Science of the Total Environment 622–623 (2018) 783–789

Contents lists available at ScienceDirect

Science of the Total Environment

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

# Litter removal does not compensate detrimental fire effects on biodiversity in regularly burned semi-natural grasslands

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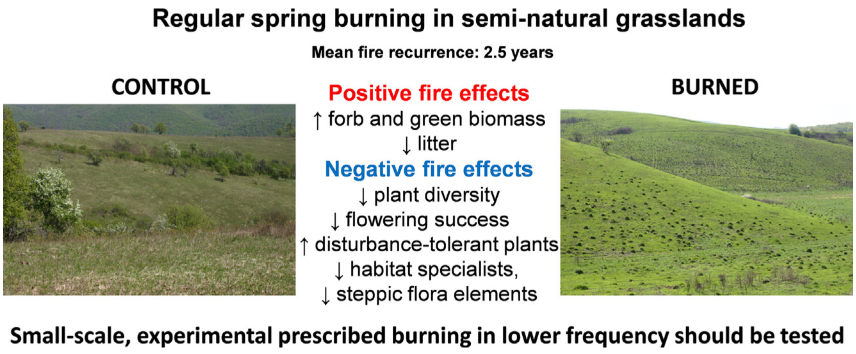
## HIGHLIGHTS

- We studied the effects of regular spring burning in species-rich foothill grasslands.
- Forb biomass and living biomass increased, litter decreased in burned grasslands.
- Plant diversity and flowering success were higher in unburned control grasslands.
- Species composition remained similar, but specialist plants declined after fire.
- Prescribed burning should be tested in small patches and lower frequency.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

*Article history:*
Received 20 September 2017
Received in revised form 30 November 2017
Accepted 30 November 2017
Available online xxxx

*Keywords:*
Biomass
Flowering success
Grassland management
Plant diversity
Prescribed burning
Restoration ecology

## ABSTRACT

Regulation of plant biomass accumulation is a key issue in effective grassland conservation in Europe. Burning is an alternative tool to regulate biomass dynamics in semi-natural grasslands even in the absence of grazing or mowing. We tested the effects of regular spring burning on the biomass fractions and fine-scale plant species composition of species-rich foothill grasslands in North-Hungary. There were five regularly burned and five control grasslands in the study; we collected twenty 20 × 20-cm sized biomass samples from each. We analyzed the main fractions (litter, graminoid and forb biomass), and the species-level biomass scores, and flowering success in the control and burned grasslands. We revealed that fire increased the amount of forb biomass and decreased the amount of litter, which suggested that regular burning might be feasible for regulating biomass dynamics. The non-metric multi-dimensional scaling (NMDS) showed a high similarity of the control and burned grasslands in species composition. However, plant diversity, and the number of flowering shoots decreased significantly in the burned grasslands. In regularly burned sites we found a significant decline of specialist species, as well as of steppic flora elements. Our results showed that besides its positive effect on biomass dynamics, high-frequency burning threatens the overall diversity and specialist plant species in semi-natural grasslands. We recommend that proper fire regimes should be first studied experimentally, to provide a scientific basis for the application of prescribed burning management in such habitats.

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https://doi.org/10.1016/j.scitotenv.2017.11.356

## 1. Introduction

In Europe semi-natural grasslands have been created and maintained by natural and anthropogenic disturbances, such as clear-cutting of forests, grazing, mowing and fire, which regularly remove the accumulated biomass and prevent the encroachment of shrubs and trees (Poschlod and Wallis de Vries, 2002). Thus, disturbance plays a crucial role in maintaining the open landscape structure in these ecosystems. Regular biomass removal decreases interspecific competition for light, controls litter accumulation and suppresses competitor species; thus, allows the co-existence of several light-demanding forbs (Dengler et al., 2014; Habel et al., 2013). Preservation of these grasslands relies on essential disturbance regimes, which control biomass dynamics and woody encroachment and thereby support the maintenance of the characteristic species composition. Such disturbance regimes usually include grazing and mowing which are the most common land use practices in grasslands (Tälle et al., 2016).

