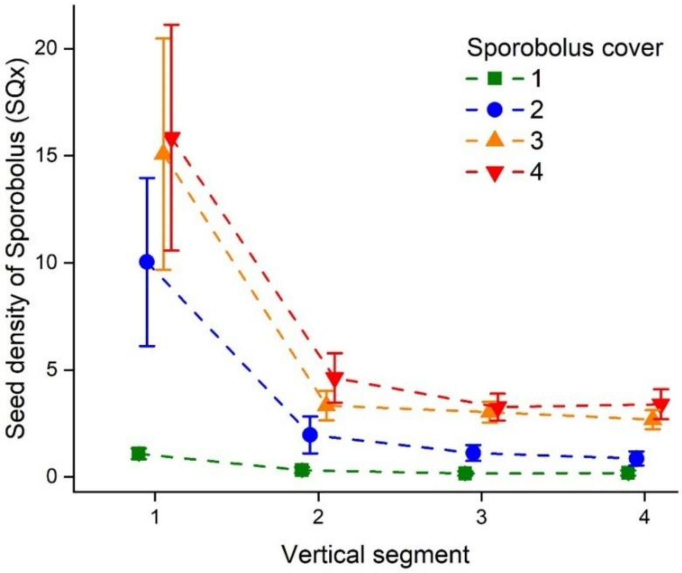


Figure. 3.2. *Sporobolus cryptandrus* seed density in various vertical segments of the soil seed bank was measured across plots with varying levels of species cover (data transformed using square root/SQ). The cover categories were as follows: no *S. cryptandrus* cover (1), *S. cryptandrus* cover between 1% and 25% (2), 26% to 50% (3), and 51% to 75% (4). The vertical soil segments analysed were: 0-2.5 cm (1), 2.5-5 cm (2), 5-7.5 cm (3), and 7.5-10 cm (4).

Discussion

Our findings offer valuable information about the vertical distribution of seed in various soil layers as well as the density and composition of the soil seed banks with respect to *Sporobolus cryptandrus* cover. The ecological implications of these observations include the potential invasiveness of *S. cryptandrus*, the alteration of seed banks in sandy grasslands, and the way in which seed banks may reflect past and present vegetation patterns.

Seed Bank Composition

One of the hypotheses was that as the cover of *S. cryptandrus* increases, the density and diversity of other species in the soil seed bank decrease. Based on the results, this hypothesis was not supported, as the increased cover of *S. cryptandrus* did not significantly alter the soil seed bank's density or diversity. Former research revealed that compared to aboveground vegetation, changes in the soil seed bank occur more slowly. Therefore, the soil seed banks frequently serve as a kind of "successional memory," preserving the composition of the previous vegetation states. (Sun et al., 2013; Tóth et al., 2022). The species richness and density of soil seed banks of the invaded communities are generally decreased by plant invasions, as demonstrated by Gioria et al. (2014). In a similar study, Hager et al. (2015) has shown that invasive species significantly reduce the diversity of soil seed banks, although the effect on seed bank density was less pronounced. By removing the invasive species' seed bank from our calculations, neither the density nor the diversity of the remaining seed bank was significantly influenced. A few reasons might explain these diverging results: Firstly, the soil seed bank's composition is often relatively stable and changes slowy, serving as a successional memory for the community. According to Gloria & Pyšek, (2016) the so-called "residence time", the time which passed since the species has been established in the area, has to beconsidered to estimate the invasive species' effect on the soil seed bank. In this study, we can assume that *S. cryptandrus* has a relatively short residence time, no longer than 10-15 years, based on field observations and monitoring activities of national park rangers. In 2016, the species was first observed close to Debrecen, Hungary (Török et al. 2018). Second, *S. cryptandrus* is a tussock-forming grass with limited clonal spread and does not form dense vegetation cover such as other grasses do (e.g., genus *Calamagrostis* or *Elymus*). During this study, its cover never reached higher than 60%, so its spread may cause less limitation on seed dispersal and establishment when compared to denser and clonally spreading species.

Instead, site characteristics and not *S. cryptandrus* cover were the decisive factor influencing the diversity and abundance of the soil seed bank (excluding *S. cryptandrus* seeds). The estimated densities of the seed bank in sandy grasslands in the top 5–10 cm of the soil ranged from a few hundred to tens of thousands of seeds per square meter in earlier studies conducted throughout Europe (Symonides, 1979; Godefroid et al., 2018; Török et al., 2018). Indeed, excluding the seeds of *S. cryptandrus* from the analyses, the highest seed bank densities recorded in this study were registered at the Debrecen site a degraded grassland which contained many weedy species which are known to regularly form permanent seed banks. This strong site effect underlines the conservative nature of soil seed banks because they often reflect past vegetation composition, as has also been determined by other studies (Wellstein et al., 2007; Bossuyt & Honnay, 2008).

According to Hopfensperger (2007), grasslands typically have standing vegetation that is more similar to the soil seed bank than wetlands or forest ecosystems. However, grasslands vary in this respect as well. For instance, in sand grasslands this similarity is usually lower (Godefroid et al. 2018; Török et al. 2018), while in fen meadows and alkali grasslands it is higher (Valkó et al. 2011, 2014). Factors, like management of the grasslands, disturbance, environmental stress, and limitation in seed dispersal and establishment, could significantly influence the similarity among the standing vegetation and the soil seed bank. In our work, we found the highest level of similarity between the above-ground flora vegetation and the soil seed bank at the Debrecen site and found a lower level of similarity at the Kiskunság sites. These results are in accordance with those obtained from the study regarding soil seed bank densities and suggest that both the seed bank's composition and its similarity to the above-ground vegetation depend strongly on specific site characteristics.

Soil seed bank density of Sporobolus cryptandrus

The second hypothesis was that the density of S. cryptandrus seeds in the soil seed bank is highly affected by its own vegetation cover: with higher cover leading to a higher density of its seeds. The results support this, and also it is also in line with other results such as those reported by Clements et al., (2007), who confirmed the species' ability to establish substantial soil seed banks within its native range. Our results further showed that *S. cryptandrus* is able to develop an impressive soil seed bank in non-native grasslands. One study by Gloria et al. (2012) identified 36 species able to form seed banks in their introduced habitats, but soil seed bank was collected for only one perennial grass, namely *Agropyron desertorum*, an invasive species in North America, which form sporadic soil seed banks reached densities as high as 93 seeds/m^2 (Gioria et al., 2012). On the contrary, *Sporobolus cryptandrus* seed densities at some of our study sites were over tens of thousands per square meter. Furthermore, the percentage of *S. cryptandrus* seeds in the soil seed bank also increased with an increase in the cover of the species. Notably, there were viable seeds in the soil in areas without *Sporobolus* cover, probably as a result of the massive seed production of the species and generally efficient dispersal mechanisms (Ingimarsdóttir et al., 2012; Shmida & Wilson, 1985). It was documented by previous studies that *S. cryptandrus* can yield up to 10,000 seeds per plant annually with seeds approximately 1 mm in diameter being readily incorporated into the soil. A small-scale sampling carried out in 2019, showed a persistent seed bank of 1,114-3,077 seeds/m^2 in autumn (Török et al. 2021), while this current sampling in spring resulted in 637-3,899 seeds/m^2, which suggests a dense and persistent soil seed bank across sites, given that the species germinates during the spring season.

This study found that in some sites, *S. cryptandrus* exhibited soil seed bank densities comparable to those of small-seeded wetland plants (hygrophytic graminoids) that typically inhabit wet grasslands. This is notable since high seed density is uncommon among dry grassland species. In primary and secondary dry grasslands, the seed banks of perennial grasses such as *Festuca vaginata* (Török et al., 2018), *Festuca pseudovina* (Valkó et al., 2014), *Poa angustifolia* (Török et al., 2009, and 2018), and some Stipa species (Török et al., 2018) are usually far less dense, reaching no more than 1,200-1,400 seeds m^2 in the upper 10 cm of soil compared to those of *S. cryptandrus* in this study. These grass species are typical C3 species adapted to the temperate climates, and often they are dominant components of dry grassland vegetation. The other perennial grasses, which also occurred in one of the study sites with at least 5% cover (reported in Török et al., 2021), like *Calamagrostis epigeios, Lolium perenne, Festuca. pseudovina* and *Poa angustifolia* had lower seed bank densities than *S. cryptandrus* and only ranged from 80 seeds m^2 for *Calamagrostis epigeios* to as high as 2,308 seeds m^2 for Poa angustifolia. In contrast, large-seeded wetland graminoids, such as *Elymus athericus* (Erfanzadeh et al., 2010), may not be expected to build up permanent soil seed banks because larger seeds are more likely to disappear from the soil over time. However, the majority of the small-seeded hygrophytic grasses show high-density seed banks with features similar, in part, to that of *S. cryptandrus*, which, therefore, emphasizes the unusual seed bank density profile of this dry grassland species.

