Short thesis for the degree of Doctor of Philosophy (PhD)

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

by Díaz Cando Patricia Elizabeth

Supervisor:
Prof. Dr. Török Péter
Scientific advisor
MTA Doctor

UNIVERSITY OF DEBRECEN
Juhász Nagy Pál Doctoral school
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Introduction

Grasslands are among the most diverse and ecologically important ecosystems, covering 40% of the Earth's terrestrial area (Gibson & Newman, 2019). They host a unique flora, fauna, and provide vital ecosystem services like carbon storage, soil stabilization, and water regulation, and they also support several agriculture and pastoral activities (Gibson & Newman, 2019; Kovacsics-Vári et al., 2023). However, these ecosystems are increasingly threatened by the invasion of alien plant species, which reduce native biodiversity, alter ecosystem functions, and challenge conservation efforts. Grasslands, characterised 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), and land - uses changes (Hopkins, & Del Prado 2007). Such disturbances create niches that alien plants can exploit, often outcompeting native species.

Invasions of alien plants, especially C4 grasses, are now considered one of the most critical global ecological processes (Kueffer, 2017). C4 grasses possess physiological traits that confer competitive advantages under conditions of high

temperature, light intensity, and low water availability, allowing them to dominate and transform the structure of invaded ecosystems (Chuine et al., 2012; Kumar et al., 2017; Boretti & Florentine, 2019). These invasive species such as *Sporobolus cryptandrus*, take advantage of disturbances like grazing, land conversion and recently climate change to colonize and alter native vegetation in grassland ecosystems (Török et al., 2021, 2024). These conditions frequently favour invasive species over native ones (Finch et al., 2021).

According to the reports of the European Environment Agency (2021) and IPCC (2023), rising temperatures, precipitation pattern changes, and increased probability of extreme weather are expected. These factors provide invasive plants opportunities to establish and spread (Boretti & Florentine, 2019; Kumar et al., 2017; Chuine et al., 2012). C4 grasses, adapted to high temperatures and arid conditions, benefit disproportionately under such circumstances (Kumar et al., 2017). They extend their geographical range into temperate and high-altitude grasslands, altering ecosystem dynamics and displacing native C3 grasses (Sage & Kubien, 2003; Kumar et al., 2017; Boretti & Florentine, 2019).

The combination of plant invasion and climate change poses complex challenges for grassland ecosystems (Buckland et al., 2001). Biodiversity loss, disrupted food webs, diminished

ecosystem services, and altered fire regimes are among the consequences (Buckland et al., 2001; Dogra et al., 2010; Raj & Singh, 2020; Bardgett et al., 2021). The dominance of invasive species like *Sporobolus cryptandrus* further compromises the ecological resilience of grasslands, threatening their capacity to support native species and provide critical ecosystem functions (Török et al., 2021, 2024).

The aim of the research presented in my dissertation is to enhance understanding of the invasion ecology of alien C4 grasses in European grasslands, with a specific emphasis on *Sporobolus cryptandrus*, an invasive C4 grass species observed in Hungarian grasslands. Through a dual approach, the work contributes to addressing the challenges posed by invasive C4 grasses while also highlighting the need for holistic strategies to enhance the resilience of European ecosystems to increasing environmental pressures.

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 and has been accepted 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 ultimate 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 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 negatively 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.

Methods and materials

Standard systematic literature review

The approach used in this systematic review was to search for the available literature to generate an updated list of the alien C4 grass species in Europe. Online databases such as Google Scholar and ISI Web of Science were employed for the literature search, using a list of keywords which refer to the alien status, C4 grass species, and European countries. More information on distribution and climate was collected from other sources including EURO+MED PlantBase and databases likeGBIF - Global Biodiversity Information Facility. Alien species were grouped according to their establishment and spread characteristics, following the framework of Richardson et al. (2000) to assign status. The species were grouped according to the country and region of distribution with the habitat preference categorized in terms of the EUNIS Habitat Classification System.