Formerly, socio-economic structure of many regions favored low-intensity and extensive agriculture, i.e. extensive grazing or hand-mowing of marginal, species-rich semi-natural grasslands (Babai and Molnár, 2014). Nowadays industrialization and urbanization, as well as agricultural intensification all resulted in the depopulation of rural areas and the abandonment of marginal semi-natural grasslands (Halada et al., 2017; Valkó et al., 2011). This situation makes the conservation of semi-natural grasslands challenging, because the implementation of formerly typical grazing or mowing regimes is problematic in regions, where there are no animal husbandry anymore; thus, there is no need for pastures and hay (Isselstein et al., 2005). The introduction of some kind of biomass removal regime in such marginal areas is urgent in order to prevent the formation of secondary scrublands or forests, and to halt the disappearance of the conservation values of semi-natural grasslands (Valkó et al., 2012). It is crucial that biomass removal should be of such an intensity, severity and frequency, which can prevent litter accumulation and woody encroachment, but is not detrimental for characteristic species of semi-natural grasslands (Valkó et al., 2014). These species have been mostly adapted to extensive biomass removal regimes (moderate grazing or hand-mowing, Isselstein et al., 2005); thus, it is still a question whether they can tolerate other types of biomass removal such as burning.

Several studies tested prescribed burning, as an alternative biomass removal tool in semi-natural grasslands (Kahmen et al., 2002; Köhler et al., 2005; Ryser et al., 1995; Wahlman and Milberg, 2002). The idea of such experiments is to seek for cost-effective and less labor-intensive alternatives to grazing and mowing. Most of these studies found that regular burning in every year leads to an untargeted species composition which is far from the desired state (Valkó et al., 2014). The likely reason is that species characteristic of nonfire-prone habitats are sensitive to high-frequency fire events and in parallel, the encroachment of re-sprouting competitor species poses an additional threat for grassland specialist plant species (Michielsen et al., 2017; Valkó et al., 2014). Even though high-frequency fires can lead to the degradation of nonfire-prone grassland vegetation (Deák et al., 2014; Milberg et al., 2014; Valkó et al., 2014; Wahlman and Milberg, 2002), low-frequency burning might be a proper tool for grassland management in such habitats (Page and Goldammer, 2004; Valkó et al., 2016). Identifying the proper fire return periods is crucial for the successful application of prescribed burning (Fuhlendorf et al., 2009).

The sensitivity of plant species to fire has still remained largely unexplored in grasslands. In European grasslands burning usually was done in small experimental plots (usually between 20–100 $m^2$), and species composition was assessed using visual cover estimation (Hansson and Fogelfors, 2000; Kahmen et al., 2002, Köhler et al., 2005; Moog et al., 2002; Ryser et al., 1995; Valkó et al., 2016) or by recording presence/absence of species in small plots (Liira et al., 2009; Wahlman and Milberg, 2002). Biomass was quite rarely studied (but see Ryser et al., 1995; Valkó et al., 2016; Vogels, 2009), and if so, only living biomass, litter and the biomass of mosses were concerned.

The novelty of our study is that we tested the effects of regular burning by comparing vegetation of grasslands regularly burned by local people with ones that have not been burned. We sampled a high number of plots to control for potential site heterogeneity and variances in species composition. We combined the advantages of studying biomass composition and sophisticated analyses of functional species groups by analyzing biomass samples at the species level. In this way we could directly detect the effect of burning on fine-scale species composition and biomass components.

Our aim was to test the effects of regular spring burning on the biomass and fine-scale plant species composition of species-rich semi-natural dry grasslands. We tested the effects of regular spring burning to evaluate whether it can be a feasible management option for suppressing litter accumulation and maintaining plant diversity in grasslands. We tested the following hypotheses: (i) Spring burning reduces accumulated litter and increases living biomass. (ii) Burning favors disturbance-tolerant and generalist species. (iii) Species confined to nonfire-prone semi-natural grasslands are suppressed by burning. (iv) Species originating from steppe and Mediterranean regions are favored by burning, as they are characteristic to ecosystems regularly exposed to wildfires.

