



Extreme drought facilitates shift to non-native C₄ perennial grass dominance in a temperate grassland in Central Europe

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Received: 5 November 2025 / Accepted: 17 May 2026 / Published online: 5 June 2026
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Abstract Climate change is expected to facilitate the spread of many alien C₄ grasses, which perform better in warmer climates than C₃ species. Furthermore, extreme climatic events may promote plant invasions by suppressing native species. Despite several well-documented cases of C₄ perennial grass invasions, the role of extreme events in facilitating plant invasions is rarely documented. *Sporobolus cryptandrus*, a North American C₄ perennial bunchgrass, has recently been established in several European locations, including mass invasions in natural grasslands. Given the early stage of *S. cryptandrus*

invasion and its potential for future spread, a better understanding of the dynamics and mechanisms of its invasion is urgently needed. In a natural sand steppe in Hungary, an EU priority habitat type with one of the largest *S. cryptandrus* populations in Europe, we monitored *S. cryptandrus* invasion and changes in species dominance in permanent plots annually from 2022 to 2024, which included an extreme drought in 2022. In the post-drought years, we found a gradual increase in both the frequency of *S. cryptandrus* and the number of plots where it was the dominant species. Following the drought-induced dieback of the dominant native grass, *Festuca vaginata*, the cover of *S. cryptandrus* almost doubled from 2023 to 2024 and approached that of *F. vaginata*. This expansion was positively related to *F. vaginata* dieback. Our study demonstrates that *S. cryptandrus* can spread and become dominant rapidly in natural grasslands. Furthermore, our results provide empirical evidence on how extreme events can accelerate an ongoing plant invasion process.

Associate Editor: C. Daehler

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10530-026-03851-1>.

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Keywords Climate change · Dominance shift · Grass dieback · Invasive grass · Sand dropseed · Sand steppe

Introduction

Climate change is predicted to expand or shift the distribution of many invasive grass species over the

twenty-first century (e.g., Lopes et al. 2023; Rad et al. 2025). Several of these grasses have a C_4 photosynthetic pathway (Williams and Baruch 2000; Díaz Cando et al. 2025), which can provide a physiological advantage over C_3 grasses in a warmer and drier climate (Sage and Kubien 2003; Taylor et al. 2014). For example, C_4 species typically exhibit a higher photosynthetic rate than C_3 species at elevated temperatures (Sage and Kubien 2003), and C_4 grasses can maintain higher net CO_2 assimilation than their C_3 relatives during drought periods (Taylor et al. 2014). Consistent with these patterns, a recent study reported a striking increase in the number of alien C_4 grasses in the European flora over the past 14 years (Díaz Cando et al. 2025). Nevertheless, alien C_4 perennial bunchgrasses are still relatively uncommon in Europe, and even fewer of these species occur in natural or semi-natural grasslands (Díaz Cando et al. 2025).

In many grassland regions of the world, climate change is projected to increase the frequency of extreme droughts by the end of the twenty-first century (Cook et al. 2020). Extreme drought events can facilitate the spread of invasive plants following the event by creating an ‘invasion window’ (Sanders et al. 2025). This ‘invasion window’ is characterised by increased resource availability and decreased biotic resistance in the resident community due to a decline in the abundance and richness of native species (Sanders et al. 2025). Invasive plant species often utilise resources that become available following drought (e.g., space, water, and nutrients) more efficiently than native species due to their functional traits, such as higher growth rates or more effective nutrient use (Williams and Baruch 2000; Sanders et al. 2025). Yet, well-documented examples of C_4 perennial grass invasions associated with drought events are scarce (but see Polyakov et al. 2010).

Sand dropseed (*Sporobolus cryptandrus* (Torr.) A. Gray) is a C_4 perennial bunchgrass native to North America (Tilley et al. 2009). The species occurs in short- and mixed-grass prairies, desert scrubs, and pinyon-juniper woodlands, typically on sandy soils (Albertson and Weaver 1944; Tilley et al. 2009). As an alien species, *S. cryptandrus* has been recorded in a number of locations across several continents, predominantly in Europe (13 countries; Török et al. 2021; Kröel-Dulay et al. 2024; Díaz Cando et al. 2025). Furthermore, *S. cryptandrus* can invade not only disturbed habitats, such as roadsides and

degraded grasslands, but also natural sand steppes in Central and Eastern Europe, where it can act as a transformer invasive species (Demina et al. 2018; Török et al. 2021; Kröel-Dulay et al. 2024). Permanent plot studies with annual monitoring are crucial to understanding how the *S. cryptandrus* invasion unfolds, including the role of extreme drought events. The urgency of this understanding is underscored by the early stage of *S. cryptandrus* invasion: there are already a few documented cases of its mass invasion in natural sand steppes in southern Russia, Ukraine, and Hungary (Demina et al. 2018; Török et al. 2021), but the species has huge potential for future spread (Kröel-Dulay et al. 2024).