Although, there is no accurate information about the residence time of *S. cryptandrus* at these sites, rough estimates and anecdotal evidence suggest 10–15-year residence time, and we can use plots with different levels of the species cover as a time proxy for invasion progression (so-called space-for-time substitution Miao et al., 2018; Wang et al., 2022a). It is in line with previous studies by Gioria & Pyšek 2016, who demonstrated that older invasions tended to have higher seed bank densities and more marked effects on native vegetation compared to recent invasions. *Sporobolus cryptandrus* rapidly building up in the soil seed bank indicates that delays in management will only act to increase the difficulty and expense of control (Simberloff, 2003). Moreover, with the increasing severity of droughts in many areas under climate change, die-offs of native plants (Miao et al., 2022; Orbán et al., 2023) may provide additional opportunities for *S. cryptandrus* to become established in natural grasslands. Therefore, developing methods for managing *S. cryptandrus* to suppress the species is increasingly urgent. Controlling populations of *S. cryptandrus*, together with additional research on its ecological and biological characteristics, is required in issuing better recommendations on control measures.

Finally, the last hypothesis suggesting that the density and diversity of the soil seed bank declines with increasing sampling depth, and this density decline is influenced by the covere of *S. cryptandrus*,was partially supported. Despite the density and diversity of soil seed banks declined as soil depth increased, *S. cryptandrus* cover had no effect on this decline. Gioria and Pyšek (2016) suggested that studies on soil seed banks and the impact of invasive species should examine seed banks at different soil depths rather than focusing only on species distribution patterns. Understanding seed persistence and the potential accumulation of invasive species' seeds in deeper soil layers can provide valuable information into their long-term ecological effects (Holmes, 2002; Gioria & Osborne, 2010; Gioria et al., 2011; Gioria & Pyšek, 2016). In this study, the soil samples were divided into four sections of 2.5 cm each and conducted a seed bank composition analysis for both the invasive and the native species. All seed bank diversity measures like richness, diversity as well as density decreased with depth, a trend which was observed in soil seed bank studies in different types of grassland vegetation (Luzuriaga et al., 2005; Godefroid et al., 2006; Qian et al., 2016; Niknam et al., 2018). Further studies also mention that deeper layers may contain viable seeds older than those in shallow layers, as the process of reaching deeper layers requires more time (Bekker et al., 1998). In most cases, there is a fast decline in seed bank density with depth, with most seeds located in the upper few centimetres of soil (Bekker et al., 1998; Ma et al., 2010; Tóth et al., 2022). This trend was corroborated in this study, where the highest seed densities for both invasive and other species were found within the top 5 cm.

A previous study by Török et al (2021) demonstrated that 1 cm of soil cover was enough to considerably hinder *S. cryptandrus* seed germination.

However, this effect is more pronounced when litter is present. This implies that the re-establishment of *S. cryptandrus* even in regions with very high seed bank densities is likely to be achieved with minor soil disturbance or gaps in the vegetation to allow bare soil exposure. Our study also demostrated that *S. cryptandrus* seed density in the upper 2.5 cm of the soil remained significantly higher in high-cover plots, while the more extensive cover categories differed in deeper layers as well. Therefore, it implies that *S. cryptandrus* seed production in areas with a high cover of the species results in high seed density in deep soil layers as well.

Conclusions and management implications

The results of this research indicated that *S. cryptandrus* can create a very large permanent seed bank in the soil reaching hundreds/thousands of seeds per square meter. In addition, this accumulation implies that there is a high dispersal and colonization potential that is particularly effective in disturbed areas. Thus, its suppression and/or eradication will be challenging. Although, its eradication could be successful in sites where the establishment of the species is very recent, and its cover is still low because at those sites the species has a relatively low seed density at least in the deeper soil layers. The actions in those sites are needed to avoid the accumulation of its soil seed bank, which may, otherwise, hinder effective management efforts. Proactive measures may help to improve the success of management strategies.

The results also indicate that despite *S. cryptandrus* exists in various gradients, the amount of vegetation cover of the invasive species did not direct impact on species diversity and the seeds bank density of the native species probably because the seed bank functions as a “successional memory” of changed vegetation over time.

Moreover, the results showed the difference in depth patterns in soil seed banks, for which seed density and diversity are low in the deeper layers of soil and high in the uppermost soil layer, which has been documented in many grassland types. Although the rate of this reduction was unchanged by *S. cryptandrus*' cover, because of its high seed output, a greater proportion of seeds were found at shallower depths especially in plots with high cover. *S. cryptandrus* seed bank accumulation seems to be persistent, which can be quite problematic for the management of the species in the future. Its combination of high fecundity, seed dispersal ability, and persistence within the soil after disturbance is likely to stimulate the invasion of this species in grassland habitats, especially with prolonged drought and die-back of the native flora. For this reason, control methods that generate soil disturbance and patches with bare soil surface should be avoided. If the physical removal of tussocks is necessary, it should be accompanied by soil covering by hay or grass litter, which was previously found to effectively prevent the germination of the seeds.

Based on our findings, *S. cryptandrus* stands as a threat that needs to be addressed early, and control practices put in place in its habitats, mostly in grassland areas which are highly vulnerable to invasions. There will be an important need for more studies focusing on the ecology and population biology of *S. cryptandrus*.

Chapter 4

Litter effects of invasive *Sporobolus cryptandrus*: Mechanisms and species-specific responses in native grasslands

Introduction

Plant litter, including both accumulation and decomposition, is well-known as a significant influence on vegetation structure and ecosystem process (Wardle et al., 1997; Yan et al., 2018; Petraglia et al., 2019; Giweta et al., 2020). Plant litter can impact multiple aspects of plant communities including germination, seedling development, species richness, and aboveground biomass (Carson et al., 1990; Hovstad & Ohlson, 2008; Kelemen, et al., 2013; Hassan et al., 2021; Zhang et al., 2022). These effects are impacting through various mechanisms, including shading, shifts in soil humidity, mechanical obstruction, nutrient cycling, and the release of chemical compounds (Weltzin et al., 2005; Letts et al., 2015; Shen et al. 2016). However, distinguishing between these mechanisms is often challenging, as their combined impacts shape litter's overall influence on plant communities, especially in the context of invasive species which can drastically change the structure and functioning of grassland ecosystems.

Invasive species can exert the effects of litter through mechanisms like physical obstruction and chemical interaction (Farrer & Goldberg, 2009). The impact of invasive plant litter may be exacerbated by the accumulation in greater amounts or by the different traits of invasive compared to native ones

(Chiba De Castro et al., 2020; Souza et al., 2023). For example, invasive grass litter can form thick dense tightly interwoven mats, impeding light and germination (Donath & Eckstein, 2008). For example, the invasive grass *Microstegium vimineum*, which produces litter that suppresses the native grass *Elymus virginicus*, promoting disease and reducing biomass of both species through competitive interactions (Benites et al., 2021). Likewise, *Bromus diandrus*, 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). A thick litter layer changes soil moisture and, in some cases, has been known to even facilitate diseases in native species (Pan et al., 2024; Ruprecht & Szabó, 2012; Benites et al., 2021). Such effects can have profound implications for native biodiversity and ecosystem stability, as invasive species often outcompete native plants by utilizing multiple strategies, including litter-mediated interactions (Benites et al., 2021; Dušanka et al., 2021).

Among these mechanisms, allelopathy, which is the release of chemical compounds that suppress or promote the growth of neighbouring plants has been extensively studied in invasive species research (Ruprecht et al., 2010; Zhang & Fu, 2010; Samedani et al., 2013; Greer et al., 2014; Guido et al. 2020; Hassan et al., 2021; Yuan, et al., 2021; Menicagli et al., 2023; Talmot et al., 2024). While allelopathy represents just one aspect of litter's influence, it may provide invasive species with a competitive advantage, as seen with *Ailanthus altissima* and *Centaurea maculosa*, which release allelochemicals to suppress native vegetation (Heisey, 1990; Ridenour, 1995; He et al., 2009). Therefore, this phenomenon reflects the multifaceted nature of litter through which physical and chemical interactions take place the structure and functioning of plant communities.

Despite considerable research on invasive plant species and their effects, the adverse effects of native species on nonnative species have received limited attention, as noted by Hierro and Callaway (2021). This gap highlights the need to explore how litter from both native and invasive species influences community interactions, particularly in ecosystems under threat from invasive grass like *Sporobolus cryptandrus.*

Sporobolus cryptandrus, an invasive C4 grass, has become a significant concern in some European regions, including Hungary, where it dominates disturbed and semi-natural sand grasslands, outcompeting native species (Török et al., 2021, 2024). Its litter may promote its invasive success by affecting germination and seedling establishment through multiple mechanisms, including allelopathy. While allelopathy has been documented in related species, such as *Sporobolus pyramidatus (*Rasmussen & Rice, 1971), its role in *S. cryptandrus* remains uncertain.

Results

When analysed across species, litter treatment only had a significant impact on seedling length (Table 1, $p < 0.001$): both native and *Sporobolus* litter increased seedling length compared to no litter. Litter treatment had no significant impact on germination rate ($p = 0.442$) and on dry weight per seedling ($p = 0.080$), (Fig. 4.1).