## 2. Materials and methods

### 2.1. Study sites

Our study sites are in the Aggtelek National Park, North-Hungary. We selected ten semi-natural grasslands, belonging to the habitat type 'Semi-natural dry grasslands and scrubland facies on calcareous substrates (Festuco-Brometalia)', a habitat of community interest in the Habitats Directive (Calaciura and Spinelli, 2008). These grasslands were formed by forest-cutting and have been maintained by extensive grazing or mowing during the past centuries. Festuco-Brometea grasslands often hold an extremely high biodiversity (Habel et al., 2013; Wilson et al., 2012). Typical grass and sedge species of this habitat are *Brachypodium pinnatum*, *Carex montana*, *Festuca valesiaca*, *Helictotrichon pubescens* and *Stipa pulcherrima*. Forbs are usually present with a high diversity; typical species are *Centaurea scabiosa*, *Cirsium pannonicum*, *Dorycnium germanicum*, *Hippocrepis comosa*, *Inula ensifolia*, *I. salicina*, *Peucedanum cervaria* and *Salvia pratensis*. Several rare and protected species, such as *Centaurea triumfettii*, *Chamaecytisus albus*, *Linum tenuifolium* and *Polygala major* occur in Festuco-Brometea grasslands. All grasslands were on South - South-East exposure, between elevations of 200 and 400 m a.s.l. Soils are leptosols formed on calcareous substrates. For location of the study sites and soil parameters, please see Appendix 1.

### 2.2. Treatments

There were five control grasslands, and five grasslands were burned. In control grasslands, there was no fire during the last century. Burned grasslands have regularly been burned since decades. Local people typically burn grasslands in early spring in the study region. The sites were burned with an average burning frequency of 2.5 years. There were slight differences between the yearly patterns of grassland burning, but all burned sites can be considered as regularly burned compared to the estimated fire return period of wildfires in Central-Europe during the Holocene (approximately 150 years, Feurdean et al., 2013). In former times, burning was a typical practice for improving fodder quality, but nowadays the traditional knowledge associated to this practice is disappearing and local people burn the grasslands mainly as a 'habit' (Deák et al., 2014). None of the grasslands are utilized by mowing or livestock grazing; however, grazing by the game population (deer and roe deer) is typical in the region.

### 2.3. Sampling setup

We designated a 10 m × 50 m-sized plot in the ten studied grasslands, where we collected twenty 20 cm × 20 cm-sized aboveground biomass samples (in total 200 samples). Biomass samples were collected between 28 May and 2 June 2012, at the peak of biomass production. Samples were air-dried for three weeks, then sorted and processed in laboratory. Litter, mosses and all species of vascular plants were separated. The use of specific biomass data provides the most reliable estimation of species abundances, enabling us to reveal the fine-scale species composition of the grasslands (Chiarucci et al., 1999; Kelemen et al., 2013). We also listed the number of flowering shoots per species in each sample. The dry mass of each biomass fraction was weighted by a Sartorius type balance with 0.01 g accuracy.

### 2.4. Species classifications

We classified all species into functional groups (forbs, and graminoids) based on their morphological features: forbs - dicots and non-graminoid monocots belonging to families *Amaryllidaceae*, *Iridaceae*, and *Orchidaceae*; graminoids - Juncaceae, Cyperaceae and Poaceae. For compiling the list of species protected at the national level we used the red list of Király (2007). Species were classified according to their ecological characteristics as follows.

*Social behavior types*. We categorized species based on their social behavior types (SBT) to weeds, disturbance-tolerants, generalists, competitors and specialists (Borhidi, 1995).

*Habitat specificity* (HS). We expressed habitat specificity based on the coenological classification system of Borhidi (1995) on a four-grade scale, where increasing HS score means that a plant is more and more confined to semi-natural grasslands. HS = 0 is for species occurring in a wide range of habitats, while HS = 3 species are confined to a certain phytosociological alliance (i.e. Festucion valesiaceae grasslands).

*Flora elements*. Species were classified to the following flora element categories based on their distribution range (Horváth et al., 1995): cosmopolitan, European, continental, steppic and Mediterranean.