Our study focused on a recent invasion of *S. cryptandrus* in a temperate grassland in Central Hungary that hosts one of the largest populations of this species in Europe. The study system is a Pannonic sand steppe, a priority habitat type in the EU Habitats Directive (Natura 2000 code: 6260*; Council Directive 2013/17/EU 2013). We monitored *S. cryptandrus* invasion in permanent plots over three consecutive years (2022–2024), which included an extreme drought in 2022. The objectives of our study were (1) to investigate changes in the frequency of *S. cryptandrus* and in the abundances of both *S. cryptandrus* and the resident native species, with a particular emphasis on their responses to drought; and (2) to assess whether the extreme drought event facilitated the invasion of *S. cryptandrus* by increasing its dominance in the post-drought years.

Materials and methods

Study site

The study site (46°24′50.4″ N, 19° 33′ 0″ E) is located in the southern part of the Danube–Tisza Interfluvium, in Central Hungary, near the city of Kiskunhalas. The region has a temperate continental climate with a sub-Mediterranean influence. The mean annual temperature is 11.2 °C, and the mean annual precipitation is 565.9 mm (1971–2024; data from the Hungarian Meteorological Service). During our study, the amount of precipitation between May and August, which is the critical period for vegetation growth, remained below the 54-year average of 249.2 mm in all three years: 195.3 mm in 2022, 198.5 mm in

2023, and 116.1 mm in 2024. However, our previous study (Mojzes et al. 2025) showed that a more reliable predictor of drought-induced mass grass dieback in open sand steppes is the maximum number of Consecutive Dry Days (CDD) between May and August, where a dry day is defined as having less than 5 mm of precipitation per day or in combination with the previous day (CDD_{5mm}). Based on this index, 2022 was an extreme drought year, with a CDD_{5 mm} of 47 days (23 June–8 August), which represents the second-highest value recorded over the past 54 years (Supplementary Fig. 1) and is similar to the duration previously reported to cause mass grass dieback events (Mojzes et al. 2025). By contrast, 2023 was a more favourable year than the long-term average, with a CDD_{5mm} of 19 days (20 May–7 June), while 2024 was also a drought year, with a CDD_{5mm} of 38 days (25 July–31 August). The soil at the study site is a coarse-textured, calcareous sandy soil with a high (>95%) sand content and a low (<2%) humus content (Kröel-Dulay et al. 2019). *Sporobolus cryptandrus* was first recorded in the area in 2016 (Török et al. 2021), likely introduced accidentally, but it was already frequent in 2022 (Kröel-Dulay et al. 2024). The study site is unmanaged and experiences moderate grazing by native ungulates.

Vegetation sampling

Within the ca. 2 km² study site, 100 randomly located 4m × 4m plots were permanently marked in 2022 (Kröel-Dulay et al. 2024). We previously found that at this site, *S. cryptandrus* only invaded open sand steppes (Fig. 1; Kröel-Dulay et al. 2024), which grow

on dunes and have low vegetation cover, and not closed sand steppes, which exhibit higher cover and are found in depressions. Therefore, the present study focused on 71 plots of open sand steppes, where the resident grassland cover (excluding *S. cryptandrus*) was below 50% in 2022. Most of these grasslands were dominated by the native bunchgrass, *Festuca vaginata* Waldst. & Kit. ex Willd., while *Stipa borys-thenica* Klokov ex Prokudin frequently occurred as a co-dominant grass. In July 2022, we visually estimated the percentage cover of *F. vaginata*, *S. borys-thenica*, and *S. cryptandrus* (referred to as the dominant perennial grass species hereafter) and each species that reached at least 1% cover. In late June 2023 and 2024, we recorded the percentage cover of all species. The data collected in 2022 were considered pre-drought because at the time of sampling, the drought had not yet unfolded. In addition, the drought in 2024 began only after our sampling and thus did not affect the results.

