Title
Carbon uptake changed but vegetation composition remained stable during transition from grazing to mowing grassland management

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Highlights

Vegetation composition and diversity did not change for six years after the conversion from grazing to mowing.

Even the detailed fine-scale analyses could not reveal differences.

Carbon uptake differed between grazed vs. mowed sites due to biomass removal intensity.

Returning from mowing to grazing would probably restore C uptake capacity at the mowed site because the vegetation composition remained stable.

Abstract

Grasslands could play an important role in supporting livestock, in carbon sequestration and in biodiversity conservation. Different grassland managements may change the vegetation composition of grasslands, which could alter these ecosystem services. We studied the effects of grazing vs. mowing on the vegetation composition (2012–2016) and on the carbon uptake (2011–2013) of sandy grasslands in Hungary to study if the vegetation composition differs and if it does, whether it affects carbon uptake. To observe differences in vegetation composition between the two types of management regimes we performed fine-scale vegetation survey in adjacent grazed and mowed sites. We compared species compositions and vegetation diversity indices between the management regimes based on permutational ANOVA, mixed effect model and information theory models. We used fine-scale vegetation survey because it has the potential to indicate vegetation changes within six years as changes in species richness and diversity are usually detected after 10-20 years. Carbon uptake was measured in parallel with eddy covariance technique at both sites. In spite of the contrasting management regimes the vegetation composition was stable (no differences observed in the diversity indices), while carbon uptake was significantly greater in the grazed
The vegetation was heterogeneous (patchy) and had a high species richness at both sites (grazed: 91 species ha\(^{-1}\), mowed: 90 species ha\(^{-1}\)) which might have contributed to the stability of the vegetation composition. We concluded that differences in carbon uptake existed between the grazed vs. mowed sites due to biomass removal intensity with no differences in the vegetation composition.

Keywords: community diversity; microcoenology; carbon uptake; grazing; mowing

1. Introduction

Grasslands could play an important role in providing feed for grazing livestock (Henwood, 2010), in carbon sequestration (Soussana et al., 2010) and in biodiversity conservation (in case of natural, semi-natural grasslands) (Báldi et al., 2013; Täll et al., 2016). Grasslands store 20% of the world soil organic carbon (SOC) while sequestrating an average of 0.03 to 1 t of C (carbon) per ha per year (Smith et al., 2008). However, grasslands could be a source of C, depending on the land type, soil parameters, climatic factors and management regimes (Smith et al., 2008; Nagy et al., 2007). To maintain and enhance these ecosystem services proper grassland management regimes and management intensities should be applied.

It was shown that different grassland managements (e.g. grazing vs. mowing) could change the composition of the vegetation (Täll et al., 2016), which can affect C sequestration of grasslands (Klumpp et al., 2011; LeCain et al., 2002). However, little is known about how changes in the management regimes (transition from grazing to mowing) affect C uptake and, in parallel with this, how the fine-scale vegetation composition changes in response to a switch in the management regimes and how this affects C uptake. It was found that intensified grassland management e.g. sowing with legumes (Conant et al., 2017), fertilization (Senapati
or increasing species richness (Cong et al., 2014) could enhance C sequestration. It was shown in a 50-year-long experiment that vegetation composition changes due to differences in grassland management regimes (grazing and grazing exclusion) influenced the C sequestration capacity of the grassland (LeCain et al., 2002). Due to the exclusion of grazing the ratio of plants with C3 photosynthetic pathway increased, while in the grazed site the proportion of C4 plants increased. This example shows as how vegetation composition affected C uptake (coupled with climatic condition) as grazing exclusion site had higher C uptake in cold years (preferable to plants with C3 pathway), while the grazed site had higher C uptake in warm years (preferable to plants with C4 pathway) compared to the other site (LeCain et al., 2002).