Seed bank study

Information on *Sporobolus cryptandrus* was collected through a combination of literature reviews, morphological observations and data on its geographical distribution and its seed bank. This C4 perennial grass species is native to North America but has been naturalized in other parts of the world such as some parts in Europe, Africa, and Australia. that the species is reported to prefer sandy, disturbed soil, it has small seeds that are both light and adhesive, which enhance its dispersal. The study sites Debrecen and Kiskunság in Hungary were chosen to represent previously documented occurrences of *Sporobolus cryptandrus*.

Both regions have a continental climate, but they differ in temperature and precipitation. Vegetation surveys were conducted on different types of grasslands and other disturbed areas in Debrecen and Kiskunság, recording habitat type, the population size of the species, and degradation level. Species cover was determined on the 40 plots for each site. Soil seed banks were analysed in Chapter 2 and 3 using the same techniques: soil coring and seed germination tests under the controlled environmental conditions in a greenhouse. Soil samples were collected from five cover categories with increasing cover of *S. cryptandrus* and required sieving to

decrease sample volume. Chapter 2 was an 11-week experiment and Chapter 3 took 32 weeks with one break that simulate a summer drought to break seed dormancy. Seedlings were classified 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).

Germination experiment

To describe the germination of *Sporobolus cryptandrus* a greenhouse experiment was carried out with a full factorial design and nine treatments which were replicated five times making the total number of pots to be 45. The applied treatments involved the effect ofseed burial depth (0, 0.5 and 1cm) and litter depth (0, 150, 300g/m²) on germination. The experimental design was based on the approach developed by Sonkoly et al. 2020. The *S. cryptandrus* seeds, collected in 2019, were stored in dry conditions at room temperature (20–25ºC). 25 seeds were distributed into each pot, totalling in 1,125 seeds. The seeds were covered with sterilized potting soil and then *Festuca rupicola* litter ó. Germination was monitored over ten weeks

(March 26–May 27, 2020). At the end of the experiment, seedlings that emerged above the litter were counted to determine successful germination rates, while those that did not survive were included in survival rate calculations.

Litter experiment

Seeds and litter for the experiment were collected on the Great Hungarian Plain in the summer of 2021:seeds of ten species: *Sporobolus cryptandrus* the invasive species, and nine species comprising the native sand grassland community; litter of *S. cryptandrus*, *Festuca vaginata* and *Corynephorus canescens* Seeds used in the study were cleaned and stored in darkness at room temperature and then used first for a seed viability test, and finally for the experiment. Litter treatments were *Sporobolus cryptandrus* leaf litter, referred to as "*Sporobolus* litter" and a mixture of *Festuca vaginata* and *Corynephorus canescens* leaves, called "native litter", both collected from semi-natural grasslands. A control treatment was also applied, where no litter was spread on the surface of the pots. Five replicates of each of the three treatments were conducted using 10 plant species and 15 pots of each species (150 pots in total) in this greenhouse experiment to assess the impact of litter on germination rates of plants. Each pot (9 × 9

cm) contained 300 g of sterilized potting soil and 25 seeds sown before the start of the litter treatment. The pots were placed in a greenhouse in the Botanical Garden, frequently randomized and watered daily. This experiment was conducted over five weeks from April 2022. At the end, seedlings that emerged above the litter were counted, and shoot length from seven randomly selected seedlings per pot was measured. Aboveground biomass was also weighed for each seedling per pot to assess growth. Fatal germination events were not included in the counts.

Statistical analyses

In the chapter 1, some of the analysis involved calculations of species densities, as well as the identification of the climatic origins of the species. Additionally, linear regression was performed to analyse the significance on species status across regions. To assess community similarity among the regions, a Detrended Correspondence Analysis was employed, and we also compare our list species with previous list of species, to see how the invasion changes over the time. Statistical analyses were conducted in R, with visualizations to present the findings.

