Ecological Engineering 186 (2023) 106824

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Early sowing is more effective in the long-term for restoring sandy grassland than six years of mowing or carbon amendment

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A R T I C L E I N F O

Keywords:
Grassland restoration
Long-term monitoring
Seeding
Mowing
Carbon amendment
Invasive species
Old fields

A B S T R A C T

In order to find the best and most reliable practices for ecological restoration of degraded lands, longer time scales should be considered when evaluating restoration efforts. We assessed the long-term (16 years) effects of different grassland restoration treatments – seeding, mowing, and carbon amendment – in the Pannonian sand grasslands. After re-plowing in 1 m × 1 m plots, treatments were carried out in two abandoned croplands. Seeding was applied only initially (2002) while mowing and carbon amendment were carried out for six years (2003–2008). Vegetation was surveyed yearly from 2003 to 2008 and re-sampled in 2019 in each permanent treatment plot. We used principal coordinates analysis to describe the trajectories of vegetation development and linear mixed-effects models to test changes in the relative cover of native sand grassland (target) and invasive (neophyte) species with time and treatments. Relative cover of target species increased while neophyte species decreased with time in both sites. There was a higher relative cover of target species from the first or third year on and a lower relative cover of neophyte species from the third year on in one site in seeded plots compared to other treatments. Seeded species also spread into non-seeded plots by 2019, obscuring the differences between treatments 16 years after sowing. Carbon amendment proved to be beneficial in the early and mowing in the later phases of restoration. Based on the long-term results, initial seeding is the best method for restoring sand grasslands in old fields by favoring the establishment of target species and controlling non-native invasion. As a supplement to seeding, carbon amendment can be suggested in the initial phases and/or low-intensity mowing in the later phases of the restoration after land abandonment. Although the spread from seeded plots obscured the long-term differences between treatments, it optimized the restoration process, suggesting that the use of small seed introduction units can be enough to restore the whole degraded area.

1. Introduction

Degradation and fragmentation of natural and semi-natural habitats and invasion of non-native species due to human activities are among the major threats to global biodiversity (Pereira et al., 2012). In order to halt biodiversity loss, besides the conservation of remaining natural ecosystems, ecological restoration is considered crucial to slow down fragmentation, decrease extinction rates and mitigate climate change (Strassburg et al., 2020). Recently, the United Nations declared that this decade is dedicated to ecosystem restoration that can be a base to accelerate existing global restoration goals and increase the number of projects associated with restoration around the world (Temperton et al., 2019; Aronson et al., 2020).

In order to meet global targets, ecological restoration should be upscaled, which implies extending restoration to unused agricultural lands (Maes et al., 2015), restoring larger landscapes, and including landscape factors in restoration prioritization (Gann et al., 2019; Strassburg et al., 2020). In addition, longer time scales should be taken

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https://doi.org/10.1016/j.ecoleng.2022.106824
Received 7 April 2021; Received in revised form 14 September 2022; Accepted 19 October 2022
Available online 4 November 2022

into account when assessing restoration efforts (Waldén et al., 2017) to comprehend better the restoration process and the effect of restoration interventions (Pakeman et al., 2002; Lepš et al., 2007; Prach et al., 2015; Reis et al., 2021) and to find best practices for ecological restoration (Cortina-Segarra et al., 2021). According to long-term monitoring studies (up to 75 years) of plant community composition from the United States (Herrick et al., 2006), many years may be needed before the impacts of management become detectable in a restored area, and initial success might fade in the longer-term. Long-term monitoring makes it possible to assess the success of restoration properly and correct its trajectory through adaptive management when necessary (Viani et al., 2017). Previously, most restoration projects were short-term monitored – a maximum of five years – mainly due to the lack of financial resources (Ruiz-Jaen and Aide, 2005). Recently the timescale of monitoring has increased (Wortley et al., 2013), varying according to the restored habitat and the studied organisms. However, studies in grasslands with more than ten years on average are still rare (Kollmann et al., 2016).

Approximately 70% of the world's grasslands have been cleared or transformed into agricultural lands over the last two centuries (UNCCD (United Nations Convention to Combat Desertification), 2013) or lost due to afforestation (Veldman et al., 2019) or by the abandonment of extensive grazing (Bakker et al., 2012; Biró et al., 2013; Habel et al., 2013; Török et al., 2018a). Despite this, little attention has been paid to conserving and restoring these habitats globally (Temperton et al., 2019). Grassy biomes and savannahs cover around a third of the land surface (Bond, 2019; Dudley et al., 2020), present high diversity, and are a suitable habitat for many endemic species (Habel et al., 2013). Grassy habitats also provide plenty of ecosystem services (e.g. water supply and flow regulation, carbon storage, erosion control, climate mitigation, pollination, food production), including cultural services due to the long tradition of extensive management (Dengler et al., 2014; Török et al., 2018a; Bengtsson et al., 2019; Veldman et al., 2019).