Vegetation composition is under the influence of the management of biomass production. In general, mowing is a sudden event when biomass is usually homogeneously removed, while during grazing the biomass removal is patchy and prolonged (Adler et al., 2011). During mowing the light penetration to the ground increases, the litter layer is reduced and due to the lack of fertilization the soil nutrients are depleted. On the other hand, grazing leads to a higher rate of nutrient turnover (due to urine and dung) compared to mowing. In many cases due to either grazing or mowing, the vegetation composition and biodiversity is usually altered (Házi et al., 2012; Jantunen, 2003; Moog et al., 2002; Socher et al., 2012; Vadász et al., 2016). However, no differences were also observed in species richness (e.g. Hansson and Fogelfors, 2000; Stammel et al., 2003). Tälle et al., (2016) reviewed that grazing generally had a more positive effect on the conservation value of grasslands, i.e. grazing led to higher biodiversity compared to mowing but the magnitude of the positive effects was generally too small to moderate. Vegetation composition was found to be rather stable under constant grazing or mowing even during long-term (>15 years) (Hellström et al., 2006; Sullivan et al., 2017) or mid-term time periods (cca. 10 years, Pavlů et al., 2011), although short term changes were
also observed (<5 years, Wan et al., 2016; Valkó et al., 2012). There is still little evidence with regard to how grazing vs. mowing changes vegetation composition at fine-scale in short or long time periods. Accurate knowledge on vegetation (type, composition, structure), soil, climate and management parameters (stocking rate, mowing intensity, timing) are needed, since due to the large differences obtained in these parameters (e.g. arid grassland vs. wet meadows etc.) no general patterns can yet be identified.

Mowing in continental grasslands generally suppresses the dominant graminoid competitors, favours forbs and decreases the mortality of light-demanding seedlings, while it is also stressed that responses of plants to mowing can be highly species specific (Valkó et al., 2012). It has been observed that due to mowing the frequency of drought tolerant species increased (Socher et al., 2012), such as Bromus inermis or Elymus repens because of the increased light and heat stress within the vegetation (Kovács and Csízi, 2004). On the other hand, due to the selective grazing of cattle it can be observed that the frequency of unpalatable (Eryngium campestre, Ononis spinosa) and trampling resistant species (Festuca pseudovina, Cynodon dactylon) increased (Kovács and Csízi, 2004). Vegetation could react species-specifically to either grazing or mowing. Thus, grazing provided clonal grasses and forbs with good conditions (e.g. Trifolium repens), whereas grasses with below-ground storage organs were better supported by mowing (e.g. Molinia caerulea) (Stammel et al., 2003). In general, grazing and mowing could also contribute to high biodiversity (Tälle et al., 2016), provided that the disturbance caused by the management regime is of intermediate level (Crawley, 1997; Török et al., 2018).

In this study we used microcoenological methodology (fine-scale vegetation survey) to study the effect of transition from grazing to mowing on the fine-scale vegetation composition of the grazed and mowed grasslands. This method was used because fine-scale (5×5 cm quadrates) diversity changes could be detected earlier compared to cover estimations in larger
quadrats (traditionally 2×2 m in these grasslands) (Bartha et al., 1995, 2004). Microcoenology provides a well-documented and precise tool (high resolution, spatially explicit, multi-scale sampling design) to indicate changes in the vegetation composition of grasslands early under varying management regimes (Bartha et al., 2004; Matus and Tóthmérész, 1990; Virágh et al., 2008). It is a tool not only for nature conservation (indication of degradation) but also for ecosystem management purposes (when vegetation composition and its changes are linked to ecosystem services) (Loreau et al., 2003; Wilcox et al., 2017). It was proved that behind the apparent larger scale stability (invariance) of vegetation there could be intensive fine-scale dynamics operating (Herben et al., 1993), suggesting that multidirectional and uncorrelated fine-scale local transitions stabilize the larger scale patterns (Wang and Loreau 2016). Any forces that synchronize the fine-scale processes will destabilize the community and will result finally in larger scale transitions. The information theory models (Juhász-Nagy and Podani 1983, Juhász-Nagy 1993) offer a methodology to describe and understand details of fine-scale patterns, therefore we used the compositional diversity (CD) index as a sensible tool for detecting initial stages of vegetation changes (Bartha et al., 1998, 2011).