### 2.5. Statistical analyses

The effects of 'management' (control/burned, fixed factor) and 'site' (random factor) on the vegetation characteristics were tested by Generalized Linear Mixed Models (GLMMs; Zuur et al., 2009) and Least Significant Difference (LSD) tests in SPSS 20.0. Dependent variables were the following: main biomass fractions (total biomass, living biomass, graminoid biomass, forb biomass, moss biomass, litter), Shannon diversity, number of flowering shoots, number of flowering species and species richness and biomass of the functional groups (social behavior types, habitat specificity, and flora elements). Species richness scores of functional groups were fitted with Generalized Linear Mixed Models (GLMMs) using a Poisson distribution with log link function. Biomass scores of the functional groups were $\log(x + 1)$ transformed to approximate them to normal distribution. For the analysis of biomass scores we used normal distribution with identity link function in the GLMMs. Level of significance was set at $p < 0.05$.

We identified the significant indicator species of the control and burned grasslands with the IndVal method, based on biomass scores (Dufrêne and Legendre, 1997). For the analyses we used the 'labdsv' package in an R environment (R Core Team, 2016). For detecting the differences in the species composition of control and burned grasslands and non-metric multi-dimensional scaling (NMDS ordination) based on presence-absence scores using Rogers-Tanimoto similarity was plotted (Legendre and Legendre, 2012) in R.

## 3. Results

### 3.1. Biomass fractions

Burned grasslands were characterized by significantly higher amount of green and forb biomass and lower amount of litter than control grasslands (Fig. 1, Table 1). The biomass of graminoids and mosses was not affected by the management type (Fig. 1, Table 1). Control grasslands were characterized by higher Shannon diversity than the burned ones (Table 1). The number of flowering shoots, number of flowering species, and the ratio of flowering species were all higher in the control grasslands compared to the burned ones (Table 1). Biomass of protected species was also higher in the control samples (Table 1).

### 3.2. Functional groups

Species richness of disturbance-tolerant plants was higher in the control grasslands, while generalist and specialist species were present in higher numbers in the burned grasslands (Table 2). Biomass of weeds and disturbance-tolerant species was higher in burned grasslands, while specialist species had higher biomass scores in control grasslands (Table 2, Fig. 2).

Both species richness and biomass of species with low habitat specificity (HS score 0) were higher in burned grasslands (Table 1, Fig. 3). Species confined to Festucion valesiacae grasslands (HB score 3) had higher biomass and species richness in the control samples (Table 2, Fig. 2).

European and steppic flora elements had higher species richness in the control grasslands than in the burned ones (Table 2). The biomass of steppic flora elements was lower in the control grasslands. Both cosmopolitan and Mediterranean flora elements were recorded with higher biomass in the burned grasslands (Table 2, Fig. 4).

### 3.3. Species composition

We found altogether 107 species in the biomass samples. There were 93 species recorded in the control and 90 in the burned grasslands. The IndVal analysis identified 16 significant characteristic species of control and 9 of burned grasslands (Table 3). The most frequent indicator species of control grasslands were *Festuca valesiaca*, *Hippocrepis comosa*, *Inula ensifolia*, *Stipa pulcherrima* and *Thymus pannonicus*. In burned grasslands *Brachypodium pinnatum*, *Elymus hispidus*, *Peucedanum cervaria*, *Salvia pratensis* and *Vicia tenuifolia* were the most frequent indicator species. The NMDS ordination based on the

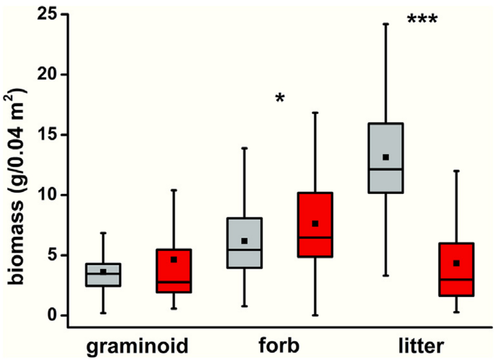

**Fig. 1.** Main biomass fractions (graminoid, forb and litter) in the control (gray) and burned (red) grasslands. Significance of the LSD tests are marked with asterisks, ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 1**
Effects of burning on the biomass characteristics of the studied grasslands analyzed by Generalized Linear Mixed Models. Significant effects ($p < 0.05$) are marked with boldface. Notations: B – biomass, SR – species richness.