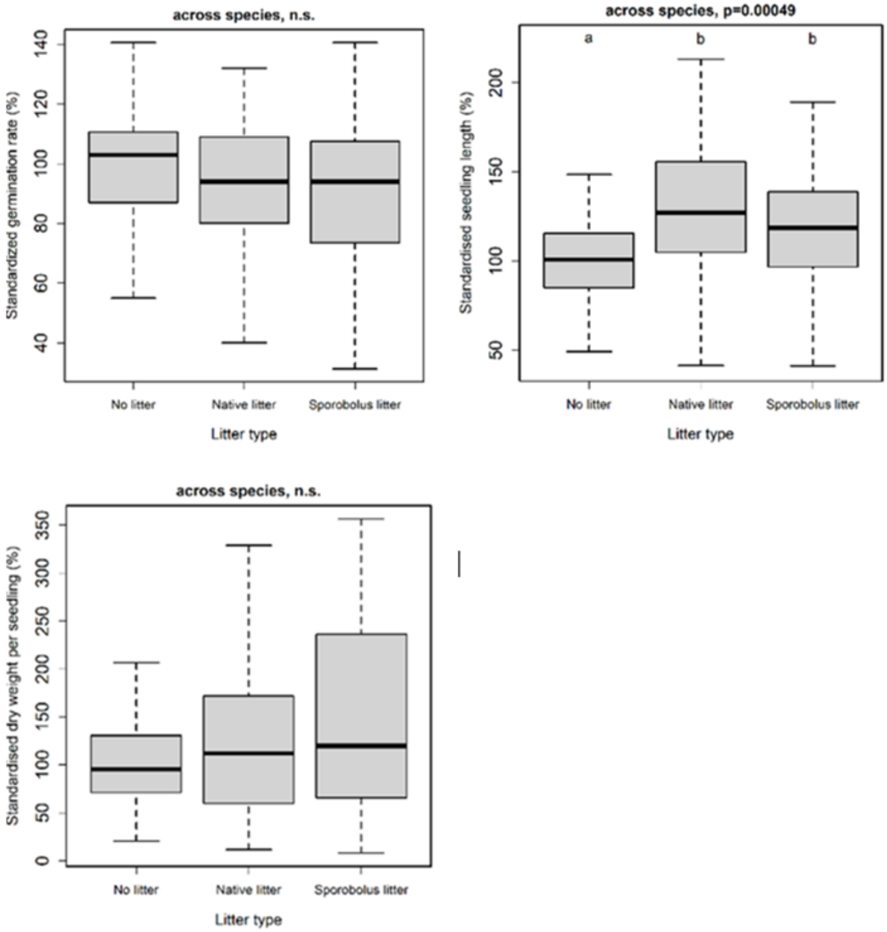


Figure 4.1. Litter treatment effect on germination rate, seedling length, and dry weight per seedling analysed between species (one-way ANOVA and Tukey tests). Standardized mean values for germination rate, seedling length and dry weight were given compared to the mean value of the given variable in the no litter (control) treatment for every species to avoid the confound effect of species identity

Regardless of the applied litter treatment, we detected that the influence of litter layering on the germination rate was highly species-specific. Thus, the litter effects were also analysed at the species level.

At the species level, the germination rate of *Bromus tectorum* and *Jasione montana* were significantly impacted by litter treatment (Fig. 4.2), but not on the germination rate of the other eight species were not affected significantly. Specifically, *Sporobolus* litter had a notable negative impact on germination compared to native litter only for *Bromus tectorum* (Fig. 4.2).

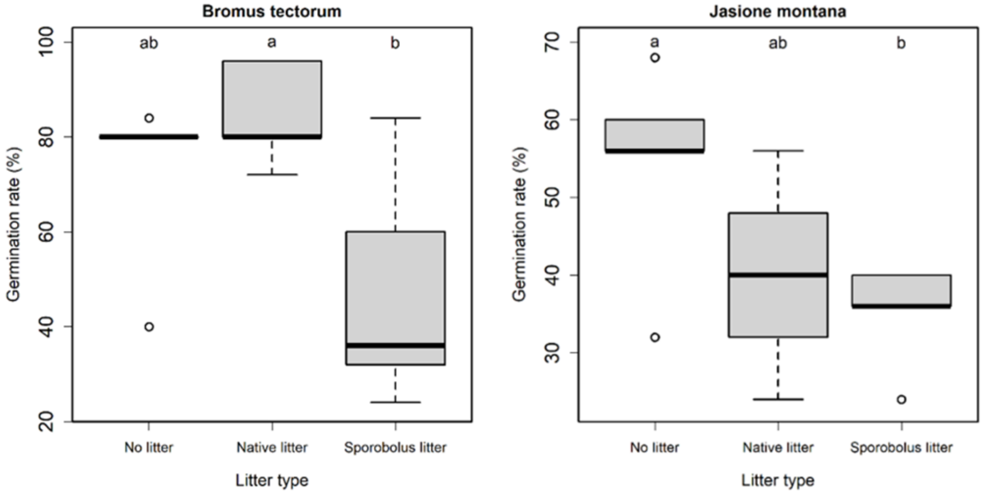


Figure 4.2. Litter treatment effect on the germination rate of *Bromus tectorum* and *Jasione montana* (one-way ANOVA and Tukey tests, only significant relationships are plotted).

Litter treatment significantly influenced the seedling length of six of the ten species (except for *Erysimum diffusum, Festuca pseudovina, Jasione montana,* and *Sporobolus cryptandrus*). For all species where litter treatment had a significant impact on seedling length, native litter increased seedling length compared to no litter. *Sporobolus* litter negatively affected seedling length compared to native litter, but this effect was significant only for *Bromus tectorum* (Fig. 4.3).

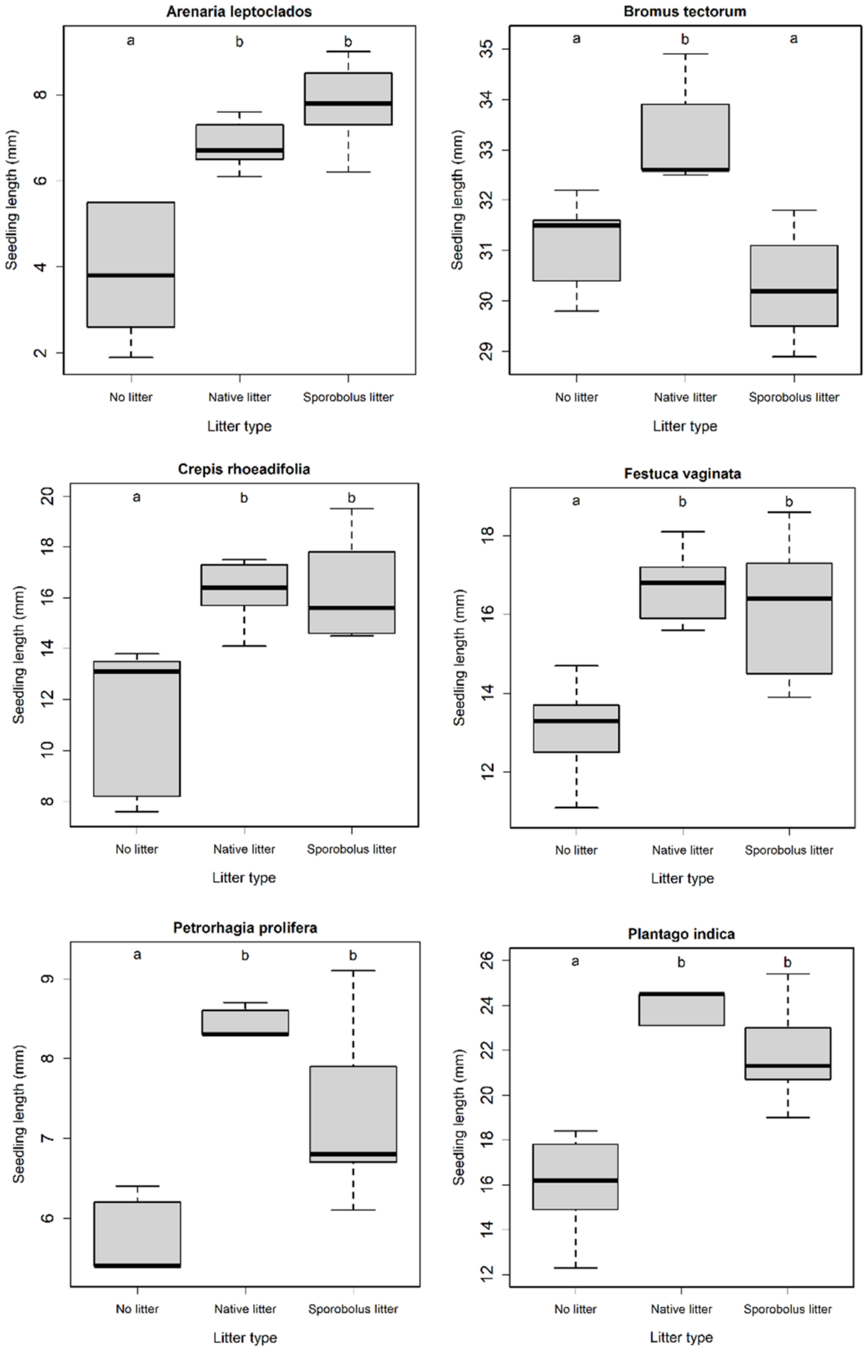


Figure 4.3. Litter treatment effect on seedling length analysed separately for each species (one-way ANOVA and Tukey tests, only significant relationships are plotted).