Our goal was to investigate the effects of grazing and mowing on the fine-scale pattern of plant species diversity in sandy, semi-arid grasslands in Hungary (Bugac) and to relate vegetation composition changes to C sequestration measured (and published; Koncz et al., 2017) at both sites. We hypothesized that the contrasting management regimes (grazing vs. mowing) had an effect on vegetation composition.

We expected that;

1) switching the management from grazing to mowing would change the fine-scale vegetation composition which could be detected after five years,
2) diversity of vegetation composition would decrease while homogeneity would increase in the mowed site, although we do not expect changes (besides inter-annul variability) at the grazed site.

3) vegetation composition changes would influence C sequestration and C sink activity.

4) C sequestration in the mowed site will be lower compared to grazed site.

In our previous study we found that changing the management from grazing to mowing in 2011 did not change the microcoenological composition between the grazed and mowed sites in the first year (2012) (Koncz et al., 2014). In the present study we analyze the results obtained since then (2012–2016). The measurements of the vegetation composition and functional parameters (C uptake) together provide an understanding about the role of contrasting grassland managements on the plant diversity and ecosystem function.

2. Materials and Methods

2.1. Study area

To investigate the effect of grazing and mowing on the vegetation composition we performed repeated microcoenological surveys (high resolution vegetation monitoring) in a closed, sandy grassland (Fig. 1) in Hungary near Bugac (N46°41'28", E19°36'42"). The soil type is sandy chernozem (Calcic Chernozem according to the World Reference Base classification; see http://www.fao.org/nr/land/soils/soil/en/), with high sand and low clay contents (Nagy et al., 2010). Total organic carbon content in the upper 10 cm soil layer is 5.2% (Nagy et al., 2010). The vegetation is classified as closed sand steppes (H5b) (Bölöni et al., 2011) and Pannonic sand steppe (6260) (Šefferová Stanová et al., 2008). Based on the 19th Century Military Surveys of the area both grazed (1 ha) and mowed grassland sites (1 ha) has been grazed in the last 150 years (Web references: MAPIRE-1; MAPIRE-2). The total grazing area is around
500 ha at the present. The average annual precipitation in the area was 575 mm and the annual mean temperature was 10.4 °C (2004-2013). Grazing period of cattle usually lasted from 15th May to 15th July and from 15th October to the first of December (0.65±0.15 livestock unit, LSU ha⁻¹, 2010–2016). The mowed area (1 ha) was fenced from the grazed area in March 2011 (Fig. 1). Thus, before the fencing both sites had the same history. The mowed site was cut once per year between June and August (except in 2014, when it was cut twice). Mowing height was 6 centimetres. After drying for a few days the hay was removed from the mowed site. No other treatments (e.g. irrigation, fertilization, or burning) were applied on the sites (these are banned in these protected grasslands according to the Law of Nature Protection, 1996. LIII., 5§ (2) 269/2007. (X. 18.) Parliament Decision). For more details on stocking rate, mowing intensity, grazed and mowed biomass, herbage use efficiency see Koncz et al., (2017).

The mowed and the grazed study areas were adjacent to each other (250 m) therefore precipitation rates and air temperatures were assumed to be similar. Precipitation (ARG 100 Tipping Bucket Raingauges, Waterra Ltd.) and air temperature (HMP35AC, Vaisala) were recorded by the meteorological station in the grazed site (Fig. 1) between 2011–2018. The weather conditions of the months were described with the Gaussen-Bagnouls index.