According to trends forecasted for the EU between 2015 and 2030, 11% of agricultural land is at high risk of abandonment (Perpiña et al., 2018). Cropland abandonment offers an opportunity for passive (i.e. spontaneous recovery) or active restoration of grasslands (Queiroz et al., 2014; Valkó et al., 2016a). Active restoration interventions aim to accelerate the recovery process and overcome the major limitations of spontaneous recovery (Prach and Hobbs, 2008; Atkinson and Bonser, 2020). Constraints in restoring abandoned fields include dispersal limitation and local abiotic and biotic factors (Halassy et al., 2016; Török et al., 2018b; Halassy et al., 2019). The most important constraint is the dispersal of propagules in time (local soil seed bank or bud bank) and/or space (including the surrounding landscape) (Halassy et al., 2016; Török et al., 2018b) that can be overcome by the introduction of target species (Kiehl et al., 2010; Kövendi-Jakó et al., 2019). Although seed introduction is a preferred restoration method, the survival of seeded species is variable and often unpredictable in the long term because of intrinsic and environmental factors (Rinella and James, 2017). One of the most important abiotic factors is the excess of nutrients (mainly nitrogen) in the soil after the abandonment of agricultural cultivation that can be reduced, e.g. by carbon amendment (Perry et al., 2010; Török et al., 2014; Halassy et al., 2021). Biotic factors, e.g. encroachment of dominant competitors (woody or herbaceous) and invasion of alien species, can be managed by mowing that increases species diversity by creating establishment gaps (Valkó et al., 2012; Török et al., 2018b). It is essential to note that the combination of restoration interventions aiming at dispersal, abiotic and biotic limitations is expected to increase restoration success (Halassy et al., 2016).

The present work aimed to evaluate the long-term effect (16 years) of initial seeding or six years of mowing or carbon amendment in restoring Pannonian sand grasslands on two abandoned agricultural fields. Previous results have already demonstrated the short-term effect (6 years) of these treatments on the vegetation development (Halassy et al., 2016, 2019) and the vegetation status and site effects (e.g. time of abandonment, soil composition, and surrounding landscape composition) in 2019 (Llumiquinga et al., 2021). The present research compiled data from the entire monitoring period to assess restoration progress and temporal vegetation trends to find best practices for sandy grassland restoration on abandoned croplands. The specific questions we addressed are 1. How does the vegetation develop on the long-term (2003–2019) due to initial seeding, or six years of mowing or carbon amendment according to trajectory analysis? 2. How do initial seeding or six years of mowing or carbon amendment impact the relative cover of target species during the vegetation development on the long-term (2003–2019)? 3. How do initial seeding, or six years of mowing or carbon amendment impact the relative cover of neophyte species during the vegetation development on the long-term (2003–2019)?

2. Material and methods

2.1. Study area

The experiment was carried out in Fülöpháza, Kiskun LTER (Long-term Ecosystem Research) site (N 46°89 E 19°44) Hungary, Pannonian biogeographic region, Europe (Fig. 1). The soil type is Calcaric Arenosol with >90% of sand and <1% humus content (Lellei-Kovács et al., 2011). The climate is continental with a sub-Mediterranean influence, characterized by warm and dry summers. The mean annual precipitation varies from 520 to 550 mm, and the mean annual temperature is 10.5 °C (Kovács-Láng et al., 2008).

The natural vegetation is forest-steppe, a mosaic of open oak forests and juniper–poplar woodland sparsely scattered in a sand grassland matrix (Erdős et al., 2018). The vegetation composition of the region is highly affected by the groundwater level, and the most widespread natural vegetation type, the open sand grassland, occupies the driest locations. These sand grasslands are considered an important part of European landscapes since they host high biodiversity and endemism, being considered a priority protected habitat at the EU level (Pannonic sand steppes 6260) (EC (European Commission), 2013). They are mainly dominated by perennial tussock grasses, such as *Festuca vaginata* and *Stipa borysthenica* (nomenclature follows Király, 2009). The average vascular plant cover is no >40–70%, with bare soil and cryptogams covering the remaining surface (Erdős et al., 2018).

In the past two centuries, 92% of open sand grasslands have been degraded in Hungary, primarily by land-use changes, i.e. conversion to arable lands, afforestation by non-native tree plantations, land abandonment, and incorrect management or biological invasion (Biró et al., 2013). The groundwater level has also been lowered during the last years because of the historical drainage of wetlands, irrigation, and drinking water extraction in the late 20th century (Biró et al., 2013). This promotes land abandonment in the region, which provides a potential for the regeneration and restoration of sand grasslands on abandoned croplands (Csecserits et al., 2011; Valkó et al., 2016a).

2.2. Sites

The restoration experiment initially involved three abandoned agricultural fields differing in the time of abandonment (Halassy et al., 2016, 2019). However, only two of them could be followed in the long term (Fig. 1), as the third one was returned to cultivation right after the end of the experimental treatments. According to historical aerial photos, one site was abandoned around 1999 and is of medium age of the original three sites; it is further referred to as the 'Medium' site. The other site was abandoned at the earliest, around 1987, and is referred to as the 'Old' site. Rye and maize were grown before abandonment at the Medium site. For the Old site, the exact crops are unknown, but rye and maize are the typical crops in the region. Before starting the experiment, the vegetation of both abandoned fields was dominated by annual weeds. However, the Medium site had a high cover (up to 50%) of generalist perennial grasses (e.g. *Cynodon dactylon, Calamagrostis*