Data analysis for seed bank and germination (Chapter 2 and 3) involved assessing vegetation and soil seed bank dynamics, seedling emergence, and growth under various treatments and conditions. For vegetation as well as soil seed bank diversity species richness (S), Shannon Wiener diversity index (H), and Pielou's evenness index (E) were calculated, excluding the *Sporobolus cryptandrus*. Analysis of variance using generalized linear mixed models tested the impact of *S. cryptandrus* cover and depth of sampling on diversity, density and proportional abundance, respectively, with site as a random factor. Two-way analysis of variance was used to analyse litter cover, burial depth's influence on seedling emergence and survival (Chapter 2), and diversity and density of soil seed bank across sites (Chapter 3). PCA and DCA ordinations inferred change and similarity in vegetation and seed bank structure.

For the litter experiment (Chapter 4), the one-way analysis of varaince (ANOVAs) and Tukey's tests were used to compare the effects of different litters (*Sporobolus* litter, native litter, and no litter) on germination rate, seedling growth and dry weight. Shapiro tests and histograms were used to assess whether the model residuals followed a normal distribution, while Q-Q plots were used to check homoscedasticity of variance. If the model did not meet these assumptions, logarithmic or square root transformations were applied. When

transformation did not sufficiently improve model fit, the non-parametric Kruskal-Wallis test and Dunn's test with Bonferroni correction for post hoc comparisons were used. Combined analyses standardized germination metrics as percentages of control values to account for species identity effects. Individual species responses to litter treatments were examined separately for germination rate, seedling length, and dry weight.

New scientific results

Standard systematic literature review

- Our study revealed a rising invasion of C4 grass in Europe. We identified 133 alien C4 grass species across the continent, with the most species found in Western and Southern Europe.
- We found a high regional variation in the alien status of the species, with more invasive ones in Southern Europe especially on agricultural area and in semi-natural vegetation with species like *Sorghum halepense* or *Sporobolus indicus*. Among the studies countries, Hungary had the highest number of alien species with an invasive status. Moreover, Northern and Eastern Europe had fewer species, mostly with casual status.
- We identified 14 species as high-risk, including *Eleusine indica, Panicum capillare, Sorghum halepense and Setaria italica.*
- We detected that from 2006 to 2020-year, 71 new species were registered, from which 25 species are native to some regions of Europe but now listed as aliens in some other European countries.

Seed bank studies

- We revelated that the spread of *Sporobolus cryptandrus* affects both the vegetation and seed banks, with varying impacts on different plant species present in the community. species-specific ways.
- We found that as *Sporobolus cryptandrus* cover increases across the sites, vegetation homogenization intensifies, negatively impacting most other plant species. At higher cover levels, S. *cryptandrus* competes with other species for light and space, leading to a reduction in biodiversity.
- In our first seed bank study revealed that *S. cryptandrus* forms a persistent seed bank, although its density is low in deeper soil layers. This suggest that the species is still in the early stages of establishment. Additionally, we observed that seed bank density in the upper layers increases with *S. cryptandrus* cover, indicating ongoing seed input and potential for further spread.
- We found that the composition and density of soil seed banks change more slowly than aboveground vegetation.
- We observed that the density and diversity of soil seed banks were strongly site-dependent, with the highest seed bank density observed in a degraded grassland site. Although, we

found densities exceeding tens of thousands of seeds per square meter in some sites.

- We confirmed in this study that *Sporobolus* seed bank density is positively correlated with its cover; where the cover of *S. cryptandrus* is high, its seed bank density was also high. However, the diversity and density of soil seed banks decreased with increasing sampling depth, which is consistent with previous studies.

- We detected viables seeds of *Sporobolus* even in areas with no *Sporobolus* cover, indicating that the species forms a persistent seed bank, and spreading ability.

- Our studies highlighted the importance of early management intervention to provide an effective suppress of *Sporobolus cryptandrus* and prevent its further spread while minimizing its impact on native species.