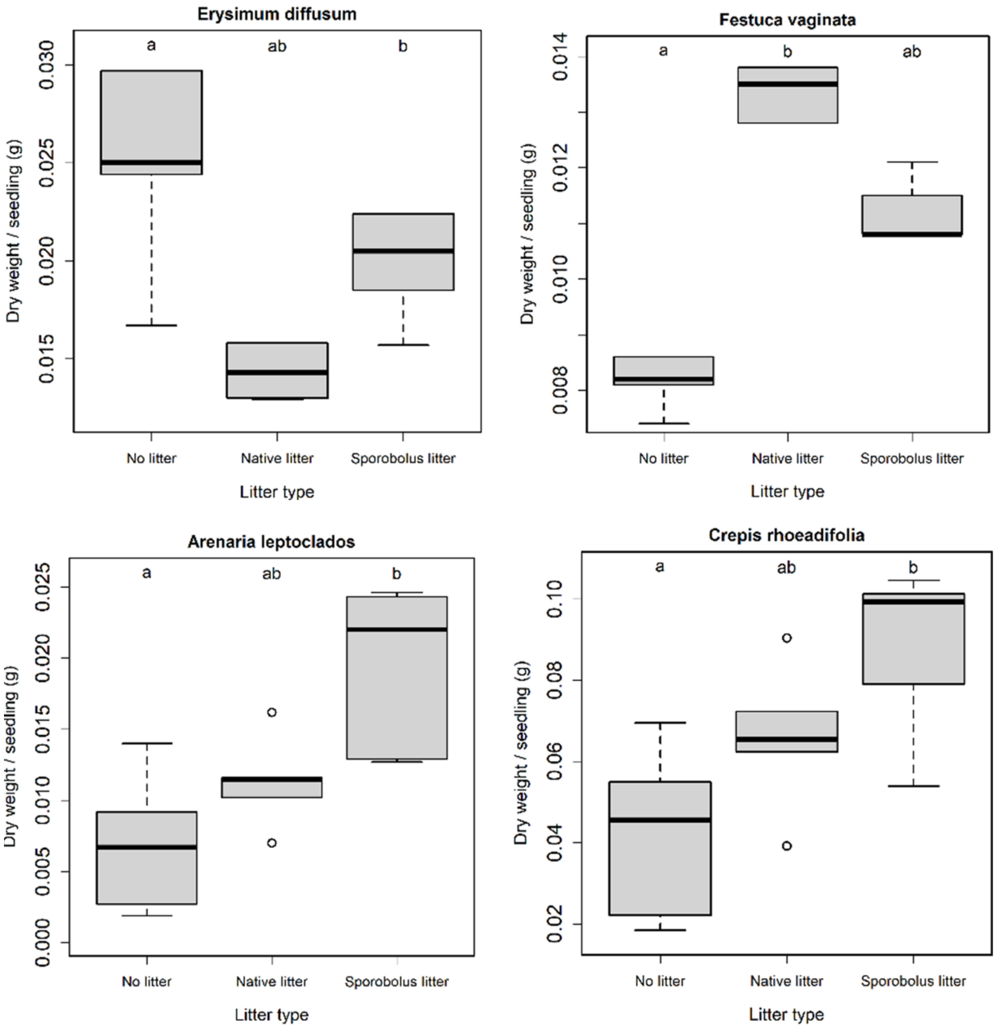


Figure 4.4. Litter treatment effect on dry weight per seedling analysed separately for each species (one-way ANOVAs and Tukey tests, only significant relationships are plotted).

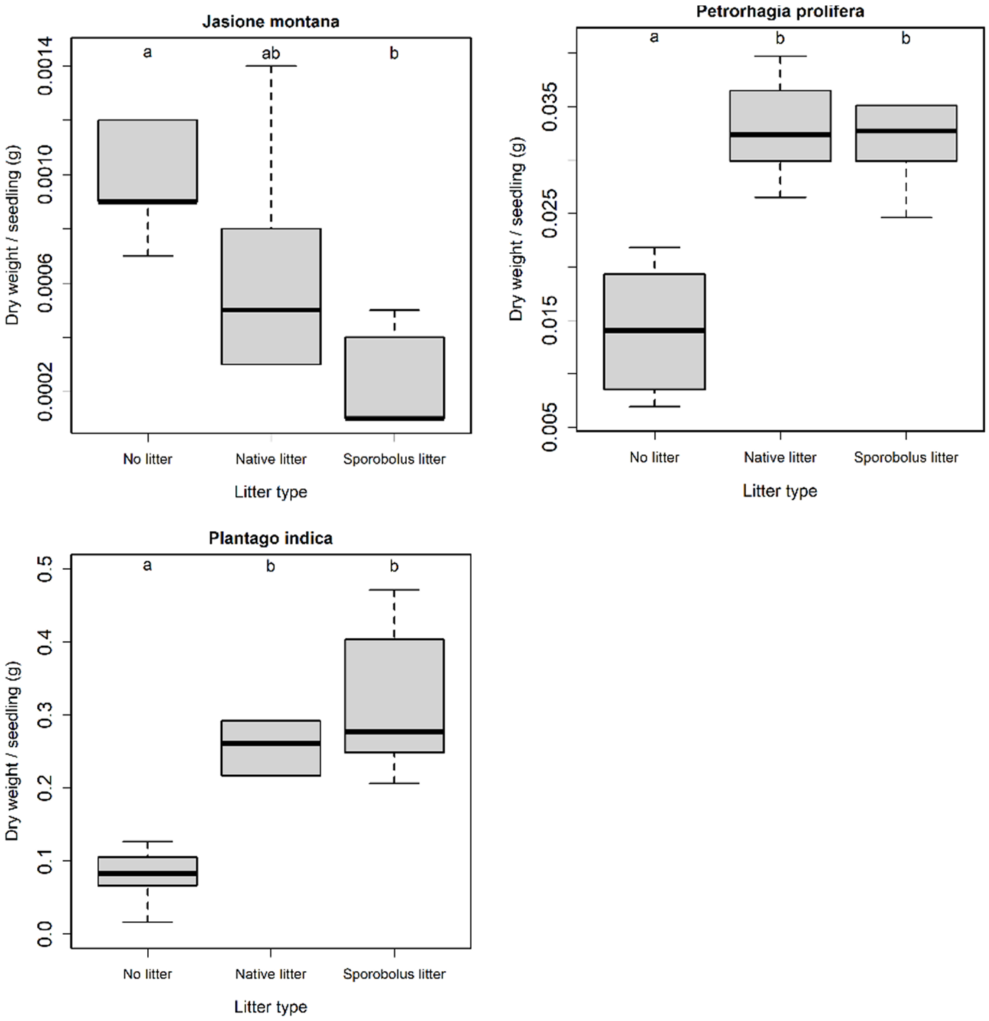


Figure 4.4. continued.

Litter treatment significantly influenced the seedling dry weight of seven of the ten species (except *for Bromus tectorum, Festuca pseudovina,* and *Sporobolus cryptandrus*). The effect of native litter and *Sporobolus* litter did not differ significantly in any of the species (Fig. 4.4).

Discussion

Results of this study underline the complex role of litter in influencing the germination and seedling establishment of sand grasslands species. In order to aid in the conservation of the impacted grasslands, this study determined that *Sporobolus cryptandrus* does not exert a universal allelopathic impact on the native vegetation, its effects are species-specific, with particular attention to the negative impact of *Sporobolus* litter on certain species like *Bromus tectorum,* which is problematic in North America. The fact that germination, seedling length, or dry weight are not uniformly inhibited across species suggests that the effects of any allelopathic compounds produced by *Sporobolus cryptandrus* may be limited and depended on specific conditions, such as species type or the environment.

The first hypothesis was partially supported by the results: both native litter and *Sporobolus* litter have a negative effect on seedling germination and establishment compared to no litter in some of the species. According to previous studies, the effects of litter vary between different species and litter types (Donath & Eckstein 2008; Ruprech et al., 2010). However, our results showed that both litter treatments (native and *Sporobolus* litter) had a significant impact on seedling length, compared with non-litter. This may be because both litters come from grass and physically are quite similar in litter form. A study by Xiong and Nilsson, (1999) found that using litter from distinct plant groups like, forbs or sedges, can have more variable effects on seedling emergence and growth. Other studies have demonstrated how varying litter types affect seedling emergence, with species-specific effects depending on litter origin (Wang et al., 2022). If we had included litter from other plant species, the results may have been different. Some studies suggest that allopathy, i.e., the ability of plants to release chemicals could affect other species, might be key to enable alien species to dominant in invaded plant communities (Callaway & Aschehoug 2000; Ruprech et al., 2008). In our study, considering all species, neither native litter nor *Sporobolus* litter significantly affected seed germination and dry weight per seedling. However, Loydi et al. (2015) showed that the non-native litter reduced the germination rate of native species and increased the seedling biomass that successfully emerged. This might suggest that allelopathy's impact on gemination may be reduced once the seeds have germinated. After germination, other factors like competition for light or nutrients, may have stronger impact on germination and early seedling growth (Loydi et al., 2015; Li et al., 2016; El-Keblawy, 2017).