### 2.2. Experimental design

Microcoenological surveys were performed at both grazed and mowed sites (Fig 1). We used permanent transects for the microcoenological survey because it provides an objective and precise baseline record to follow fine-scale changes in species frequencies and composition (Bartha et al., 2004; Virágh et al., 2008). Plant presences were recorded in small 5×5 cm quadrates along 5-meter transects (100 quadrates per transect). Species abundances were represented by the number of presences to avoid subjective bias from cover estimates (%).
This type of sampling was used successfully in previous comparative studies in various grassland types from tall-grass prairie to semi-deserts (Margóczi 1993; Bartha et al., 1995, 2004, 2008, 2011; Virágh et al., 2008; Bakacsy 2019). Alternative methods, e.g. line-intercept method (Collins and Xie, 2015) could not be used because of the relatively high species density (majority of 5×5 cm quadrates had more than 4 species, cf. Supplementary Material 1. Fig S1) and the presence of clonal species in our data.

Microcoenological surveys were done parallel on both sites at the peak of the vegetation period (13–14th June 2012, 11–12th June 2013, 29–30th May 2014, 4–5th June 2015, 30–31th May 2016). Permanent transects started at 40 meters from the eddy-covariance (EC) stations at both sites (Fig. 1). Transects were at an angle of 60 degrees to each other (Fig. 1). In each transect the presence of all rooting plant species was recorded in 100 contiguous 5×5 cm micro-quadrates to determine species frequencies and composition. Identification to species level was not always possible due to the lack of flowers, seeds or due to the lack of the main part of the stem; therefore, for the analysis we combined certain species at genus level (e.g. Carex spp., in which case three-quarter of the Carex spp. were Carex stenophylla and the rest were C. divisa, C. praecox and C. liparicarpos).

We surveyed two sites (1 ha each) because the experiment was originally designed to be used by the carbon uptake surveys (because of the labour work and expenses required for EC measurement it was not feasible to have more replicates or performing a landscape scale survey). Carbon uptake was studied by net ecosystem exchange measurements (NEE) by eddy-covariance systems at both sites (described in our previous study; Koncz et al., 2017). This experimental design tried to cover the heterogeneity of the vegetation in both sites surrounding the meteorological stations in an area of one hectare, where the NEE measurements were performed (Fig. 1).
Figure 1. The experimental design of the microcoenological survey conducted in the grasslands of Bugac, Hungary (eddy covariance measurements: +; meteorological station: o; microcoenological transects: ---).

2.3. Diversity indices

Vegetation patterns were characterized at the level of transects and also at finer scale (representing vegetation patterns within transects). Alpha diversity (species richness and Shannon diversity index) and species frequency were measured at each transect. Species frequency was calculated based on the occurrence (counts) of a species in the quadrates along the transects (100 quadrates). Plant species were grouped into functional groups (monocotyledons, forbs – dicotyledons except legumes –, legumes, bryophytes), and into disturbance resistance and annual species. The frequencies (%) of the different functional groups at site level were calculated as the ratio of the counts of a given functional group to the total counts of all functional groups (2012-2016 average).

Beta diversity indices were used to characterize composition variability within transects. Each transect was subdivided into five (20 units long) sub-transects and species abundances were calculated in each sub-transects (summarizing presences of species ranging from 0 to 20).
Based on these abundance scores, composition variability (beta diversity) within a transect was characterized by the mean Bray–Curtis dissimilarity between sub-transects. Variability of these indices (based on the 6 transects per site) was compared between the grazed and mowed sites.