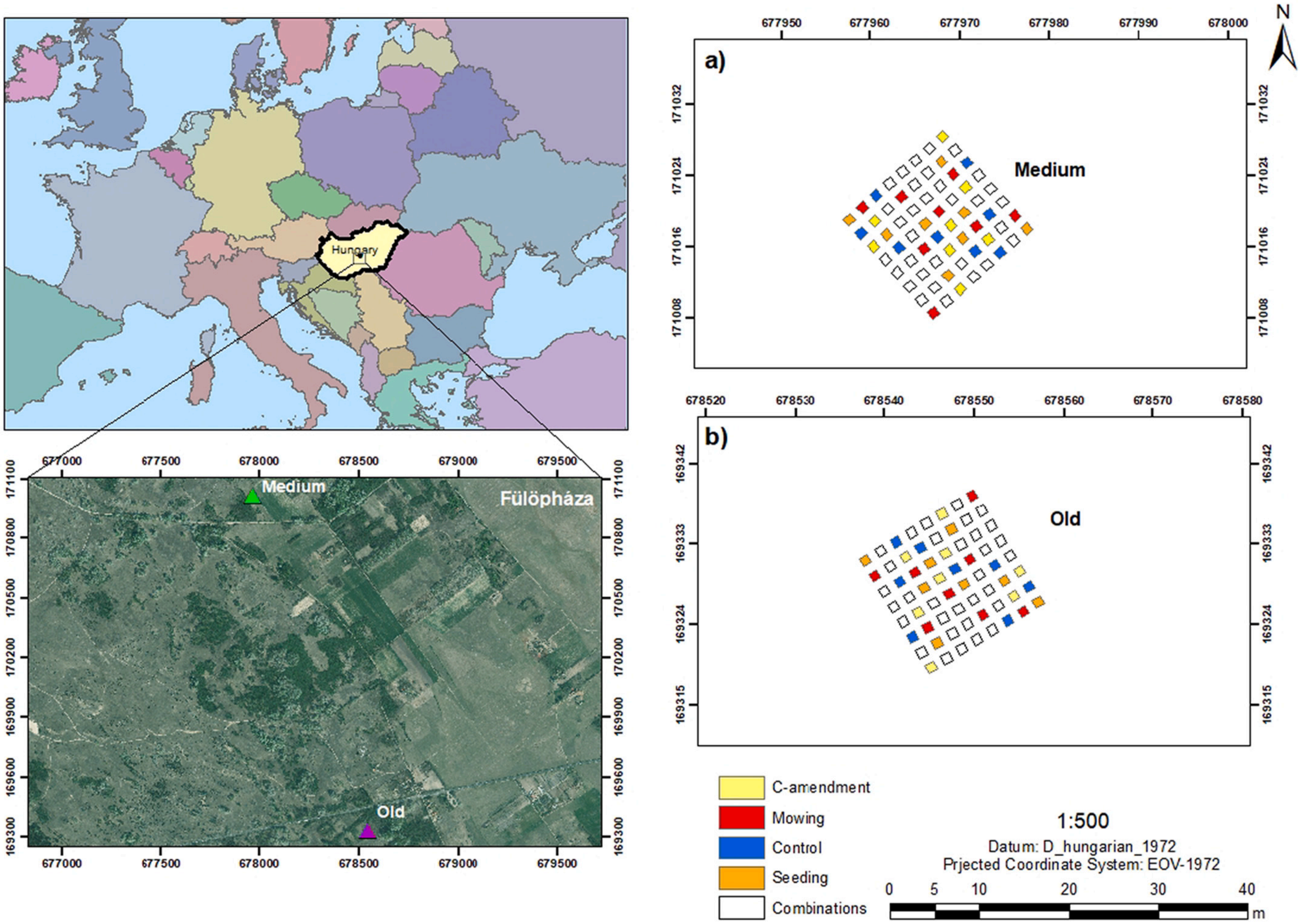

Fig. 1. Location and treatment design of the experimental sites in Hungary at the village Fülöpháza. a) Medium site and b) Old site. Treatments were performed on 1 m^2 plots with 1 m wide paths among the plots. The assigned colors differentiate the main treatments. The hollow plots represent treatment combinations that were not considered in the analyses. The aerial photo was taken in 2019 (with a 0.4 m spatial resolution).

epigeios, Elymus repens) and few sand grassland species (e.g. *Stipa borysthenica*) were already present at Old site. Slight differences in the soil were also observed before the experiment started. The medium site presented silty rough sand and fine sand with some clay and silt in soil layers 120–170 cm deep, while the Old site presented rough sand and sand with concretions in soil layers between 260 and 270 cm deep. For further details, see Llumiquinga (2020) and Llumiquinga et al. (2021).

2.3. Experimental design and monitoring

Plowing and harrowing were applied to a 20 m by 20 m area in each site as a preparatory treatment in 2002 to reduce the effect of standing vegetation. In this area, a block with 64 plots of 1 m^2 with 1 m paths between the plots was marked for the treatments. The same design, but with a different orientation, was applied in both sites that consisted of eight types of treatments randomly assigned to eight plots within a row, and eight rows served as replicates (Fig. 1a, b). The treatments were: No treatment (control), seeding, mowing, carbon amendment, plus combinations. For this paper, the combinations were excluded from further analyses as we wanted to evaluate the effect of the main treatments at this stage.

Seeding involved five open sand grassland species collected by hand in the Fülöpháza Sand Dune area during the summer of 2002. The five species included the two dominant grass species, *F. vaginata* (1.55 g/m^2) and *S. borysthenica* (1.05 g/m^2), a subordinate grass, *Koeleria glauca* (1.00 g/m^2), plus two subordinate forb species *Dianthus serotinus* and *Euphorbia seguieriana* (0.20 g/m^2 together). All species were seeded on the open soil surface in September 2002. We had to re-seed *S. borysthenica* (1.31 g/m^2) in September 2003 because of no survival due to the intense drought in the summer of 2003. Mowing with hay removal was applied twice (June and September) in 2003 and once a year (in September) from 2004 until 2008. Carbon amendment was applied in the form of sucrose addition (45 g/m^2 at a time) four times per year (April–August) from 2003 to 2008. For further details of the experimental design, see Halassy et al. (2016).

To monitor the vegetation development, we visually estimated the percentage cover of each vascular plant species in each permanent treatment plot twice a year (in June and August) during the treatment period (2003–2008). We re-sampled the plots in 2019 to evaluate the long-term effects of treatments. We used the maximum cover value for each species of the two estimations per plot per year for further analysis.