Germination experiment

- We detected that the germination and seedling survival of *Sporobolus* are affected by both litter and soil cover, but these two factors did not interact with each other.
- We found that the *Sporobolus* germination was less successful under high litter cover over soil burial, although some seedlings germinated even under these conditions.
- We also detected that *Sporobolus cryptandrus* has high viability even after extended dry storage, suggesting that the seeds can survive long periods without significant loss of their viability.

Litter experiment

- We found that litter treatment had a significant effect on the seed germination and seedling establishment; both native and *Sporobolus* litter negatively affected the germination of the studied species compared to no litter treatment, indicating a general inhibitory effect rather than a species-specific response.
- We found that *Sporobolus* litter inhibited the germination of *Bromus tectorum* but had a similar effect to native litter on most of the other studied species. Additionally, physical barriers created by *Sporobolus* litter appeared to play

a more significant role in suppressing germination than any potential allelopathic effects.

- We discovered that there is an inhibitory effect of *Sporobolus* litter on the germination of *Bromus tectorum*. This offers a great opportunity for developing natural suppression strategies for invasive stands of *Bromus tectorum* in North American prairie ecosystems where *Sporobolus cryptandrus* is native.

- Additionally, we noticed that both *Sporobolus* and native litter influence seedling development by affecting elongation, biomass allocation, and germination rates, highlighting the need for species-specific conservation strategies.

Conclusions and outlook

We emphasise that there is a complex interplay among climate change, biological invasion, and the dynamics of grassland ecosystems in Europe, while recognizing that the role of climate change in fostering the invasion of C4 species remains uncertain and requires further investigation. Currently, alien C4 grasses are considered as strong competitor species in disturbed and ruderal habitats due to anthropogenic influence and climate change.

From 2006 to 2020, alien C4 grasses have become more abundant, 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 dieback of native C3 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 high impact on steppe grasslands and dry sand areas, especially within the steppe climatic zones of Eurasia. The results point out that this species is a persistent seed bank builder showing high fecundity and dispersal potential, making its management difficult. Seed

density and species richness of *Sporobolus cryptandrus* are higher in the top layers and decrease with the depth of the soil. While the species has invasive potential, interactions with other species, like *Bromus tectorum*, which is invasive in the native range of S. cryptandrus, indicate possible ways in which invasion dynamics could be managed based on ecological interactions between invaders and native species. For instance, the suppression of *B. tectorum* by *S. cryptandrus* points toward the use of native species to control invasive one. Such strategies should be approached very carefully to avoid accidental effects on native species.

Based on these findings, we recommended prevention and early intervention strategies that include species-specific management methods to limit the expansion and establishment of *S. cryptandrus*. Effective strategies include minimizing soil disturbance, covering with hay or grass litter to reduce germination after removal, and using biological control methods, like natural enemies alongside traditional techniques like 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 effects 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 better understand the factors influencing the invasion of *Sporobolus cryptandrus*, including its response to climate change and its impact on grassland ecosystems. 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 interconnected threats of climate change and biological invasions require a broad, evidence-based approach to grassland conservation. In fact, there is needed to integrate ecological, biological, and socio-economic consideration for effective strategies in safeguarding such ecosystems. Therefore, in mitigating the impacts of invasive species like *S. cryptandrus* and preserving the ecological integrity of European grasslands, continued vigilance, research, and adaptive management are essential.

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List of publications related to the dissertation

Foreign language scientific articles in international journals (3)

1. **Díaz Cando, P. E.**, Fenesi, A., Sonkoly, J., Perera, P. C. D., Török, P.: Enemy behind the gates?: Predicted climate change and land-use intensification likely speed up C4 grass invasions in Europe.
   J. Veg. Sci. "Accepted by Publisher", 2025. ISSN: 1100-9233.
   IF: 2.2 (2023)