| | *p* | F | Estimate |
|---|---|---|---|
| Litter (g/0.04 m$^2$) | **0.000** | **311.165** | **−0.488** |
| Living B (g/0.04 m$^2$) | **0.005** | **8.133** | **0.066** |
| Graminoid B (g/0.04 m$^2$) | 0.421 | 0.65 | 0.022 |
| Forb B (g/0.04 m$^2$) | **0.032** | **4.675** | **0.063** |
| Moss B (g/0.04 m$^2$) | 0.792 | 0.070 | 0.007 |
| Shannon diversity (/0.04 m$^2$) | **0.010** | **6.742** | **−0.021** |
| Flowering species SR (/0.04 m$^2$) | **0.000** | **12.809** | **−0.340** |
| Number of flowering shoots (/0.04 m$^2$) | **0.000** | **52.913** | **−0.485** |
| Ratio of flowering species (/0.04 m$^2$) | **0.004** | **8.284** | **−0.017** |
| Protected species SR (/0.04 m$^2$) | 0.579 | 0.308 | −0.124 |
| Protected species B (g/0.04 m$^2$) | **0.038** | **4.346** | **−0.050** |

species composition showed that there was a considerable overlap between the control and burned grasslands; they were not separated along the first two axes (Fig. 5). Burned grasslands had a more heterogeneous species composition compared to the control.

## 4. Discussion

We found that burned grasslands produced higher amounts of living biomass than control ones; thus, burning increased biomass production (Dhillion and Anderson, 1994; Kitchen et al., 2009; Valkó et al., 2016). We also found that regular spring burning is a highly effective tool for decreasing litter accumulation in semi-natural grasslands (in agreement with Köhler et al., 2005 and Ryser et al., 1995). Decreasing the amount of litter is one of the most important tasks in conservation of semi-natural grasslands; thus, spring burning is an effective tool to overcome this problem. Besides the evident advantages of burning in controlling biomass dynamics, we demonstrated that regular spring fires have substantial effects on grassland conservation values; thus, the applicability of prescribed burning management should be carefully considered in the studied habitats.

**Table 2**
Effects of burning on the biomass and species richness of the functional groups analyzed by Generalized Linear Mixed Models. Significant effects ($p < 0.05$) are marked with boldface. Notations: B – biomass, SR – species richness.

| | *p* | F | Coefficient |
|---|---|---|---|
| Social behavior types | | | |
| Weed SR | 0.264 | 1.252 | 0.233 |
| Weed B | **0.002** | **9.629** | **0.043** |
| Disturbance-tolerant SR | **0.008** | **7.121** | **0.257** |
| Disturbance-tolerant B | **0.000** | **33.171** | **0.184** |
| Generalist SR | **0.000** | **23.469** | **−0.259** |
| Generalist B | 0.647 | 0.210 | 0.014 |
| Competitor SR | 0.723 | 0.126 | −0.04 |
| Competitor B | 0.303 | 1.068 | 0.034 |
| Specialist SR | **0.003** | **9.369** | **−0.392** |
| Specialist B | **0.000** | **13.719** | **−0.113** |
| Habitat specificity (HS) | | | |
| HS0 SR | **0.033** | **4.633** | **0.186** |
| HS0 B | **0.000** | **17.32** | **0.158** |
| HS1 SR | 0.146 | 2.126 | −0.099 |
| HS1 B | **0.002** | **9.486** | **0.095** |
| HS2 SR | **0.000** | **19.489** | **0.309** |
| HS2 B | 0.335 | 0.936 | −0.034 |
| HS3 SR | **0.003** | **9.311** | **−0.417** |
| HS3 B | **0.001** | **11.455** | **−0.101** |
| Flora elements | | | |
| Cosmopolitan SR | 0.102 | 2.699 | 0.642 |
| Cosmopolitan B | **0.001** | **11.16** | **0.065** |
| European SR | **0.016** | **5.912** | **−0.135** |
| European B | 0.399 | 0.714 | 0.025 |
| Continental SR | 0.442 | 0.593 | −0.079 |
| Continental B | 0.803 | 0.063 | 0.009 |
| Steppic SR | **0.015** | **6.040** | **−0.292** |
| Steppic B | **0.003** | **8.809** | **−0.108** |
| Mediterranean SR | 0.164 | 1.954 | −0.131 |
| Mediterranean B | **0.002** | **10.115** | **0.120** |