We also classified the species according to their role in restoration as desirable (target), undesirable (alien species that represent a current or future threat), and neutral (non-target species, e.g. common weeds). Target species were selected according to Csecserits et al. (2011) classification of characteristic species of sand grasslands in the Kiskunság region. For the alien species, we included those introduced to Hungary after the discovery of America, referred to as neophyte species, and identified based on Balogh et al. (2004). For the complete list of species and their categorization, see Appendix S1. The relative cover of target species and the relative cover of neophyte species were used as indicators of restoration success.

2.4. Data analysis

To evaluate the development of the vegetation between 2003 and 2019 in response to the applied treatments (seeding, carbon amendment, mowing), we carried out a Principal Coordinate Analysis (PCoA) using the Euclidean distance as a distance measure in the package "*vegan*" in R (Oksanen et al., 2018). We analyzed the data from all plots and sites together in a single ordination. We calculated the centroids of control and treatments (seeding, carbon amendment, and mowing) for each year and site along the first two axes to draw vegetation development trajectories depicting changes in vegetation composition for the study period.

Linear mixed-effects models (LME) were applied to investigate the differences in the relative cover of target and neophyte species between the treatments and years for each site separately using the '*nlme*' package (Pinheiro et al., 2017). Treatment and Year were treated as fixed categorical explanatory variables, while Plot identification was treated as a random effect in the models. Treatment included four levels (control, seeding, carbon amendment, and mowing), whereas Year included seven levels (2003–2008 and 2019). The relative cover was square root-transformed both for target and neophyte species to meet the assumptions of normality and homoscedasticity. VarIdent variance structure was used in the models given the high variance of residuals within the analyzed groups (treatment and year). The significance of fixed factors was based on Type II Wald chi-square tests. When significant interactions between fixed factors occurred, we applied the Wald test using the 'contrast' package (Kuhn et al., 2016) as a post hoc pairwise test to detect significant differences between the treatments. If no interactions were found, fixed factors were analyzed separately by the Tukey HSD test by the "*multcomp*" package (Hothorn et al., 2008). All statistical analyses were performed using R v 3.5.1 (R Core Team, 2018). Means and SE reported in the figures, and the text are based on untransformed data.

3. Results

3.1. Vegetation development trajectories

The first two axes of PCoA explained 46.01% and 12.19% of the variation. The PCoA separated the trajectories of the Medium and Old sites from the third year until 2008 along axis 2, but they converged by 2019 (Fig. 2). Vegetation development due to treatments is clearly shown by the directional changes of trajectories along axis 1. Seeding plots separated from other treatments (mowing, carbon amendment, control) from 2004 on, showing a faster vegetation development in both sites until 2008 (Fig. 2). The rest of the treatments did not separate from the control in the Medium site. On the Old site, the trajectories showed an order of speed in vegetation development: from the fastest development in Seeding plots followed by mowing plots, control, and finally, carbon amended. However, in 2019, all trajectories approximated each other in the ordination space (Fig. 2).

3.2. Relative cover of target species

The relative cover of the target species was affected by year, treatment, and the interactive effect of year and treatment in both sites (Table 1). The relative cover of target species increased in all treatments with year, achieving around 80% and 90% in the Medium site and the Old site, respectively, by 2019 (Fig. 3). The increase in the relative cover of target species was primarily due to seeded species. These species achieved an average total cover of 69.41% in the Medium site and 65.90% in the Old site by 2019. Non-seeded target species (e.g. *Centaurea arenaria, Verbascum lychnitis, Poa angustifolia*) also spread in the Old site, primarily in non-seeded plots. Similar trends were observed in the Medium site, but seeded species had a stronger dominance here, resulting in a subordinate role of non-seeded target species.

In the Medium site, seeding plots presented a significantly higher relative cover of target species than the other treatments from the beginning of the experiment (2003) and continued to be different until 2008 (Fig. 3a). The rest of the treatments did not show significant differences among them, except for carbon amendment having a