2. Török, P., Espinoza-Ami, F. D., Tóth, K., **Díaz Cando, P. E.**, Guallichico, S. L. R., Buday, A., Hábenczyus, A. A., Törő-Szijgyártó, V., Kovacsics-Vári, G., Tölgyesi, C., Tóthmérész, B., Sonkoly, J.: Accumulated soil seed bank of the invasive sand dropseed (Sporobolus cryptandrus) poses a challenge for its suppression.
   Land Degrad. Dev. 35 (13), 4105-4120, 2024. ISSN: 1085-3278.
   DOI: http://dx.doi.org/10.1002/ldr.5208
   IF: 3.6 (2023)

3. Török, P., Schmidt, D., Bátori, Z., Aradi, E., Kelemen, A., Hábenczyus, A. A., **Díaz Cando, P. E.**, Tölgyesi, C., Pál, R. W., Balogh, N., Tóth, E., Matus, G., Táborská, J., Sramkó, G., Laczkó, L., Jordán, S., Buday, A., Kovacsics-Vári, G., Sonkoly, J.: Invasion of the North American sand dropseed (Sporobolus cryptandrus) - A new pest in Eurasian sand areas?
   Glob. Ecol. Conserv. 32, 1 -15, 2021. ISSN: 2351-9894.
   DOI: http://dx.doi.org/10.1016/j.gecco.2021.e01942
   IF: 3.969

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List of other publications

Foreign language scientific articles in international journals (4)

4. Buday, A., Sonkoly, J., Molnár, A., Tóth, K., Törő-Szijgyártó, V., Madar, S., Károlyi, E., **Díaz Cando, P. E.**, Kovacsics-Vári, G., Tóthmérész, B., Török, P.: Grime's ecological strategies reveal contrasting patterns in alkaline and loess grasslands.
Glob. Ecol. Conserv. 54, 1-13, 2024. ISSN: 2351-9894.
DOI: http://dx.doi.org/10.1016/j.gecco.2024.e03132
IF: 3.5 (2023)

5. Kovacsics-Vári, G., Sonkoly, J., Tóth, K., Buday, A., **Díaz Cando, P. E.**, Törő-Szijgyártó, V., Balogh, N., Guallichico-Suntaxi, L. R., Espinoza-Ami, F. D., Matus, G., Tóthmérész, B., Török, P.: High species richness of sheep-grazed sand pastures is driven by disturbance-tolerant and weedy short-lived species.
Ecol. Evol. 14 (9), 1-12, 2024. ISSN: 2045-7758.
DOI: http://dx.doi.org/10.1002/ece3.70282
IF: 2.3 (2023)

6. Kovacsics-Vári, G., Sonkoly, J., Tóth, K., Buday, A., **Díaz Cando, P. E.**, Törő-Szijgyártó, V., Balogh, N., Suntaxi Guallichico, R. L., Espinoza-Ami, F. D., Demeter, L., Tóthmérész, B., Török, P.: Intensity-dependent effects of cattle and sheep grazing in sand grasslands - Does livestock type really matter?
Appl. Veg. Sci. 26 (2), 1-14, 2023. ISSN: 1402-2001.
DOI: http://dx.doi.org/10.1111/avsc.12727
IF: 2

7. Törő-Szijgyártó, V., Balogh, N., Henn, T., Buday, A., Sonkoly, J., Takács, A., Kovacsics-Vári, G., **Díaz Cando, P. E.**, Molnár, V. A., Matus, G., Teleki, B., Süveges, K., Lukács, B. A., Lovas-Kiss, Á., Tóthmérész, B., Tóth, E., Tóth, K., Török, P.: New thousand-seed weight dataset for plant species of Central Europe.
Data in Brief. 48, 1-5, 2023. EISSN: 2352-3409.
DOI: http://dx.doi.org/10.1016/j.dib.2023.109081
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References

Bardgett, R. D., Bullock, J. M., Lavorel, S., et al. 2021. Combatting Global Grassland Degradation. *Nature Reviews Earth and Environment* 2: 720–735.