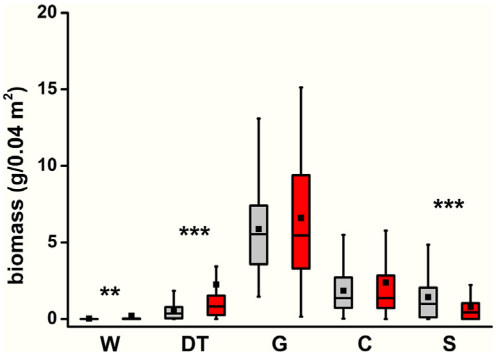

**Fig. 2.** Biomass of species groups of social behavior types, namely weeds (W), disturbance-tolerants (DT), generalists (G), competitors (C) and specialists (S) in the control (gray) and burned (red) grasslands. Significance of the LSD tests are marked with asterisks, ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Frequent burning was often found to decrease the conservation value of grasslands (Kahmen et al., 2002; Milberg et al., 2014) when fire return periods were much shorter than the optimum (Valkó et al., 2014). In former studies, where regular burning was applied, both Kahmen et al. (2002) and Moog et al. (2002) detected strikingly different species composition between the burned and control grasslands. In our study, species composition of burned and control grasslands were similar even though the burned sites have been regularly burned for decades (see Fig. 5). A possible reason is that, even though the studied grasslands were burned regularly (average fire return frequency was 2.5 years), but not in every year as in the former studies (Kahmen et al., 2002; Moog et al., 2002). Thus, in the years between fire events, the vegetation could at least partially recover. The similar species composition of burned and control grasslands may suggest that regular spring burning can regulate biomass dynamics without any major effect on grassland species pools. But if we look at other attributes, we can identify several unfavorable effects of regular burning on grassland conservation values.

Plot-level plant diversity was lower in the regularly burned grasslands. Decreased diversity was associated with a significantly decreased reproduction rate, shown by the decreased number of flowering species and flowering shoots in burned grasslands. After fire, several species have to allocate a lot of energy to re-sprouting (Cummings et al., 2007) to compensate for the loss of vegetative biomass, and therefore

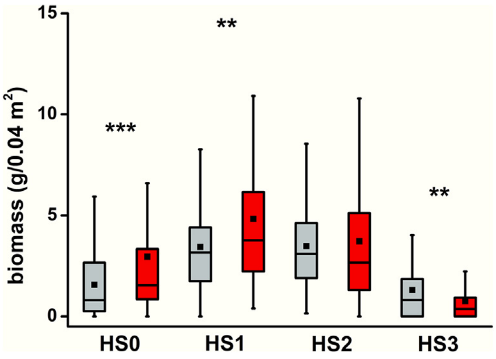

**Fig. 3.** Biomass of species groups of habitat specificity in the control (gray) and burned (red) grasslands. HS0 means species occurring in a broad range of habitats, HS3 means species confined to semi-natural grasslands. Significance of the LSD tests are marked with asterisks, ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

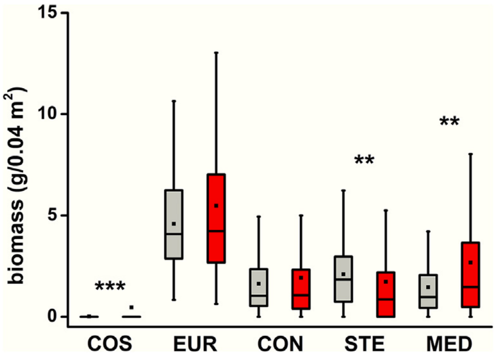

**Fig. 4.** Biomass of species groups of flora elements (cosmopolitan, European, continental, steppic and Mediterranean) in the control (gray) and burned (red) grasslands. Significance of the LSD tests are marked with asterisks, ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

they can allocate fewer resources to generative reproduction. Decreased flowering success poses a threat for plant species and decreases genetic variability of the populations on the long run. Moreover, decreased amount of flowering shoots decreases food availability for pollinating insects and thus it has a negative effect on the ecosystem functioning (Baude et al., 2016; Kovács-Hostyánszki et al., 2017).