Data analyses

All statistical analyses were conducted using the R Statistical Software (version 4.4.1; R Core Team 2024). To analyse changes in the cover of each dominant perennial grass species over the three years, we applied separate generalised linear mixed models (GLMMs). We fitted the models using an ordered beta distribution with a logit link function ('glmmTMB' package; Brooks et al. 2025), which is well-suited for analysing proportional cover data that includes zeros, without the need for transformation or the addition of artificial constants. Plot



Fig. 1 *Sporobolus cryptandrus* (large tussocks in the foreground) invading an open sand steppe near the city of Kiskunhalas, Central Hungary (left), and a fast-growing individual of



S. cryptandrus among dead individuals of the dominant native grass, *Festuca vaginata* (right). Photographs by György Kröel-Dulay

identity was included as a random factor to account for the repeated sampling of the same plots across years. We classified the other species into annuals and other perennials and conducted the same test for the two life forms separately. When the effect of the explanatory variable (i.e., year) was significant ($p < 0.05$), we performed Tukey-adjusted pairwise comparisons of the estimated marginal means as post hoc tests by using the ‘emmeans’ package (Lenth et al. 2025). To evaluate whether variation in the abundance of the dominant native grass, *F. vaginata*, and the drought-related dieback of this species were associated with the invasion of *S. cryptandrus*, we tested the relationships between changes in *S. cryptandrus* cover from 2022 to 2024 and two predictor variables: (1) *F. vaginata* cover in 2022 (pre-drought) in all plots and (2) the dieback rate of *F. vaginata* from 2022 to 2024 in plots where its cover was greater than 10% in 2022. The dieback rate was calculated as the difference between the covers recorded in 2022 and 2024, divided by the 2022 cover. The 10% threshold was chosen based on a previous, long-term study in an open sand steppe in the region, which showed that *F. vaginata* had an average cover of 21–23% in stands dominated by this species (Mojzes et al. 2025); thus, a cover exceeding 10% can be regarded as substantial. We applied separate linear regressions to test these relationships using zero-inflated GLMMs with a Gaussian distribution, because the response variable in our dataset contains negative values and a high number of zero values. Model assumptions were checked by using the ‘DHARMa’ package (Hartig et al. 2024), which indicated an adequate model fit.

Fig. 2 Percentage of plots where *Sporobolus cryptandrus* was **a** present and **b** the dominant species (the species with the highest cover) over the study period

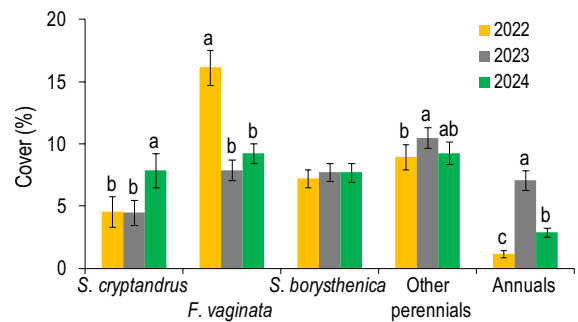
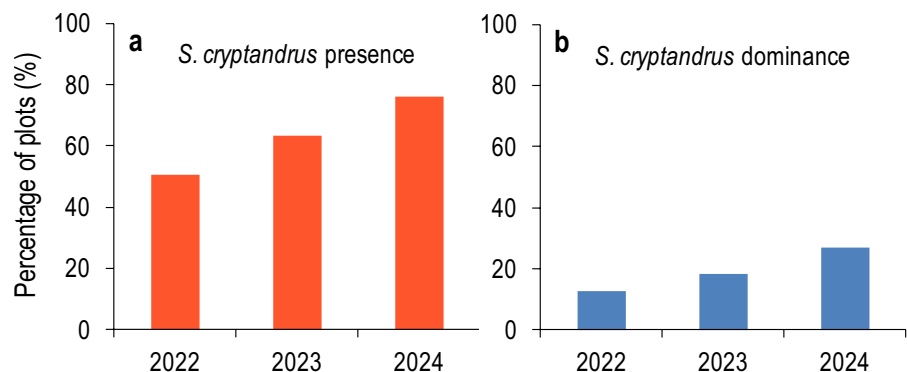


Fig. 3 Cover (mean $\pm$ SE) of dominant perennial grass species (*Sporobolus cryptandrus*, *Festuca vaginata*, and *Stipa borysthena*) and life forms from 2022 to 2024 ($n = 71$). Different letters above the bars denote significant ($p < 0.05$) differences between years for each species or life form separately. Results of post hoc Tukey-adjusted pairwise comparisons of the estimated marginal means are shown (except for *S. borysthena*, for which the effect of year in the generalised linear mixed model was not significant; Supplementary Table 1)

Results

Over the three years, we observed a gradual increase in both the percentage of plots containing *S. cryptandrus* (from 51% in 2022 to 76% in 2024) and those in which it was the dominant species (from 13% in 2022 to 27% in 2024; Fig. 2). *Sporobolus cryptandrus* was considered dominant when it had the highest cover in a plot, including cases where its cover was equal to that of another species.