2.4. Indicators for fine-scale species coexistence, compositional diversity index

Fine-scale spatial variability of species co-occurrences was further analysed by information theory models (Juhász-Nagy, 1993). The Compositional Diversity index (CD) describes the diversity of realized species combinations (where a particular combination is formed by the species which co-occur in the same sampling unit). It is calculated as the Shannon entropy for the frequency distribution of the observed species combinations within the sampling units:

\[
CD = -\sum_{k=1}^{\omega} p_k \log_2 p_k
\]

where \( \omega = 2^N \) is the number of possible species combinations, \( N \) is the number of species and \( p_k \) is the frequency of the \( k \)th species combinations in the sample. In contrast to beta diversity indices based on pairwise comparisons of plots (e.g. Bray–Curtis index), CD considers all plots (a multiple-site beta diversity measure, Bartha et al., 1998, 2011). As the number of realized species combinations depends on the spatial scale (Juhász-Nagy, 1993; Podani et al., 1993; Bartha et al., 2004), CD is calculated at a series of plots of increasing sizes (gradually merging 2, 3, 4 etc. adjacent micro-quadrats along the transects) (cf. Supplementary Material 2., Fig. S2-S6). Spatial scaling was performed by computerized resampling of the base-line transects (Podani 1987) with sampling units of gradually increasing sizes (changing resolution, i.e. grain sizes) from 5 cm to 100 cm. CD showed a unimodal maximum curve if it was plotted against the grain size (for detailed explanation cf. Supplementary Material 2., Fig. S2-S6). We usually present only the maximum of this
function (Bartha et al., 1998) that appeared in this data set at very fine scales at 5 cm and 10 cm (Supplementary Material 2., Fig. S5, Fig. S7, Fig. S9).

The length of the transects (100 quadrates) determines the possible detectable number of realized species combinations (100 combinations), thus to calculate unbiased CD (Tóthméрезsz and Erdei, 1992) only those species were kept which had at least 20 occurrences along one transect (for detailed reasoning cf. Supplementary Material 2. Fig. S7, Fig S8).
2.5. Statistics

During the statistical analysis the dependent variables were diversity indices (1-4, see explanation below), plant groups (5-10, see explanation below), and the nine most frequent species (11-19). Diversity indices were 1) species richness, 2) Shannon index, 3) Bray–Curtis dissimilarity index, and 4) compositional diversity. Plant groups were: 5) disturbance resistance species (Poptcheva et al., 2009), 6) annual species, 7) monocotyledons, 8) forbs (Dumont et al., 2012), 9) legumes, and 10) bryophytes. Finally, dependent variables included the frequency of the nine most frequent species (or their agglomeration) as well as the 11) Achillea millefolium agg., 12) Arenaria serpyllifolia, 13) Bromus hordeaceus, 14) Carex spp., 15) Cynodon dactylon, 16) Elymus repens, 17) Festuca pseudovina, 18) Medicago falcata, 19) Poa angustifolia. Differences of these dependent variables were compared with mixed effects models (Pinheiro et al., 2018) between years and managements. To perform mixed effects models we used the lme function from the nlme package (Pinheiro et al., 2018) in R (R Core Team 2018). Random effects were the transects. Independent variables included the years (2012‒2016) and the managements (with interaction).

To compare the effects of managements on the vegetation composition we also performed Redundancy Analysis (RDA). During RDA communities that have similar species composition appear as points near each other, whereas communities that have different species compositions are further away from each other on the plot. Following RDA, permutational ANOVA (PERMANOVA) was performed to test significant differences among managements. RDA, PERMANOVA were performed in R (R Core Team 2018).
3. Results

3.1. Meteorological conditions

The climatic conditions differed considerably between the years. Year 2011 and 2012 were dry (Psum<512 mm, T average 10.45 °C, based on Bagnouls-Gaussen index six months were arid), year 2013 and 2015 could be regarded as average years (P sum=562±50 mm, T average=10.97°C, based on Bagnouls-Gaussen index three months were arid in both years), whereas year 2014 and 2016 were wet (Psum>612 mm, T average= 10.99 °C, based on Bagnouls-Gaussen index only one month was arid in 2014 and two in 2016) (Fig. 2). Shortly before the study period climatic conditions probably greatly affected the general vegetation compositions at both sites, since 2010 was an extremely wet year (960 mm), while 2011 was a dry year (471 mm).