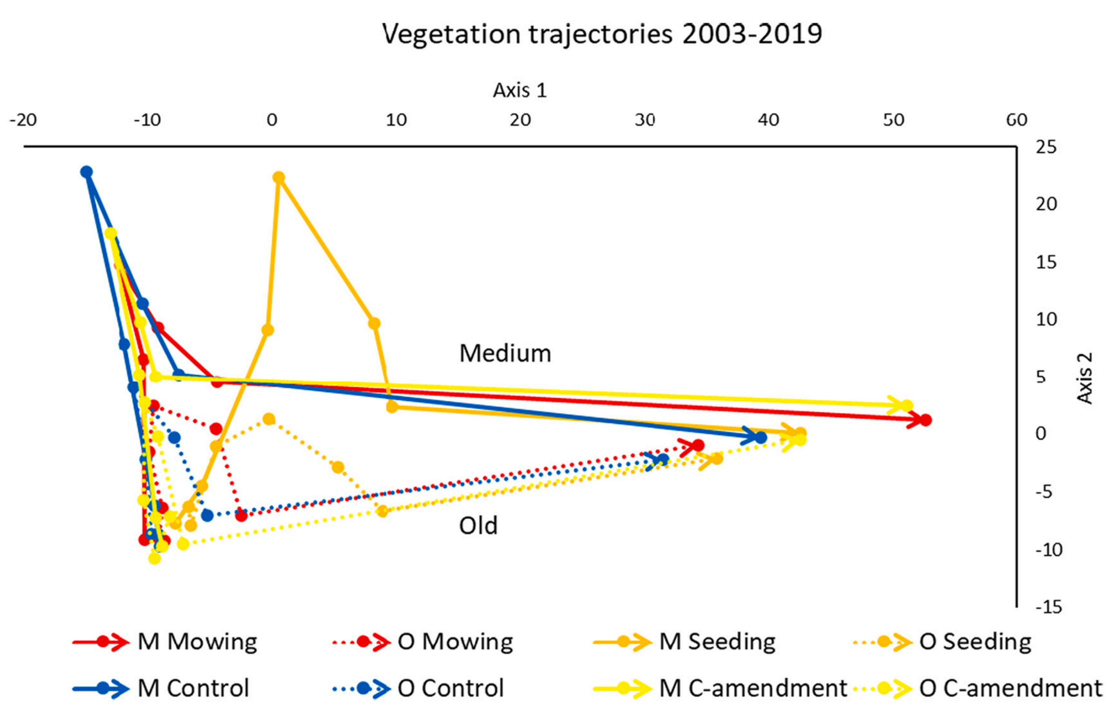

Fig. 2. Vegetation development trajectories between 2003 and 2019 based on Principal Co-ordinate Analysis of cover data using the Euclidean distance for Medium and Old sites. Abbreviations: M = Medium site, O = Old site. C-amendment – carbon amendment.

Table 1
Results of Type II Wald chi-square (χ2) test of fixed effects (treatment and year) on the relative cover of target and neophyte species from linear mixed-effects models (LME) for Medium and Old site.

	Site	
	Medium	Old
Fixed effects		
	target species	
year	$\chi2 = 4202.70$, df = 6, $\boldsymbol{p < 0.001}$	$\chi2 = 1756.185$, df = 6, $\boldsymbol{p < 0.001}$
treatment	$\chi2 = 144.99$, df = 3, $\mathbf{p < 0.001}$	$\chi2 = 33.700$, df = 3, $\mathbf{p < 0.001}$
year * treatment	$\chi2 = 282.34$, df = 18, $\mathbf{p < 0.001}$	$\chi2 = 74.314$, df = 18, $\mathbf{p < 0.001}$
	neophyte species	
year	$\chi2 = 303.89$, df = 6, $\mathbf{p < 0.001}$	$\chi2 = 522.555$, df = 6, $\mathbf{p < 0.001}$
treatment	$\chi2 = 49.24$, df = 3, $\mathbf{p < 0.001}$	$\chi2 = 42.497$, df = 3, $\mathbf{p < 0.001}$
year * treatment	$\chi2 = 37.44$, df = 18, $\mathbf{p = 0.005}$	$\chi2 = 20.882$, df = 18, $p = 0.285$

Note. Significant results ($p < 0.05$) are given in bold.

significantly higher relative cover of target species than mowed plots in 2004, with control plots showing an intermediate value. By 2019, all plots became similar due to the increase in the relative cover of target species. For the complete statistical results, see Table S2.

In the Old site, treatments did not differ from each other in the first two years (Fig. 3b). From 2005, seeding plots presented a significantly higher relative cover of target species than mowing or control plots, and from 2006 on also higher than carbon amendment. From the rest of the treatments, mowed plots became different from control from 2006 on, having a higher relative cover of target species. By 2019, all treatments became similar due to the increase in the relative cover of target species, except for control, which had a significantly lower relative cover of target species (ca. 85%). For the complete statistical results, see Table S3.

3.3. Relative cover of neophyte species

A significant effect of year, treatment (both $p < 0.001$), and interactions ($p < 0.005$) was observed for neophyte species in the Medium site. The same was observed for the Old site, except for the interactions, which did not show a significant effect (Table 1). Generally, the relative cover of neophyte species decreased with the year in all treatments and sites.

In the Medium site, the relative cover of neophyte species was smaller in seeded plots than in the other treatments during the whole experimental period (2003–2008). However, significant differences were observed only from 2004 to 2006 (Fig. 4a). Mowing plots had a significantly higher cover of neophytes than control in 2004 and a significantly lower cover in 2007. Carbon amendment plots did not differ from control. By 2019, the relative cover of neophyte species became similar in all treatments reaching <8%. The dominant neophytes in the Medium site were *Ambrosia artemisiifolia, Conyza canadensis, Oenothera biennis,* and *Asclepias syriaca*, achieving a relative cover of 1.53%, 0.5%, 0.87%, and 1.67%, respectively by 2019. For the complete statistical results, see Table S4.

In the Old site, there was an overall decrease in the relative cover of neophyte species with year, independent of treatment, resulting in significantly lower values observed from 2007 compared to earlier years and achieved the lowest values in 2019 (1.23%) (Fig. 4b). When comparing treatments independent of year, the relative cover of neophyte species was significantly lower in seeding and mowing plots (< 18%) than in carbon amendment and control plots (> 24%) (Table S6). The dominant neophyte species in the Old site were *A. artemisiifolia* and *C. canadensis,* presenting 1.2% and 0.002% relative cover, respectively, in 2019. In the last measurement, *A. syriaca* also appeared in the Old site (c.a. 0.23%). For the complete statistical results, see Table S5, S6.

4. Discussion

Our results reinforce the importance of long-term monitoring for detecting changes in vegetation development during and after active restoration measures. Although we found an overall increase in target species due to treatments, differences from control became visible in the trajectory analysis only after two years. The same was true for the direct comparison between treatments based on the relative cover of species groups, some differences between treatments became visible only after some years. There was a general decline in invasive alien species, but significant differences became visible only five years after the experiment started, indicating that the community grew more resistant to invasion with time (Richardson and Pyšek, 2006). Data from 2008 showed that the seeding of key species has kick-started the restoration of sandy grasslands in the studied old fields and has efficiently shortened the time required for recovery (Halassy et al., 2016, 2019). Revisiting the site eight years after the end of the experiment revealed that seeded species could spread to non-seeded plots, which has optimized the restoration of old fields in our study. At the same time, it also obscured the differences between treatments in the long term. The short distance of dispersal necessary to reach the neighboring different treatment can be the reason for this vegetation similarity achieved in the long term. Species dispersal distance decreases exponentially from the source (Vos et al., 2001); in the case of larger buffer areas, the differences between treatments are less masked. Experimental design should consider this constraint for evaluating the long-term effects of treatments involving seeding (Pakeman et al., 2002).