The second hypothesis was also partially supported: *Sporobolus* litter has a stronger negative effect compared to native grass litter in some of the species. Although *Sporobolus* litter significantly inhibited the germination and seedling growth of *Bromus tectorum* (an invasive species) its effects on most other species were equivalent to native litter. This may suggest that the effects of *Sporobolus* litter are mainly chemical, and its physical effects are not considerably different compared to native litter. The lack of difference between the effects of both native and *Sporobolus* litter in most species indicates that it is improbable that allelopathy from *S. cryptandrus* alone can explain its success as an invader. Further, we identified that *Sporobolus* litter presented a negative effect on the germination and seedling length compared to native litter only for *Bromus tectorum*, and native litter had significant effect on the germination on *Bromus tectorum* and *Jasione montana* (Fig. 4.2.).

Such variability in responses underlines the need for further research on the exact mechanisms of such interactions, including allelochemicals that could be released during litter decomposition (Wang et al., 2022b).

The third hypothesis was strongly supported by the results: The effect of litter type is species-specific. Litter can have different effects on plants because of various factors (Kortessis et al. 2022). It mostly benefits by maintaining soil moisture, which favours seed germination and seedling development (Letts et al., 2015; Shen et al. 2016). However, litter might also form a physical barrier for seedling germination and growth to reach sunlight (Olson & Wallander, 2002; Tormo et al., 2020). In our study, we found that responses to litter treatment were highly variable across species. The presence of litter treatment significantly affected the seedling length of six species (except for *Erysimum diffusum*, *Festuca pseudovina*, *Jasione montana*, and *Sporobolus cryptandrus*), and also the seedling dry weight of seven species (except for *Bromus tectorum*, *Festuca pseudovina*, and *Sporobolus cryptandrus*). Thus, litter treatment promoted seedling elongation but not necessarily resulted in greater biomass accumulation. This may imply that though seedlings are taller, they may not necessarily be more robust or healthier as suggested by their biomass (Liu et al., 2017), as seen in species like *Bromus tectorum*. This result could indicate that species face a trade-off between elongation (growing taller) and accumulating biomass (building size) in order to compete for sources like light, especially in environments where litter acts as a physical barrier (Quested & Eriksson, 2006; Kortessis et al. 2022; Sparks & Rasmussen, 2023). Besides, the highly variable effect on seedling length and dry weight across different species confirms the hypothesis that litter effects are species-specific. While native litter generally favours seedling growth, *Sporobolus* litter tends to suppress it in some species. However, these effects are not consistent across species. as certain species have developed adaptations that allow them to survive and even thrive under different litter conditions (Facelli & Pickett, 1991). The litter reduces light availability for seedling emergence and its impact seems to be stronger in species with smaller seeds than in species with have larger seeds (Ruprecht et al. 2010; Loydi et al. 2013; Molinari & D'Antonio 2014). At the same time, according to several studies, including meta-analysis, litter inhibits the germination of small-seeded species more significantly than that of large-seeded species (Jensen & Gutekunst, 2003; Eckstein & Donath 2005; Loydi et al. 2013; Sonkoly et al., 2020). These findings are supported by our data, the small-seeded species *Jasione montana* exhibited lower germination rates in the presence of native litter than the larger-seeded species such as *Bromus tectorum*. Besides, it is important to consider that grasses used in this study are larger-seeded species with long and narrow leaves arranged vertically. Thus, it is easier for grasses to grow through deep litter than dicots with flat leaves (Grimes, 1979). For instance, the three grasses species *Bromus tectorum*, *Festuca pseudovina* and *Festuca vaginata* germinated more effectively in the presence of litter than dicots, because the narrow blades made it easier to emerge through litter (Germino et al., 2016; Szabo et al., 2017)

The differential effect of *Sporobolus* litter on *Bromus tectorum* has interesting implications for the interaction between native and invasive species. In North America prairies, where *Sporobolus cryptandrus* is native, this interaction may offer insight into natural mechanisms that could be used to manage invasive species such as *Bromus tectorum* (Mack, 1981; Leger & Goergen, 2017). Although our results only provide indirect evidence for a presumable allelopathic effect of *S. cryptandrus* on *B. tectorum*, our findings imply that the issue deserves additional investigation, especially identification of the particular compounds involved and the ecological relevance.

In summary, the species-specific responses observed in this study corroborate that litter plays a crucial role in influencing germination and seedling development. Native and *Sporobolus* litter can have contrasting impacts, but these effects are highly dependent on the species in question. *Sporobolus* litter and native litter had similar effects on most species, suggesting that *Sporobolus* litter primarily exerts the same physical effect on germinating seeds as native litter. In contrast, *Sporobolus* litter had a significantly greater negative effect on the germination of *B. tectorum* than native litter, suggesting a specific, presumably chemical effect.

Conclusion and Outlook

The findings of this study highlight the complex role litter plays in affecting the germination and seedling establishment of sand grassland species. By examining the effects of native litter and *Sporobolus cryptandrus* litter, we have highlighted the multifaceted nature of litter's impact, showing that these effects are highly species-specific and cannot be generalized across all native and invasive species. Most notably, the inhibition of *Bromus tectorum* by *Sporobolus cryptandrus*, suggesting possible ways to manage the interactions of invasive species, particularly where one invasive species may naturally control another. Such an interaction implies the analysis of chemical and physical factors, as well as investigation of specific allelochemicals and their ecological role. Also, it was observed that the physical effects of litter (most notably, moisture retention and shading) vary according to species-specific traits related to seed size and germination requirements, which suggests that litter may differentially create microsites either favourable for seedling elongation or unfavourable for seedling establishment.

From an ecological point of view, these results present important information on the role of litter in managing plant species interactions in invaded ecosystems. The proof that *S. cryptandrus* litter has no overall higher impact than native litter challenges assumptions about invasive dominance being largely chemical and underscores the complexity of these interactions. Instead, future research should focus on specific mechanisms (physiological and chemical) that are responsible for these species-specific effects. Studying the decomposition of *S. cryptandrus* litter and its effects on nutrient dynamics and microorganisms will be most useful. Furthermore, future research may extend these investigations to other invasive and native species pairs to understand litter dynamics and impacts of invasive species in grassland communities.

In practical terms, the findings reported here provide a basis for applying a rational understanding when it comes to managing grasslands. Subsequent management strategies should seek to address invasions by *Sporobolus cryptandrus*, with special focus on its ability to suppress other invasives such as *Bromus tectorum* while avoiding impacts on native species. Using interventions that share both advantages and disadvantages of litter accumulation could be useful to maintain the densities and species diversity in affected grasslands.

General conclusions

The synthesis of the findings in this dissertation emphasises that there is a complex interplay among climate change, biological invasion, and the dynamics of grassland ecosystems in Europe. Presently, alien C4 grasses are established as serious competitor weeds in disturbed and ruderal habitats due to anthropogenic influence and climate alteration. Their competitive advantage, driven by physiological flexibility, herbicide resistance, and invasive traits make them formidable challengers to native flora. While most C4 species are not typically frost-tolerant, some exhibit adaptations that allow them to withstand cooler temperatures to a certain degree, further contributing to their ecological success.

Over the past 14 years, alien C4 grass has become more widespread, with 133 species recorded in 39 European countries. Their richness is highest in regions with high anthropogenic impacts, such as Southern and Western Europe. Climate change enhances this invasion through creating ecological niches, resulting in a dye-back of native C_3 grasses, which may enhance the colonization ability of C4 grass species (Churchill et al., 2022). Our studies about *Sporobolus cryptandrus* affirm that this species is a transformer species with significant impact on steppe grasslands and dry sand areas, particularly in the steppe climatic zones of Eurasia. The results point out that this species is able to build up a persistent seed bank, showing high fecundity and dispersal potential, making its management difficult. The density and diversity of the seeds are high in the top layers and decrease with the depth of the soil. While *Sporobolus cryptandrus* has invasive potential, its interactions with other species, like *Bromus tectorum*, problematic in North America, provide insights into invasion dynamics and possible managed approaches. For instance, the suppression of *B. tectorum* by *S. cryptandrus* suggests that competition between species may influence invasion outcomes. However, the idea of using one non-native to suppress another is highly complex and must be approached with caution to prevent unintended consequences for native species.

Based on these findings, prevention and early intervention strategies presented as management recommendations include species-specific methods to avoid the expansion and establishment of *S. cryptandrus*. Effective strategies include not disturbing the soil, covering hay or grass litter to reduce germination following tussock removal, and natural enemies and classical management techniques that include grazing and mowing. Moreover, the interventions concerned must aim at the overall goal of eradicating invasives while conserving the native species' diversity, and the results did emphasize the interconnection between litter dynamics and seedling growth.

Future research directions for addressing these challenges are therefore crucial. Long-term monitoring and experimental studies are essential to refine management practices and forecast how climate change will affect on grassland invasibility. Other information for an adaptive management strategy may also be provided by studies on decomposition and ecological roles of invasive litter and effects on microorganisms and nutrient dynamics.

The general message from this work is clear: the challenges of climate change and biological invasions combined require a broad, evidence-based approach to grassland conservation. In fact, there is an ecological, biological, and socio-economic integration for effective strategies in safeguarding such ecosystems. Therefore, to reduce the impacts of invasive species like *S. cryptandrus* and preserving the ecological integrity of European grasslands, continued vigilance, research, and adaptive management are essential.