![Figure 2. Mean monthly temperature (black line with dots) and the amount of precipitation (grey columns) in the study area.](image)

3.2. Diversity indices at the grazed vs. mowed sites

During the survey we found a total of 114 species, 91 on the grazed and 90 on the mowed site. The experimental design represents one hectare for both sites, thus the grasslands were species rich.

Species number differed between years (due to annual fluctuations) but not between the managements (grazed: 25.4 ± 1.9 species; mowed 24.7 ± 1.2 per 0.25 m²) (Fig. 3a, Table 1).
Shannon diversity index varied considerably between the years but the course of the change was similar in both sites (Fig. 3b) and no differences were observed between the managements (grazed: 2.5 ± 0.1; mowed 2.4 ± 0.1 per 0.25 m²) (Table 1). Throughout the years the grazed (34 ± 0.6) and mowed (33.6 ± 1.9) sites remained similar as is shown by the Bray–Curtis dissimilarity (grazed: 34 ± 0.6; mowed 33.6 ± 1.9) (Fig. 3c) and compositional diversity index (grazed: 5 ± 0.4; mowed 4.8 ± 0.5) (Fig. 3d) and the results of the mixed effect model (Table 1). The different management regimes (grazing vs. mowing, i.e. the management change from grazing to mowing) had no effect on the diversity indices (Table 1). The effects of the management regimes were not manifest in the interaction term either (Table 1). Within each management regime (site) the diversity indices greatly differed among transects as seen by the large standard deviations (Fig. 3), which indicated that the vegetation composition in both the grazed and the mowed sites were heterogeneous (patchy).
Figure 3. Diversity indices of grazed and mowed sites; a) species richness, b) Shannon diversity, c) Bray–Curtis dissimilarity index, and d) compositional diversity along the transects. Average and standard deviations values are based on six transects per year per management (one transect was 500 cm long and 5 cm wide, i.e. 0.25 m$^2$).

### 3.3. Plant groups and frequency of species

Based on the mixed effect model the different managements had no effect on the plant groups and on the most frequent species (Table 1). The frequencies of the functional groups were the following (2012-2016) in the grazed and mowed sites, respectively: monocotyledons (53% 56%), forbs (30%, 34%), legumes (13%, 8%), and bryophytes (4%, 2%). All plant groups except bryophytes were greatly affected by the years (Table 1). Yearly fluctuations can also
be seen in Fig 4, especially in case of annuals and forbs in 2014 (Fig 4b, 4d). In case of these two groups the effects of years may have caused a difference between the two sites in 2014 (the post hoc analysis of ANOVA was significant in case of annuals at p=0.02 level and in case of forbs but only at p=0.07 level), but these differences did not persist, thus there were not the consequences of the different managements (Table 1).

The nine most frequent species were always the same and the managements (sites) had no effect on the frequencies of these species, except on *Arenaria serpyllifolia* and *Cynodon dactylon* (Table 1). The frequency of *Arenaria serpyllifolia* became higher by 2014 at the mowed site, while the frequency of *Cynodon dactylon* decreased constantly at the mowed site (data not shown). Besides these two species the frequency of *Bromus hordeaceus* and *Elymus repens* was affected by the years (Table 1).
Figure 4. Frequencies of the functional groups (monocotyledons, forbs, legumes, and bryophytes), as well as the disturbance resistance and annual species in the grazed and mowed sites (number of occurrence transect$^{-1}$). One transect consisted of 100 contiguous 5×5 cm micro-quadrates.
Table 1. Summary of the results of mixed effect model (p-values) performed for the grazed vs. mowed sites by diversity indices (1‒4), plant groups (5‒10), and by the most frequent species (or their agglomeration) (11‒19). Independent variables include the years and managements with interaction.

* indicates significant differences at level=0.05.