In response to the extreme drought of 2022, the average cover of *F. vaginata* fell to about half in 2023 ($7.9 \pm 0.8\%$) compared to 2022 ($16.1 \pm 1.4\%$), and it showed no significant recovery by 2024 ($9.2 \pm 0.8\%$; Fig. 3, Supplementary Tables 1 and 2). The cover of annuals exhibited a temporary increase in 2023. The

cover of *S. cryptandrus* did not change from 2022 ($4.5 \pm 1.2\%$) to 2023 ($4.5 \pm 1.0\%$), but almost doubled by 2024 ($7.9 \pm 1.4\%$), approaching the cover of the originally dominant *F. vaginata*.

The expansion of *S. cryptandrus*, measured as the change in cover between 2022 and 2024, was not related to the cover of *F. vaginata* in 2022 (pre-drought), but was positively related to the rate of *F. vaginata* dieback observed in the post-drought years (from 2022 to 2024; Fig. 4).

Discussion

To date, many studies have documented the spread of invasive C₄ perennial grasses in natural or semi-natural habitats (Williams and Baruch 2000; Ryan-Colton et al. 2024; Díaz Cando et al. 2025). By contrast, only a few studies have examined the impacts of drought on the invasion success of C₄ perennial grasses, particularly in relation to how the resident native community responds to the drought (but see Polyakov et al. 2010; Fahey et al. 2018). In our study, the marked increase in both the frequency and abundance of *S. cryptandrus*, along with a shift towards its dominance within two years, demonstrates that *S. cryptandrus* can spread extremely fast in open sand steppes. To our knowledge, such a high expansion

rate in undisturbed grasslands, together with the ability to replace the dominant native species in just a few years, is unprecedented among alien C₄ perennial bunchgrasses in Europe. The high invasion potential of *S. cryptandrus* can be largely attributed to its reproductive traits, such as abundant seed production and an efficient seed dispersal mechanism (Tilley et al. 2009), being primarily self-fertilized (Fryxell 1957), and a dense soil seed bank (Török et al. 2021). Previous research in the region reported that the high cover of *S. cryptandrus* was associated with a decrease in species richness and the abundance of subordinate species (Török et al. 2021). Therefore, the rapid increase in *S. cryptandrus* dominance observed in our study likely poses a major threat to the persistence of the unique Pannonic sand steppes.

Our results on the invasion of *S. cryptandrus* may provide empirical evidence for the hypothesis that extreme drought events can promote the invasion of alien species by reducing the abundance of resident native species, thereby creating an ‘invasion window’ (Sanders et al. 2025). The finding that the sharp decline in the cover of *F. vaginata* (from 2022 to 2023) preceded the increase in the cover of *S. cryptandrus* (from 2023 to 2024) indicates that the mass mortality of the previously dominant native grass was primarily caused by the extreme drought, as observed following drought events of similar