Summary

The dissertation studied the invasion of C4 grasses in European grasslands, focusing on *Sporobolus cryptandrus* in Hungary as a case study. It highlighted how climate change and human activities facilitate the spread of invasive C4 grasses thriving under warmer and drier conditions. The research identified 133 alien C4 grass species in Europe, showing regional differences in species richness, distribution, and invasion status. Southern and Western Europe have the highest number of naturalized and invasive species, while Northern Europe mostly hosts casual species. Through field experiments and statistical analyses, the study reveals that invasive C4 grasses, such as *S. cryptandrus*, alter plant community composition, reduce biodiversity, and impact soil seed banks, favoring their own dominance. It was revealed that the species forms a persistent seed bank, which enables a competitive advantage over native C3 species under warming conditions. The findings highlighted the urgent need for adaptive management strategies to mitigate invasive grass spread, particularly through early detection, ecological restoration, and land-use adjustments. The study contributes valuable insights into invasion dynamics and conservation strategies for European grasslands facing increasing environmental pressures.

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Appendix

Appendix 1.1. The number of casual, naturalised and invasive C4 grass species in each European country (n=39) and in the two islands treated separately (Corsica and the Canary Islands, see Materials and methods). All alien species are shown also for the four European regions of the continent: Northern, Eastern, Southern, and Western.

European regions and countries	Casual	Naturalised	Invasive	All alien species
Northern Europe				**69**
Denmark	19	3	3	25
Estonia	11	2	0	13
Finland	12	1	0	13
Iceland	1	0	0	1
Ireland	13	4	1	18
Latvia	15	2	0	17
Lithuania	19	1	1	21
Norway	22	2	0	24
Sweden	23	3	0	26
United Kingdom	44	13	3	60
Eastern Europe				**81**
Belarus	7	10	0	17
Bulgaria	23	4	0	27
Czech Republic	43	7	4	54
Hungary	16	17	14	47
Moldova	3	2	0	5
Poland	26	6	1	33
Romania	11	5	10	26
Slovakia	38	8	1	47
Ukraine	10	21	1	42

Appendix 1.1. continued

European regions and countries	Casual	Naturalised	Invasive	All alien species
Southern Europe				**96**
Albania	11	5	1	17
Bosnia and Herzegovina	12	1	4	17
Canary Island*	0	2	1	3
Corsica*	0	3	1	4
Croatia	12	9	7	28
Greece	15	11	8	34
Italy	24	30	11	65
Kosovo	11	5	0	16
Macedonia	13	1	1	15
Montenegro	11	6	0	17
Portugal	20	18	2	40
Serbia	12	6	2	20
Slovenia	9	13	2	24
Spain	18	39	12	69
Western Europe				**103**
Austria	35	13	3	51
Belgium	50	13	2	65
France	22	33	9	64
Germany	37	20	1	58
Liechtenstein	8	0	0	8
Luxembourg	1	2	0	3
Netherlands	16	13	0	29
Switzerland	29	8	1	38

Appendix 1.2. Native climatic zones and habitat preferences of alien C4 grass species in Europe. The data covers 133 species, highlighting their origins (tropical, subtropical, temperate) and habitat preferences within European regions. The table is based on an extensive data search, reporting the number of habitats each species occupies and their specific preferences for various habitat categories. Habitat classification follows Chytrý et al. (2020).

Species	**Origin**	**Number of habitat types covered**	**Primary habitat preferences by Chytrý et al. (2020)**
Andropogon gerardi	Temperate	4	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Heaths, scrublands and tundra, Forests
Andropogon virginicus	Temperate	6	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests, Arable, gardens, fallow, Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Aristida adscensionis	Tropical	1	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes)
Axonopus compressus	Tropical	5	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; Arable, gardens, fallow; Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Axonopus fissifolius	Tropical	3	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Bothriochloa bladhii	Tropical	0	No data found

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Bothriochloa ischaemum	Temperate	2	Sparsely vegetated (rocks, caves); -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Bothriochloa pertusa	Tropical	0	No data found
Cenchrus alopecuroides	Temperate	1	Arable, gardens, fallow
Cenchrus americanus	Tropical	0	No data found
Cenchrus biflorus	Tropical	0	No data found
Cenchrus caudatus	Tropical	0	No data found
Cenchrus ciliaris	Subtropical	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Heaths, scrublands and tundra
Cenchrus clandestinus	Tropical	4	Coastal habitats (dunes, shingle, rock/cliffs); -Forests; -Arable, gardens, fallow; -Lawns, trampled vegetation
Cenchrus echinatus	Tropical	1	Lawns, trampled vegetation
Cenchrus flaccidus	Temperate	1	Lawns, trampled vegetation

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Cenchrus longisetus	Tropical	3	Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Cenchrus longispinus	Temperate	5	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Cenchrus orientalis	Subtropical	0	No data found
Cenchrus setaceus	Tropical	6	Coastal habitats (dunes, shingle, rock/cliffs); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Heaths, scrublands and tundra; Arable, gardens, fallow; -Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Cenchrus spinifex	Tropical	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Sparsely vegetated (rocks, caves).
Chloris barbata	Tropical	0	No data found
Chloris divaricata	Tropical	0	No data found

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Chloris gayana	Tropical	5	Wetlands (mires, bogs and fens); -Sparsely vegetated (rocks, caves); -Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Chloris radiata	Tropical	0	No data found
Chloris virgata	Temperate	0	No data found
Coix lacryma-jobi	Tropical	1	Arable, gardens, fallow
Cynodon dactylon	Subtropical	5	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Heaths, scrublands and tundratundra; Forest; Sparsely vegetated (rocks, caves)
Dactyloctenium aegyptium	Tropical	3	Sparsely vegetated (rocks, caves); -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Dichanthelium acuminatum	Temperate	2	Scrubs, heathlands and tundra; -Forests
Dichanthium sericeum	Tropical	0	No data found
Digitaria aequiglumis	Subtropical	0	No data found
Digitaria ciliaris	Tropical	4	Forests; -Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Digitaria debilis	Tropical	2	Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Digitaria ischaemum	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Digitaria radicosa	Tropical	0	No data found
Digitaria sanguinalis	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Digitaria setigera	Tropical	0	No data found
Digitaria violascens	Tropical	0	No data found
Diplachne fusca	Tropical	3	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation
Echinochloa colonum	Tropical	2	Arable, gardens, fallow; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Echinochloa crus-galli	Subtropical	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow
Echinochloa esculenta	Temperate	1	Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Echinochloa frumentacea	Tropical	1	Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Echinochloa muricata	Temperate	2	Arable, gardens, fallow; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Echinochloa oryzicola	Temperate	2	Arable, gardens, fallow; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Echinochloa oryzoides	Temperate	0	No data found
Ehrharta calycina	Subtropical	4	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; Lawns, trampled vegetation
Ehrharta erecta	Subtropical	7	Coastal habitats (dunes, shingle, rock/cliffs); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Scrubs, heathlands and tundra; -Forests; -Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Eleusine coracana	Tropical	0	No data found
Eleusine indica	Tropical	6	Coastal habitats (dunes, shingle, rock/cliffs); -Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eleusine tristachya	Tropical	5	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; -Sparsely vegetated (rocks, caves); -Arable, gardens, fallow; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eragrostis atrovirens	Tropical	0	No data found
Eragrostis barrelieri	Temperate	2	Scrubs, heathlands and tundra; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eragrostis cilianensis	Subtropical	4	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow; -Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eragrostis ciliaris	Tropical	1	Lawns, trampled vegetation

Appendix 1.2. continued.

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Eragrostis curtipedicellata	Temperate	0	No data found
Eragrostis curvula	Tropical	3	Coastal habitats (dunes, shingle, rock/cliffs); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation
Eragrostis elongata	Tropical	0	No data found
Eragrostis lugens	Subtropical	0	No data found
Eragrostis mexicana	Temperate	0	No data found
Eragrostis minor	Subtropical	1	Arable, gardens, fallow
Eragrostis multicaulis	Subtropical	3	Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eragrostis multiflora	Tropical	0	No data found
Eragrostis papposa	Subtropical	1	Lawns, trampled vegetation
Eragrostis parviflora	Tropical	1	Arable, gardens, fallow
Eragrostis pectinacea	Subtropical	3	Wetlands (mires, bogs and fens); -Forests; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Eragrostis pilosa	Temperate	2	Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eragrostis plana	Tropical	0	No data found
Eragrostis schweinfurthii	Tropical	0	No data found
Eragrostis spectabilis	Temperate	1	Arable, gardens, fallow
Eragrostis tef	Tropical	2	Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Eragrostis virescens	Temperate	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation
Eriochloa villosa	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow; -Lawns, trampled vegetation
Heteropogon contortus	Tropical	0	No data found
Hyparrhenia hirta	Tropical	2	Sparsely vegetated (rocks, caves); Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Hyparrhenia rufa	Tropical	0	No data found