The long-term monitoring revealed that from the treatments applied, initial seeding with a low diversity seed mixture (five species only) had the most visible impact on vegetation development, including an increase in target species and a decrease in invasive species in both sites, resulting in a different successional trajectory compared to non-seeded plots. These results correspond to earlier findings, but some differences between seeded and non-seeded plots were masked with time (Halassy et al., 2016, 2019; Llumiquinga et al., 2021). The high impact of seeding is a sign of a strong propagule limitation in the region. In our study area, research revealed the lack of viable sand grassland specialists seeds and the dominance of undesired species in the seed bank (Halassy, 2004). However, this limitation is less evident in terms of spatial dispersal since there are still fragments of semi-natural grasslands in the neighboring areas (Biró et al., 2013; Reis et al., 2022) that can be a source of target propagules. In addition, the presence of secondary grasslands can also be an important source for regeneration according to their age since abandonment, as 20–40 years old abandoned land can host several grassland species (Csecserits et al., 2011; Csecserits et al., 2016).

Seeding mixtures of target species is a recognized restoration method for grasslands where dispersal limitation is an important constraint (Török et al., 2011; Halassy et al., 2016; Török et al., 2018b). Our results confirmed that the initial seeding of target species has a long-term impact on vegetation development. Seeded species were able to survive, spread and colonize neighboring areas, resulting in dominance also in non-seeded plots 16 years after seeding. This aligns with the idea that small sown plots can serve as a propagule source for larger areas (Valkó et al., 2016b). Furthermore, seed introduction can also effectively suppress invasive species (Bucharova and Krahulec, 2020). Our long-term results confirmed this, as initial seeding reduced the relative cover of neophyte species. At the species level, *Ambrosia artemisiifolia* was the most repressed invasive species (Llumiquinga et al., 2021). This species can rapidly colonize areas with soil disturbance, especially agricultural fields, and poses a threat to public health in Europe due to its highly allergenic pollen (Kröel-Dulay et al., 2019). Based on our results, early