<table>
<thead>
<tr>
<th>Dependent variables</th>
<th>year</th>
<th>management</th>
<th>year×management</th>
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<tbody>
<tr>
<td>Diversity indices</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 Species richness</td>
<td>0.01*</td>
<td>0.96</td>
<td>0.83</td>
</tr>
<tr>
<td>2 Shannon index</td>
<td>&lt;0.0001*</td>
<td>0.67</td>
<td>0.79</td>
</tr>
<tr>
<td>3 Bray–Curtis dissimilarity index</td>
<td>0.55</td>
<td>0.65</td>
<td>0.35</td>
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<tr>
<td>4 Compositional diversity</td>
<td>0.25</td>
<td>0.60</td>
<td>0.35</td>
</tr>
</tbody>
</table>

| Plant groups                |       |            |                 |
| 5 Disturbance resistance species | 0.0002* | 0.76       | 0.21            |
| 6 Annual species            | <0.0001* | 0.06       | 0.0003*         |
| 7 Monocotyledons            | 0.01*  | 0.77       | 0.49            |
| 8 Forbs                     | <0.0001* | 0.59       | 0.008*          |
| 9 Legumes                   | 0.0001* | 0.23       | 0.49            |
| 10 Bryophytes               | 0.20  | 0.16       | 0.57            |

| Frequent species            |       |            |                 |
| 11 Achillea millefolium agg.| 0.69  | 0.42       | 0.52            |
| 12 Arenaria serpyllifolia   | <0.0001* | 0.34       | 0.00*           |
| 13 Bromus hordeaceus        | <0.0001* | 0.11       | 0.38            |
| 14 Carex spp.               | 0.08  | 0.65       | 0.60            |
| 15 Cynodon dactylon         | 0.02*  | 0.19       | 0.049*          |
| 16 Elymus repens            | 0.007* | 0.52       | 0.29            |
| 17 Festuca pseudovina       | 0.61  | 0.55       | 0.19            |
| 18 Medicago falcata         | 0.08  | 0.55       | 0.26            |
3.4. Results of PERMANOVA

According to the PERMANOVA the vegetation remained similar between the grazed and mowed sites i.e. there was no compositional differences (p>0.05) (Fig. 5). Grazed and mowed plant communities had similar species composition.

Figure 5. Results of Redundancy Analysis (RDA) and permutational ANOVA (PERMANOVA).
3.5. Carbon uptake

Details of carbon uptake and greenhouse gas balance of the managements (sites) have been analysed in details and published elsewhere (Koncz et al., 2017). We found that the grazed site had higher C sink capacity (+1±0.7 t C ha⁻¹ year⁻¹) compared to the mowed site, which was C source (-0.3±0.6 t C ha⁻¹ year⁻¹) (Fig. 6). The average difference in C uptake between the grazed and mowed site was 1.3±0.2 t C ha⁻¹ year⁻¹. Vegetation composition did not differ between the grazed and mowed sites, thus it could not have been the reason behind the differences in C uptake.

Figure 6. Net ecosystem exchange (NEE, carbon uptake) of the grazed and mowed sites. Calculations were based on data published in Koncz et al., (2017).
4. Discussion