Appendix 1.2. Continue

Species	**Origin**	**Number of habitat types covered**	**Primary habitat preferences by Chytrý et al. (2020)**
Megathyrsus maximus	Tropical	0	No data found
Melinis repens	Tropical	0	No data found
Miscanthus sacchariflorus	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; Lawns, trampled vegetation
Miscanthus sinensis	Temperate	2	Arable, gardens, fallow; -Lawns, trampled vegetation
Moorochloa eruciformis	Tropical	1	Arable, gardens, fallow
Muhlenbergia frondosa	Temperate	3	Wetlands (mires, bogs and fens); -Scrubs, heathlands and tundra; -Sparsely vegetated (rocks, caves)
Muhlenbergia schreberi	Temperate	4	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; Sparsely vegetated (rocks, caves); -Lawns, trampled vegetation
Panicum capillare	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Panicum dichotomiflorum	Temperate	2	Arable, gardens, fallow; -Lawns, trampled vegetation

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Panicum miliaceum	Tropical	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Panicum miliaceum subsp. Ruderale	Tropical	1	Arable, gardens, fallow
Panicum philadelphicum	Temperate	0	No data found
Panicum repens	Tropical	3	Wetlands (fens, mires and bogs); Heaths, scrublands and frost plain; -Sparsely vegetated (rocks, caves)
Panicum virgatum	Temperate	2	Wetlands (fens, mires and bogs); Sparsely vegetated (rock/cliffs, scree, caves)
Paspalum dilatatum	Tropical	5	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Forests; Arable, gardens, fallow; Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Paspalum distichum	Tropical	4	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Paspalum notatum	Tropical	0	No data found
Paspalum urvillei	Subtropical	0	No data found

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Paspalum vaginatum	Tropical	3	Coastal habitats (dunes, shingle, rock/cliffs); -Wetlands (mires, bogs and fens); -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Phalaris paradoxa	Subtropical	1	Arable, gardens, fallow
Phyllostachys aurea	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Saccharum officinarum	Tropical	1	Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Saccharum spontaneum	Tropical	2	Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Schizachyrium scoparium	Temperate	0	No data found
Setaria adhaerens	Tropical	2	Arable, gardens, fallow; -Lawns, trampled vegetation
Setaria faberi	Temperate	1	Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Setaria globulifera	Subtropical	0	No data found

Appendix 1.2. Continue

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Setaria italica	Temperate	3	Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Setaria parviflora	Temperate	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation
Setaria pumila	Subtropical	3	Forests; -Lawns, trampled vegetation; Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Setaria verticillata	Subtropical	1	Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Setaria viridis	Temperate	2	Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Sorghum bicolor	Tropical	3	Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Sorghum drummondii	Tropical	0	No data found
Sorghum halepense	Subtropical	3	Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Sporobolus ×townsendii	Temperate	1	Coastal habitats (dunes, shingle, rock/cliffs)

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Sporobolus africanus	Tropical	1	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes)
Sporobolus alterniflorus	Temperate	2	Wetlands (mires, bogs and fens); -Lawns, trampled vegetation
Sporobolus anglicus	Temperate	1	Coastal habitats (dunes, shingle, rock/cliffs)
Sporobolus copei	Subtropical	0	No data found
Sporobolus cryptandrus	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Sporobolus elongatus	Subtropical	0	No data found
Sporobolus indicus	Tropical	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); -Lawns, trampled vegetation
Sporobolus michauxianus	Temperate	0	No data found
Sporobolus montevidensis	Temperate	3	Coastal habitats (dunes, shingle, rock/cliffs); -Wetlands (mires, bogs and fens); -Sparsely vegetated (rocks, caves)

Appendix 1.2. continued

Species	**Origin**	**Number of habitat types covered**	**Primary habitat preferences by Chytrý et al. (2020)**
Sporobolus neglectus	Temperate	2	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation
Sporobolus pumilus	Temperate	2	Coastal habitats (dunes, shingle, rock/cliffs); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes)
Sporobolus pyramidalis	Tropical	0	No data found
Sporobolus vaginiflorus	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Sporobolus versicolor	Temperate	2	Coastal habitats (dunes, shingle, rock/cliffs); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes)
Stenotaphrum secundatum	Tropical	4	Wetlands (mires, bogs and fens); Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Arable, gardens, fallow; -Lawns, trampled vegetation
Tragus berteronianus	Tropical	1	Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).

Appendix 1.2. continued

Species	Origin	Number of habitat types covered	Primary habitat preferences by Chytrý et al. (2020)
Tragus racemosus	Temperate	3	Grasslands (dry, mesic and wet grasslands; alpine and subalpine grasslands, forest edges and open glades; dense herbaceous vegetation; barely forested grasslands, non-coastal saline steppes); Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).
Tripidium ravennae	Subtropical	3	Coastal habitats (dunes, shingle, rock/cliffs); -Wetlands (mires, bogs and fens); -Scrubs, heathlands and tundra
Urochloa mutica	Subtropical	0	No data found
Zea mays	Tropical	3	Arable, gardens, fallow; -Lawns, trampled vegetation; -Industrial, artificial habitats (buildings of settlements, transport networks, industrial sites, waste deposits).

Appendix 1.3. Widely distributed species in Europe and rank sum data for selected alien C4 grass species, indicating widespread and high-risk status across Europe and within each European region.

Descriptions of Abbreviations:
Eur Dist (NoC): European Distribution (Number of Countries)
RS (IR): Rank Sum (Invasion Risk)
RS: Rank Sum
MFR: Most Frequent Rank
NoC: Number of Countries
Alien status values: Casual = 1; Naturalised = 2; Invasive =

Species	Eur Dist (NoC)	RS (IR)	Western Europe			Northern Europe			Southern Europe			Eastern Europe		
			RS	MFR	NoC	RS	MFR	NoC	RS	MFR	NoC	RS	MFR	NoC
Andropogon gerardi	1	1	1	1	1									
Andropogon virginicus	1	3	3	3	1									
Aristida adscensionis	2	3	1	1	1				2	2	1			
Axonopus compressus	1	1							1	1	1			
Axonopus fissifolius	3	3	1	1	1				2	1	2			
Bothriochloa bladhii	1	2										2	2	1
Bothriochloa ischaemum	2	2							2	2	2			
Bothriochloa pertusa	2	2				1	1	1	1	1	1			
Cenchrus alopecuroides	6	6	1	1	1				1	1	1	4	1	4
Cenchrus americanus	2	3							1	1	1	2	2	1
Cenchrus biflorus	1	1							1	1	1			
Cenchrus caudatus	2	2	1	1	1	1	1	1						
Cenchrus ciliaris	5	6	1	1	1	1	1	1	3	1_2	2	1	1	1
Cenchrus clandestinus	3	3							3	1	3			
Cenchrus echinatus	7	7	3	1	3	1	1	1	2	1	2	1	1	1

Species	Eur Dist (NoC)	RS (IR)	Western Europe			Northern Europe			Southern Europe			Eastern Europe		
			RS	MFR	NoC	RS	MFR	NoC	RS	MFR	NoC	RS	MFR	NoC
Cenchrus flaccidus	3	3	1	1	1				2	1	2			
Cenchrus longisetus	7	10	1	1	1	1	1	1	5	1	4	3	3	1
Cenchrus longispinus	16	31	4	1_3	2	1	1	1	18	1	10	8	3	3
Cenchrus orientalis	3	3				2	1	2	1	1	1			
Cenchrus setaceus	9	19	3	3	1	2	1	2	13	3	5	1	1	1
Cenchrus spinifex	16	27	2	1	2	1	1	1	15	2	8	9	1_2	5
Chloris barbata	2	3										3	1_2	2
Chloris divaricata	2	2										2	1	2
Chloris gayana	2	5							5	2_3	2			
Chloris radiata	1	1										1	1	1
Chloris virgata	4	5	1	1	1				2	2	1	2	1	2
Coix lacryma-jobi	7	9	3	1	3				5	2	3	1	1	1
Cynodon dactylon	23	39	13	2	7	3	1	3	12	1_3	6	11	1	7
Dactyloctenium aegyptium	7	11	1	1	1				7	3	3	3	1	3
Dichanthelium acuminatum	6	8	5	1	4				2	2	1	1	1	1
Dichanthium sericeum	2	2										2	1	2
Digitaria aequiglumis	3	4	4	1	3									
Digitaria ciliaris	27	35	5	1	5	10	1	9	13	2	8	7	1	5
Digitaria debilis	2	3	1	1	1				2	2	1			
Digitaria ischaemum	19	30	4	1	4	14	2	9	2	2	1	10	2	5
Digitaria radicosa	2	2	1	1	1				1	1	1			
Digitaria sanguinalis	21	29	5	1	5	10	1	9				14	1_3	7
Digitaria setigera	1	1	1	1	1									
Digitaria violascens	4	7	2	1	1				5	2	3			
Diplachne fusca	13	19	5	1	3	2	1	2	8	1_3	4	4	1	4
Echinochloa colonum	24	30	5	1	4	4	1	4	14	1	10	7	1	6
Echinochloa crus-galli	20	35	7	1	5	13	1	8	3	3	1	12	1_2_3	6
Echinochloa esculenta	6	7	2	1	2	1	1	1				4	1	3