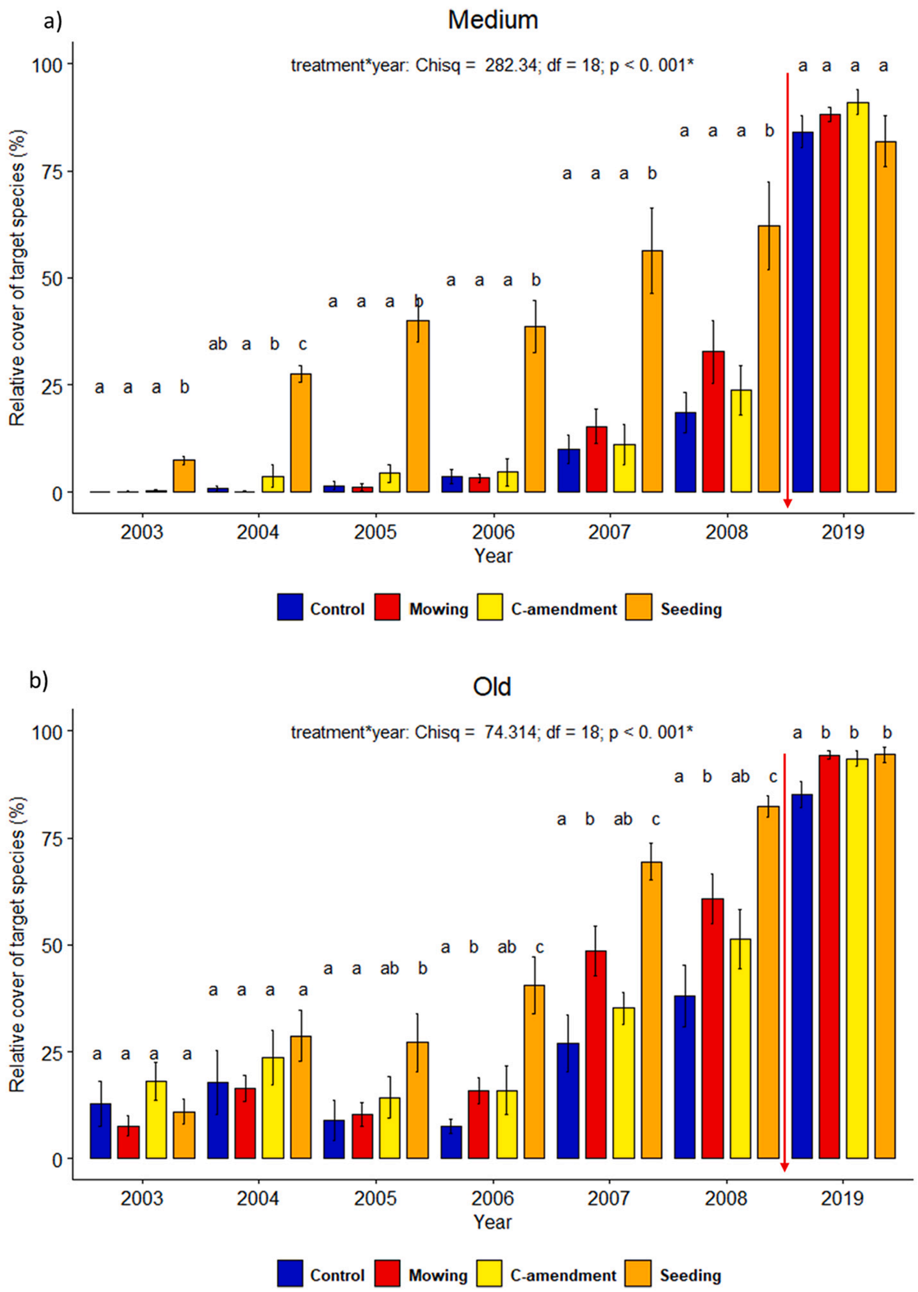

Fig. 3. Changes in the relative cover of target species according to treatment between 2003 and 2019 for a) Medium and b) Old site. A within-year significant difference (p < 0.05) between treatments based on the Wald test is indicated by lowercase letters. The red arrow represents the cessation of mowing and carbon amendment (2008). Means and SE are reported based on untransformed data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

seeding of grassland species after cropland abandonment can control its spread.

Mowing was the second most important treatment in the short-term (Halassy et al., 2016, 2019). In the long-term, mowing favored target species at one site and lowered the relative cover of invasive species at the other site from 2006 and 2007 onwards. Modification of biotic interactions (e.g. competition) is known to have a more substantial influence in the later phases of succession (Halassy et al., 2016; Török et al., 2018b) when the vegetation canopy is already closed by competitive perennials or mid-successional dominant species (Bartha et al., 2014). Since we applied plowing as a pretreatment that creates open sites for germination and species establishment, the closure of vegetation was necessary to develop before a visible impact of mowing. Mowing is a widely used management for maintaining the diversity of natural grasslands, often applied also in grassland restoration (Kelemen et al., 2014). However, when mowing opens up the sward creating establishment gaps, invasive species might be the first to colonize if present in the landscape (Reis et al., 2021; Reis et al., 2022).

The impact of carbon amendment on the success of restoration projects is reported to be contradictory (Perry et al., 2010). Many studies proved that carbon application benefits target species and controls invasive species, but opposite and neutral results were also reported (Perry et al., 2010). In our case, the relative cover of target species increased while neophyte species decreased in carbon amendment plots, similar to mowing. However, these changes were statistically different only in the early years of applications. Our previous results demonstrated that carbon amendment diminished the nitrogen content in the soil, as expected, and consequently reduced the cover of mosses and increased the bare ground in the short term (Halassy et al., 2016). However, in the long-term, these differences were not sufficient to accelerate the recovery of sand grasslands compared to control. Our results are in line with previous findings that the high nutrient content is not a limiting factor to restoration in the region (Halassy et al., 2021), but other abiotic (e.g. climatic) or biotic factors may play a more