Burning was the most detrimental for species with highly specialized habitat requirements, i.e. for those confined to dry semi-natural Festucion valesiacae grasslands. Contrary, species occurring in a wide range of habitats were supported by burning. These results highlight the homogenizing effect of too frequent burning and the vulnerability of habitat specialist species (see also Milberg et al., 2014). The GLMMs showed that burned grasslands were characterized by a high number and biomass of disturbance-tolerant species. Many of them are effective seeders or re-sprouters. Legumes with hard seed coat, such as *Medicago falcata* and *Vicia tenuifolia* can effectively germinate after fire, as fire can break their seed dormancy and initiate germination (Ruprecht et al., 2013). Disturbance-tolerant grasses, such as *Brachypodium pinnatum* and *Poa angustifolia* are able to re-sprout vigorously after fire from their basal meristems (Köhler et al., 2005; Wiegmann and Waller, 2006). Direct fire effects and also the increased abundance of disturbance-tolerant plants decreased the biomass and species richness of specialist species in the burned grasslands (see also Ruprecht et al., 2016).

**Table 3**
Significant characteristic species ($p < 0.05$) of the control and burned grasslands based on the IndVal analysis. Species protected at the national level are marked by an asterisk.

| | IndVal score | p | Frequency |
|---|---|---|---|
| Control grasslands | | | |
| *Festuca valesiaca* | 0.547 | 0.001 | 145 |
| *Inula ensifolia* | 0.395 | 0.015 | 115 |
| *Stipa pulcherrima** | 0.376 | 0.001 | 41 |
| *Hippocrepis comosa* | 0.325 | 0.001 | 45 |
| *Thymus pannonicus* | 0.195 | 0.017 | 39 |
| *Carex michelii* | 0.190 | 0.001 | 19 |
| *Seseli varium* | 0.190 | 0.001 | 19 |
| *Selinum carvifolia* | 0.132 | 0.003 | 16 |
| *Peucedanum oreoselinum* | 0.129 | 0.001 | 14 |
| *Viola hirta* | 0.127 | 0.024 | 22 |
| *Genista tintoria* | 0.122 | 0.041 | 22 |
| *Pulsatilla grandis** | 0.120 | 0.003 | 12 |
| *Melampyrum arvense* | 0.112 | 0.021 | 20 |
| *Scorzonera austriaca* | 0.103 | 0.028 | 16 |
| *Hieracium hoppeanum* | 0.095 | 0.007 | 11 |
| *Potentilla arenaria* | 0.093 | 0.014 | 12 |
| Burned grasslands | | | |
| *Brachypodium pinnatum* | 0.533 | 0.003 | 159 |
| *Peucedanum cervaria* | 0.367 | 0.001 | 80 |
| *Elymus hispidus* | 0.310 | 0.001 | 31 |
| *Salvia pratensis* | 0.255 | 0.005 | 51 |
| *Vicia tenuifolia* | 0.208 | 0.002 | 36 |
| *Carex tomentosa* | 0.168 | 0.002 | 26 |
| *Dactylis glomerata* | 0.150 | 0.001 | 15 |
| *Salvia verticillata* | 0.097 | 0.028 | 17 |
| *Euphorbia virgata* | 0.067 | 0.049 | 8 |