Species	**Eur Dist (NoC)**	**RS (IR)**	**Eestern Europe**			**Northern Europe**			**Southern Europe**			**Eastern Europe**		
			RS	**MFR**	**NoC**	**RS**	**MFR**	**NoC**	**RS**	**MFR**	**NoC**	**RS**	**MFR**	**NoC**
Echinochloa frumentacea	6	7	2	1	2	1	1	1				4	1	3
Echinochloa muricata	14	21	9	1_2	6	2	1	2	2	2	1	8	1	5
Echinochloa oryzicola	6	8	4	1	3				4	1	3			
Echinochloa oryzoides	12	18	2	2	1				8	2	5	8	1	6
Ehrharta calycina	2	4							4	2	2			
Ehrharta erecta	6	9	2	1	2	1	1	1	6	2	3			
Eleusine coracana	5	5	1	1	1				2	1	2	2	1	2
Eleusine indica	29	61	12	1	6	7	1	4	28	2	12	14	1_3	7
Eleusine tristachya	13	18	4	1	3				8	2	5	6	1	5
Eragrostis atrovirens	6	6	3	1	3	2	1	2	1	1	1			
Eragrostis barrelieri	9	10	3	1	3	2	1	2	3	1_2	2	2	1	2
Eragrostis cilianensis	19	24	7	1	5	8	1	8				9	1_2	6
Eragrostis ciliaris	2	2	2	1	2									
Eragrostis curtipedicellata	1	1	1	1	1									
Eragrostis curvula	19	25	8	2	5	2	1	1	13	1	11	2	1	2
Eragrostis elongata	3	3	2	1	2	1	1	1						
Eragrostis lugens	4	4	2	1	2	1	1	1				1	1	1
Eragrostis mexicana	14	15	7	1	6	2	1	2	2	1	2	4	1	4
Eragrostis minor	16	26	8	2	4	11	1	8				7	2	4
Eragrostis multicaulis	14	19	9	1_2	6	1	1	1	1	1	1	8	1	6
Eragrostis multiflora	1	1										1	1	1
Eragrostis papposa	2	2	2	1	2									
Eragrostis parviflora	7	9	4	1	4	1	1	1				4	2	2
Eragrostis pectinacea	14	20	6	1	5	1	1	1	9	2	5	4	1	3
Eragrostis pilosa	17	27	7	2	4	7	1	6				13	2	7
Eragrostis plana	5	5	4	1	4	1	1	1						
Eragrostis schweinfurthii	2	3				1	1	1				2	2	1
Eragrostis spectabilis	1	2										2	2	1

Species	**Eur Dist (NoC)**	**RS (IR)**	**Eestern Europe**			**Northern Europe**			**Southern Europe**			**Eastern Europe**		
			RS	**MFR**	**NoC**	**RS**	**MFR**	**NoC**	**RS**	**MFR**	**NoC**	**RS**	**MFR**	**NoC**
Eragrostis tef	10	10	5	1	5	1	1	1	1	1	1	3	1	3
Eragrostis virescens	14	17	6	1	5	1	1	1	5	1	4	5	1	4
Eriochloa villosa	8	14	3	1_2	2	1	1	1				10	1	5
Heteropogon contortus	1	2							2	2	1			
Hyparrhenia hirta	3	4							2	2	1	2	1	2
Hyparrhenia rufa	1	2							2	2	1			
Megathyrsus maximus	4	4							2	1	2	2	1	2
Melinis repens	5	8	4	2	2	1	1	1	3	1_2	2			
Miscanthus sacchariflorus	7	10	5	2	3	1	1	1				4	1	3
Miscanthus sinensis	12	15	5	1	4	4	1	4	4	2	2	2	1	2
Moorochloa eruciformis	5	7	2	1	1				3	1_2	2	2	1	2
Muhlenbergia frondosa	1	2							2	2	1			
Muhlenbergia schreberi	5	10	2	1	1				8	2	4			
Panicum capillare	33	59	12	2	6	8	1	8	23	2	11	16	2	8
Panicum dichotomiflorum	24	44	12	2	6	2	2	1	15	1_2	10	15	2	7
Panicum miliaceum	38	52	11	1	8	9	1	9	15	1	12	17	2	9
Panicum miliaceum subsp. Ruderale	15	24	9	2	5	2	1	2	3	1_2	2	10	1	6
Panicum philadelphicum	7	8	2	1	2				4	1	3	2	1	2
Panicum repens	4	5	1	1	1				4	1	3			
Panicum virgatum	5	6	2	1	2	1	1	1	3	1_2	2			
Paspalum dilatatum	17	26	6	1	5	2	1	2	17	2	9	1	1	1
Paspalum distichum	18	37	5	1	3	2	2	1	24	3	11	6	1_2_3	3
Paspalum notatum	5	7	2	1	2				5	2	3			
Paspalum urvillei	3	5							5	2	3			
Paspalum vaginatum	4	8	2	2	1				6	2	3			
Phalaris paradoxa	17	21	5	1	5	10	1	7				6	1	5
Phyllostachys aurea	4	8	3		1	1	1	1	4	1_3	2			

Species	**Eur Dist (NoC)**	**RS (IR)**	**Eestern Europe**			**Northern Europe**			**Southern Europe**			**Eastern Europe**		
			RS	**MFR**	**NoC**	**RS**	**MFR**	**NoC**	**RS**	**MFR**	**NoC**	**RS**	**MFR**	**NoC**
Saccharum officinarum	2	2							2	1	2			
Saccharum spontaneum	4	6	2	2	1				4	1	3			
Schizachyrium scoparium	1	1										1	1	1
Setaria adhaerens	16	21	2	1	2	2	1	2	15	1	10	2	1	2
Setaria faberi	25	39	12	2	7	2	1	2	14	1	10	11	2	6
Setaria globulifera	1	1										1	1	1
Setaria italica	35	43	9	1	7	9	1	9	14	1	10	11	1	9
Setaria parviflora	11	19	6	1	4	3	1	3	10	2_3	4			
Setaria pumila	20	27	6	1_2	4	10	1	8	3	1_2	2	8	1	6
Setaria verticillata	26	39	10	2	6	8	1	8	10	2_3	4	11	1	8
Setaria viridis	18	31	3	1_2	2	12	1_2	8	5	2_3	2	11	2	6
Sorghum bicolor	29	35	7	1	6	6	1	6	14	1	10	8	1	7
Sorghum drummondii	13	15	3	1	3				3	1	3	9	1	7
Sorghum halepense	34	57	13	2	6	7	1	7	26	2	12	11	2	9
Sporobolus ×townsendii	9	16	7	2	4	6	2	3	3	1_2	2			
Sporobolus africanus	2	2	1	1	1	1	1	1						
Sporobolus alterniflorus	4	11	3	3	1	6	3	2	2	2	1			
Sporobolus anglicus	8	19	9	3	4	10	3	4						
Sporobolus copei	1	2							2	2	1			
Sporobolus cryptandrus	13	17	6	1	5	1	1	1	3	1_2	2	7	1	5
Sporobolus elongatus	3	3	1	1	1							2	1	2
Sporobolus indicus	19	41	11	1	6				25	3	10	5	2	3
Sporobolus michauxianus	4	6	1	1	1	4	2	2	1	1	1			
Sporobolus montevidensis	2	4							4	1_3	2			
Sporobolus neglectus	8	15	7	2	4				6	2	3	2	2	1
Sporobolus pumilus	4	6	1	1	1	2	2	1	3	1_2	2			
Sporobolus pyramidalis	1	3										3	3	1
Sporobolus vaginiflorus	14	19	5	1	4				11	1	8	3	1_2	2

Species	Eur Dist (NoC)	RS (IR)	Eestern Europe			Northern Europe			Southern Europe			Eastern Europe		
			RS	MFR	NoC	RS	MFR	NoC	RS	MFR	NoC	RS	MFR	NoC
Sporobolus versicolor	4	8	2	2	1				6	2	3			
Stenotaphrum secundatum	9	13	3	1_2	2	1	1	1	8	2	5	1	1	1
Tragus berteronianus	2	2	1	1	1	1	1	1						
Tragus racemosus	11	20	7	1	4				5	2_3	2	8	1	5
Tripidium ravennae	1	1										1	1	1
Urochloa mutica	2	2	1	1	1				1	1	1			
Zea mays	34	38	8	1	7	7	1	7	14	1	12	9	1	8

Appendix 1.4. Detrended Correspondence Analysis of species-pool similarity and dissimilarity of widespread alien C4 grass species across four European regions. The DCA analysis highlighted the Southern European region as the most distinct in terms of alien C4 grass species composition compared to other regions. In contrast, the species pool and alien statuses of the species are highly similar in Western, Eastern and even Northern European countries, with only a few exceptional countries (e.g., Moldova, Liechtenstein, Luxembourg, and France). Both Eastern and Western European countries form a compact cluster, sharing numerous species with similar statuses. For example, central clusters of countries include commonly shared species such as *Setaria pumila*, *S. verticillata*, and *S. viridis*. Description: Composition of country wise C4 grass flora of Europe. DCA ordination where the 30 most widespread alien C4 grass species are shown. Notations: northern countries in blue (DNK Denmark); eastern countries in red (BLR Belarus); southern countries in orange (ALB Albania); and western countries in green (AUT Austria). Species abbreviations are in black: CENCLONG *Cenchrus longisetus*,