Blair, J., Nippert, J., and Briggs, J. 2014. Grassland Ecology. *Ecology and the Environment* 14: 389–423.

Boretti, A., and Florentine, S. 2019. Atmospheric CO2 Concentration and Other Limiting Factors in the Growth of C3 and C4 Plants. *Plants* 8: 931–942.

Buckland, S. M., Thompson, K., Hodgson, J. G., and Grime, J. P. 2001. Grassland invasions: effects of manipulations of climate and management. *Journal of Applied Ecology* 38: 301–309.

Burai, P., Deák, B., Valkó, O., and Tomor, T. 2015. Classification of herbaceous vegetation using airborne hyperspectral imagery. *Remote Sensing* 7: 2046–2066.

Chuine, I., Morin, X., Sonié, L., et al. 2012. Climate change might increase the invasion potential of the alien C4 grass *Setaria parviflora* (Poaceae) in the Mediterranean Basin. *Diversity and Distributions* 18: 661–672.

Churchill, A. C., Zhang, H., Fuller, K. J., et al. 2022. Pastures and climate extremes: impacts of cool season warming and drought on the productivity of key pasture species in a field experiment. *Frontiers in Plant Science* 13: 836968.

Dogra, K. S., Sood, S. K., Dobhal, P. K., and Sharma, S. 2010. Alien plant invasion and their impact on indigenous species diversity at global scale: A review. *Journal of Ecology and the Natural Environment* 2: 175–186.

European Environment Agency. 2021. What will the future bring when it comes to climate hazards? Overview — European Environment Agency. 1–7. Retrieved from https://www.eea.europa.eu/publications/europes–

changing–climate–hazards–1/what–will–the–future–bring

Finch, D. M., Butler, J. L., Runyon, J. B., et al. 2021. Effects of climate change on invasive species. In Invasive species in forests and rangelands of the United States: A comprehensive science synthesis for the United States forest sector, 57–83. Springer Nature Switzerland AG.

Gibson, D. J., and Newman, J. A. 2019. Grasslands and climate change, 3–19. Cambridge University Press.

Hopkins, A., and Del Prado, A. 2007. Implications of climate change for grassland in Europe: Impacts, adaptations, and mitigation pptions: A Review. *Grass and Forage Science* 62: 118–126.

IPCC. 2023. Climate change 2023: Synthesis report. Contribution of working groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate change. Core Writing Team, H. Lee, and J. Romero, eds. IPCC, Geneva, Switzerland.

Kovacsics-Vári, G., Sonkoly, J., Tóth, K., et al. 2023. Intensity-dependent effects of cattle and sheep grazing in sand grasslands. Does livestock type really matter? *Applied Vegetation Science* 26: e12727.

Kueffer, C. 2017. Plant invasions in the Anthropocene. Science 358: 724–725.

Kumar, V., Sharma, A., Soni, J. K., and Pawar, N. 2017. Physiological response of C3, C4 and CAM plants in changeable climate. The Pharma Innovation 6: 70.

Linder, H. P., Lehmann, C. E., Archibald, S., Osborne, C. P., and Richardson, D. M. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93: 1125–1144.

Rai, P. K., and Singh, J. S. 2020. Invasive alien plant species: their impact on environment, ecosystem services and human health. *Ecological Indicators* 111: 106020.

Sage, R. F., and Kubien, D. S. 2003. Quo vadis C4? An ecophysiological perspective on global change and the future of C4 plants. *Photosynthesis Research* 77: 209–225.

Török, P., Espinoza Ami, F. D., Szél-Tóth, K., et al. 2024. Accumulated soil seed bank of the invasive sand dropseed (*Sporobolus cryptandrus*) poses a challenge for its suppression. *Land Degradation and Development 3*5: 4105–4120.

Török, P., Schmidt, D., Bátori, Z., et al. 2021. Invasion of the North American sand dropseed (*Sporobolus cryptandrus*)–A new pest in Eurasian sand areas? *Global Ecology and Conservation* 32: e01942.