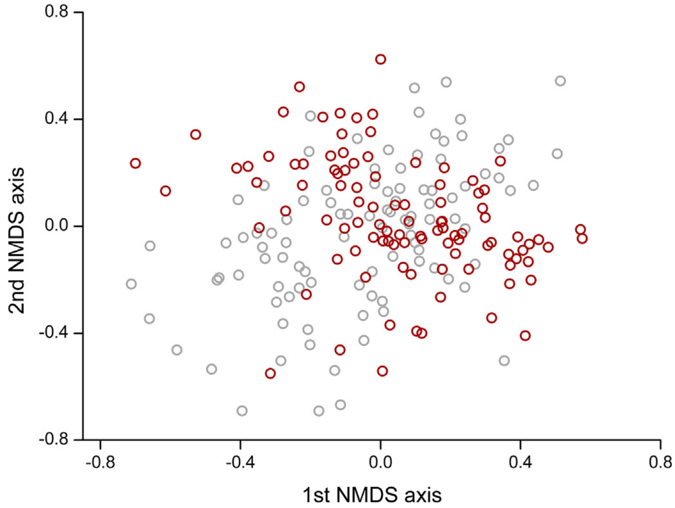

**Fig. 5.** Species composition of the biomass samples in the control (gray circles) and burned (red circles) grasslands, based on presence-absence data (Rogers-Tanimoto similarity, NMDS ordination, stress = 0.2721). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Species of pan-European distribution decreased in number in burned areas, likely because pan-European species usually occur in nonfire-prone habitats, thus they are evolutionarily not adapted to fire. These species formed the largest group of flora elements, and their decrease is responsible for the general decrease of species richness in burned grasslands. We hypothesized that species of dry ecosystems where wildfires are typical, such as Mediterranean and steppic species will be supported by fire. Traits adaptive for dry ecosystems are often similar to those adaptive for fire-prone ecosystems (Keeley et al., 2012). We found that species of Mediterranean distribution were supported by burning, as they had significantly higher biomass scores in the burned grasslands. This is likely because Mediterranean ecosystems are highly fire-prone (Francos et al., 2016; Keesstra et al., 2017; Lucas-Borja et al., 2017; Pereira et al., 2014) and their species are adapted to regular fires (Keeley et al., 2012). An interesting finding was that contrary to our expectations both the biomass and species richness of steppic species decreased significantly in the burned grasslands. Even though steppes are exposed to regular wildfires, steppic flora elements were suppressed by frequent fires in the studied semi-natural grasslands. This result has a crucial importance from the nature conservation viewpoint, as steppic elements include several rare and protected species, such as *Chamaecytisus albus*, *Iris pumila* and *Pulsatilla grandis*. The latter two species have the peak of flowering season in springtime, which can explain their vulnerability to regular spring burning. There are several field observations, that single early spring fire events before flowering season support steppic plants, such as *Adonis*, *Pulsatilla* and *Stipa* species, by supporting their re-sprouting or by providing better germination conditions by decreasing the litter layer (Deák et al., 2014; Sandström et al., 2017). Several European forest steppe regions are characterized by low-frequency cool-season low severity fires, with an average fire return interval of several decades (Archibald et al., 2013; Lysenko, 2008), thus, their characteristic species cannot tolerate very short fire return periods.

## 5. Conclusions

Our results showed that regular spring burning can effectively regulate biomass dynamics and can be a proper tool for decreasing litter accumulation. However, regular burning does not maintain the conservation values of semi-natural grasslands in the long run. We identified species groups that are the most vulnerable to regular spring burning. These species were steppic elements, and specialist species of semi-natural grasslands, which are the ones being most threatened by anthropogenic effects and changes in management regimes (Dengler et al., 2014; Habel et al., 2013). As semi-natural grasslands are unique biodiversity hotspots and refuges for these species, it is crucial to mitigate the negative effects of regular fire. Thus, we highly recommend controlling the practice of ‘habitual’ burning of grasslands. Controlled prescribed burning experiments would be essential to test the effects of fires with longer fire-return periods (Valkó et al., 2014). We recommend that proper fire regimes should be first studied experimentally, to provide a scientific basis for the application of prescribed burning management in such habitats.

## Acknowledgements

We are thankful to the rangers of Aggtelek National Park Directorate for their help in fieldwork. Authors were supported by OTKA PD 111807 (OV), NKFI FK 124404 (OV), NKFI KH 126476 (OV), OTKA PD 116200 (AK), OTKA K 116239 (BT), NKFI KH 12647 (BT), NKFIH K 119225 (PT), NKFI PD 124548 (TM), OTKA PD 115627 (BD) and the Bolyai János Fellowship of the Hungarian Academy of Sciences (OV, BD). OV and BD were supported by the ÚNKP-17-4-III-DE-151 and ÚNKP-17-4-III-DE-160 New National Excellence Program of the Ministry of Human Capacities. AK and TM were funded by the MTA's Post Doctoral Research Program.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2017.11.356.

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