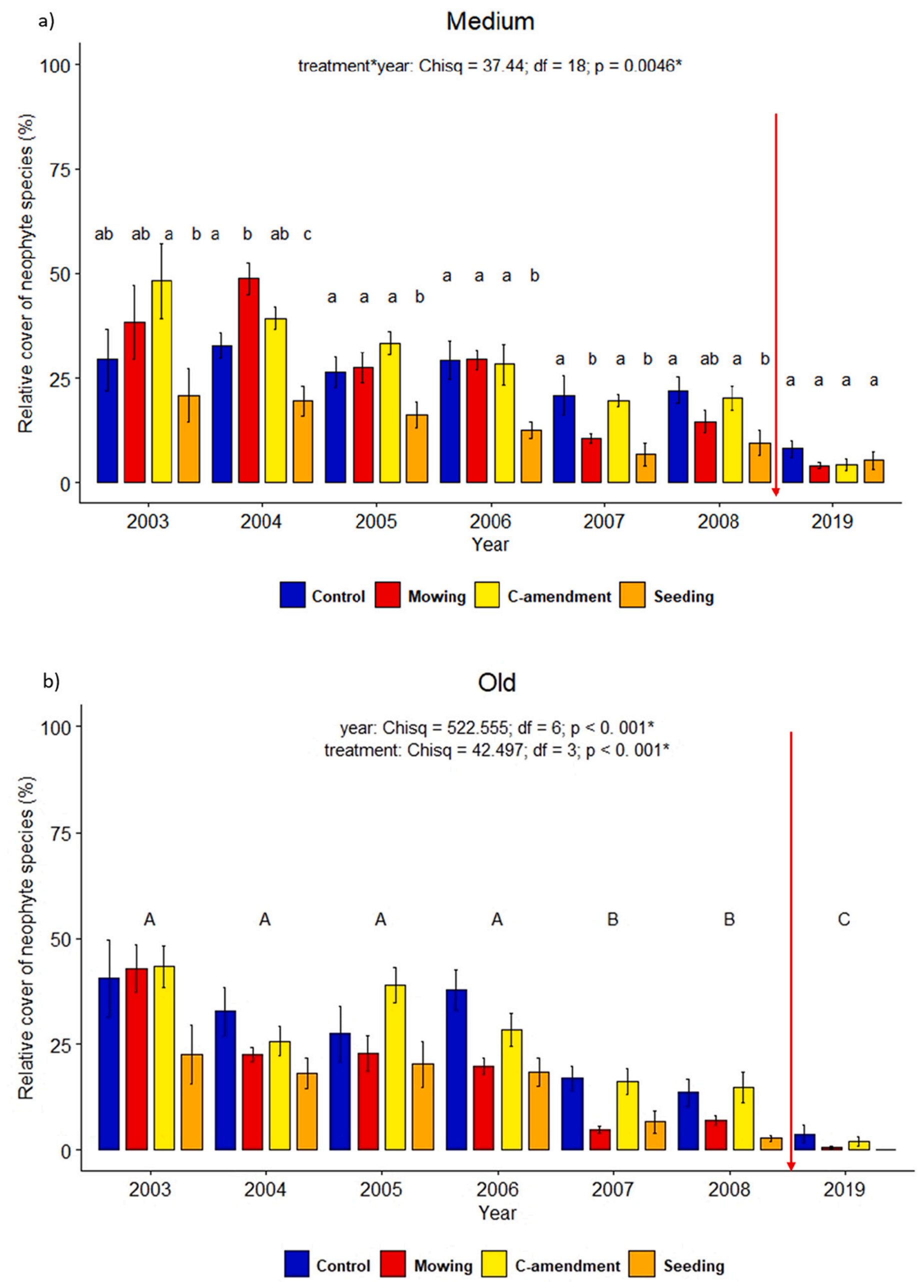

Fig. 4. Changes in the relative cover of neophyte species with treatments between 2003 and 2019 for a) Medium site and b) Old site. A within-year significant difference ($p < 0.05$) between treatments based on the Wald test is indicated by lowercase letters for the Medium site. A between-year significant difference ($p < 0.05$) is indicated by capital letters based on the Tukey HSD for the Old site. The red arrow represents the cessation of mowing and carbon amendment (2008). Means and SE are reported based on untransformed data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

important role in grassland restoration (Török et al., 2018b; Buisson et al., 2021).

The two sites showed slightly different vegetation development and differences in the impact of treatments. Most importantly, the relative cover of target species increased, and neophyte species decreased faster in the Old site than in the Medium site. Contrary to the Old site, only seeding significantly affected target species in the Medium site. These results can be due to the differences in the time of abandonment of the old fields (Medium site four years, Old site 16 years old before restoration) that is known to affect species composition (Csecserits et al., 2011). However, the age effect in our case cannot be separated from the landscape effect or the differences in soil characteristics (Llumiquinga, 2020; Llumiquinga et al., 2021). Semi-natural grasslands were present in a greater proportion in the landscape surrounding the Old site, which can be an excellent source of propagules of target species (Reis et al., 2022). On the other hand, the presence of agricultural fields near the Medium site may represent a threat of invasion, as agricultural land is home to many invasive species (Csecserits et al., 2016). As for the soil, the soil properties of the Medium site were more suitable for closed sand grasslands, while the soil of the Old site was more suitable for open sand grasslands (Llumiquinga, 2020; Llumiquinga et al., 2021).

5. Conclusion

We conclude that long-term monitoring is essential in restoration ecology. It may take many years for certain treatment effects to be detected in a restored system (cf. Herrick et al., 2006), and continuous monitoring can show if the vegetation development continues in the desired direction or adaptive management is needed to correct the restoration trajectory (Viani et al., 2017).

From the three treatments applied, initial seeding with a low diversity seed mixture of target species, including dominant grasses and subordinate species, is the most effective tool for restoring sand grasslands in the long term. This also indicates that dispersal limitation is the most critical constraint in sand grassland restoration (Halassy et al., 2016; Török et al., 2018b). Furthermore, target species can spread from small introduction plots and colonize larger areas. This supports the idea that instead of sowing or planting the whole degraded area, it is enough to create smaller establishment windows (or lines) from where the species can spread to the entire area (Valkó et al., 2016b; Martins, 2018). This is very important to reduce the costs that enable the restoration of larger areas to meet global restoration targets. Early seeding of native species can also hinder alien invasion, but further research is necessary to assess which target species should be planted and when to control invasive spread.

The manipulation of other limiting factors presented secondary importance in sand grassland restoration (Halassy et al., 2016; Halassy et al., 2019) and is suggested rather as a supplement to other treatments. Low-intensity mowing should be applied at the later phases of succession when the vegetation canopy is already closed due to other treatments, e.g. as a post-management after seeding of target species and/or control of invasive species (e.g. Reis et al., 2021). Furthermore, mowing should be used with caution as the establishment gaps created can also be occupied by invasive species if they are present in the surrounding landscape (Reis et al., 2021; Reis et al., 2022). Carbon amendment can also create establishment gaps, as it hinders vegetation development by decreasing productivity (Halassy et al., 2021). We suggest applying it in combination with the introduction of target species and preferably right after cropland abandonment when the nutrient content of the soil may be the highest.

Based on our results, the best practice for restoring sand grasslands after cropland abandonment in the region would be to sow a low-diversity seed mixture immediately after plowing in small scattered patches, supplemented by carbon amendment in case of high soil nitrogen content, followed by low-intensity management, such as infrequent mowing (or grazing) to reduce the cover of invasive and weed species.

Credit author statement

Katalin Török and Melinda Halassy conceived and designed the study; all authors participated in fieldwork; Katalin Szitár and Anna Kövendi-Jakó advised on statistical analysis; Bruna Paolinelli Reis performed statistical analyses; Bruna Paolinelli Reis and Melinda Halassy prepared the first version of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

The study was funded by the National Science Foundation of Hungary (NKFI-OTKA FK127996) and by the ELKH – Eötvös Loránd Research Network (ELKH SA-66/2021). Anna Kövendi-Jakó and Edina Csákvári were supported by the National Talent Program (NTP-NFTÖ-19-B-0159; NTP-NFTÖ-21-B-0034). Bruna Paolinelli Reis and Yesenia Belén Llumiquinga were supported by the Stipendium Hungaricum Program. We would like to thank the several surveyors for field data collection, principally Rebeka Szabó.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2022.106824.

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