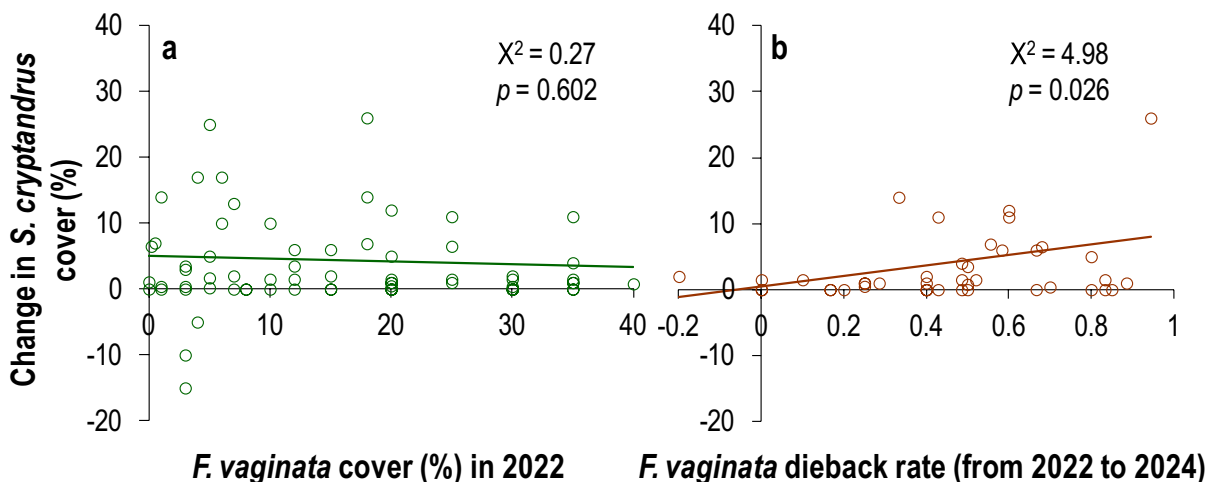


Fig. 4 The relationship between changes in *Sporobolus cryptandrus* cover from 2022 to 2024 and **a** the cover of the dominant native grass, *Festuca vaginata*, in 2022 (pre-drought) in all plots ($n = 71$) and **b** the dieback rate of *F. vaginata* from

2022 to 2024 in plots where its cover exceeded 10% in 2022 ($n = 42$). Results of zero-inflated generalised linear mixed models (with a Gaussian distribution) are shown

magnitude (Mojzes et al. 2025), rather than by the invasion of *S. cryptandrus*. The pronounced increase in the cover of *S. cryptandrus* following the dieback of *F. vaginata*, together with its positive relationship with *F. vaginata* mortality, suggests that the loss of the native species created an opportunity for *S. cryptandrus* to expand. Collectively, these results support the interpretation that the extreme drought facilitated the invasion of *S. cryptandrus* by removing (or reducing the cover of) the formerly dominant native grass, *F. vaginata*, thereby allowing *S. cryptandrus* to exploit the newly available resources. Drought-induced mass dieback of dominant perennial grasses has previously occurred in open sand steppes of the region (Orbán et al. 2023; Mojzes et al. 2025). However, the mass dieback was followed by a shift in dominant species from *F. vaginata* to *S. borys-thenica*, another native grass, until the recovery of the former species (Mojzes et al. 2025). The dominance shift from *F. vaginata* to *S. cryptandrus* following drought in our study suggests that the invasion of *S. cryptandrus* is likely to disrupt these natural recovery dynamics of open sand steppes, particularly if the accelerating climate change increases the prevalence of drought-induced mass mortality events.

The positive effect of drought on *S. cryptandrus* invasion may be explained by the species' ability to withstand high interannual rainfall variability (Winkler et al. 2019) and, more importantly, to establish a large number of seedlings in a favourable year following drought (Weaver and Mueller 1942). The increasing dominance of *S. cryptandrus* after extreme drought in our study system is consistent with the dynamics of this grass documented in the mixed prairie within its native range. Specifically, in the central Great Plains, *S. cryptandrus* often became abundant on bare soil after the dieback of previously dominant short grasses caused by a severe drought (Albertson and Weaver 1944). Similar to *S. cryptandrus* in our study, a rapid invasion and dominance takeover was reported for the exotic *C₄* perennial bunchgrass, *Eragrostis lehmanniana*, in a desert grassland in Arizona, following drought-induced mortality of the originally dominant native grasses and shrubs (Polyakov et al. 2010).

Collectively, our results demonstrate that *S. cryptandrus* is spreading and has gained dominance at an alarming rate in open sand steppes, and that an extreme drought event played a key role in mediating

its invasion. These results suggest that *S. cryptandrus* is likely to establish and spread as a dangerous invasive species in many areas within its potential range, threatening open grasslands in Central and Eastern Europe and possibly in other regions. Furthermore, the ability of *S. cryptandrus* to disrupt natural post-drought regeneration dynamics exemplifies how extreme climatic events can accelerate ongoing invasions by non-native plant species.

Acknowledgments We thank the two anonymous reviewers for their valuable suggestions, which helped improve the manuscript.

Author contributions The study concept was developed by György Kröel-Dulay, with contributions from Gábor Ónodi and Andrea Mojzes. Data collection was carried out by György Kröel-Dulay, Gábor Ónodi, Attila Rigó, and Andrea Mojzes. Katalin Sztár performed the statistical analyses. Andrea Mojzes wrote the first draft of the manuscript. All authors critically reviewed earlier versions of the manuscript and approved the final version.

Funding The support received from the National Laboratory for Health Security programme (RRF-2.3.1-21-2022-00006) and from the Sustainable Development and Technologies National Programme of the Hungarian Academy of Sciences (FFT NP FTA) is greatly appreciated.

Data availability Data that support the findings of this study are available in Figshare: <https://doi.org/10.6084/m9.figshare.30253447>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval Not applicable.

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