4.1. Vegetation composition and grassland managements

In general, grazing causes a gradual and patchy decrease in the vegetation height, compacts and re-fertilizes the soil, while mowing causes a sudden and homogeneous drop in the vegetation height and depletes the soil minerals provided there is no fertilization. In consequence, vegetation composition is assumed to be altered by management differences. However, due to contrasting management regimes (grazing vs. mowing) the vegetation composition showed no differences in our study in adjacent grazed and mowed grassland sites during the six years of the experiment. At the scale of individual vegetation patches (represented by total species richness of transects and Shannon diversity calculated from transect-level relative abundances), we did not observe diversity changes of the vegetation. At finer scales (within individual patches), in contrast to our expectations, beta diversity measures (Bray–Curtis dissimilarity index and the diversity of species combinations) were also similar throughout the years between the grazed and mowed sites (Table 1). PERMANOVA (Fig. 5) did not reveal any differences either in the vegetation composition between grazed vs. mowed managements. Thus, the fine-scale composition and spatial organization of vegetation remained unchanged, which showed high stability of the studied sandy grasslands. High stability might be the consequence of the high species number belonging to various functional types as we observed 91 species in the grazed (1 ha) and 90 species in the mowed site (1 ha), a total of 114 species. However, species diversity and vegetation stability is not necessarily linked, as e.g. grasslands with long term reservation were found to have lower biodiversity but higher stability in a study in a steppe site of Mongolia compared to an enclosed grassland with or without mowing, which had higher biodiversity but lower stability (Zhang, 2016).
Remarkable yearly changes in the vegetation composition in our study were observed in case of the frequency of two plant groups (annual species and forbs) and in the frequency of two frequent species (*Arenaria serpyllifolia, Cynodon dactylon*) during the six years of the experiment (Table 1). Due to mowing (the mowed site was fenced in 2011 to exclude grazing) the frequency of annual species apparently increased possibly due to the appearance of small openings in the grassland caused by the hay harvesting, although after 2014 these differences disappeared. The apparent increase of forbs was unexpected and should further be studied as in contrast to our study, mowing was found to suppress tall growing forbs (Billeter et al., 2007; Valkó et al., 2012). Due to mowing the vegetation before seeding would reduce the seed germination capability of plants, which was expected to decrease the frequency of forbs. However, it is possible that the forbs simply survived under the blades of the cutting machine and further forbs emerged from the soil seed bank (as space became available). In other study, due to intensive grazing the cover of tall grasses such as *Bromus inermis* or *Elymus repens* decreased, while due to mowing the frequency of drought and disturbance tolerant species increased (Grime, 2001; Kovács and Csízi, 2004).

High stability/resilience in species richness and diversity was also observed in other studies. There were no changes found in species richness and diversity at fine-scale even after 25 years of grazing vs. mowing in mesotrophic grasslands (Sullivan et al., 2017). In another study no shift was observed to a different plant community despite 10 years of contrasting management (mowing vs. abandonment) of a mountain hay meadow (Pavlů et al., 2011). In a mountainous grassland plot Csergő and Demeter (2011) found that long term mowing increased the persistence of the dominant *Festuca* species, and allowed the co-existence of several other species adapted to low nutrient content of soil, rapid nutrient recycling, and open microsites. On the other hand, short-term rapid vegetation changes were observed in a few studies, e.g. Wan et al., (2016) found that within three years mowing management regime
(twice per year) reduced the abundance of semi-xeric and xeric forbs (Wan et al., 2016). Also, yearly mowing in a mountain fen and dry-mesophilous hay meadow in Hungary increased the species richness of forbs and target forbs between 2006 and 2007 (Valkó et al., 2012). In mid-term, after seven years of experiment, grazing supported the dominance of grasses, while mowing enhanced non-leguminous forbs in a species rich grassland of the White Carpathian Mountains (Mládková et al., 2015). There is a great need for long-term (10-20 years) comparative (comparing managements) micro-coenological experiments (to be more detailed as using only species cover) taking into consideration the local conditions and legacy effects.

4.2. Inter-annual and spatial variability of vegetation composition

In our study the inter-annual variability of the vegetation composition was high for both grazed and mowed sites, which is a characteristic of numerous grasslands (Loeser, 2001). Climatic conditions affected both sites simultaneously, e.g. when the precipitation was relatively high during the springs of 2013 and 2016 species richness and Shannon diversity indices were also high at both the grazed and the mowed sites. Climatic conditions appeared to be even stronger drivers than the effects of the management regime; as the yearly differences were larger than the differences between the managements. Of the 19 dependent variables analysed with the mixed effect model, the effects of years were found to be significant, while the type of management regime (sites) had no effect at all and year-management interaction was significant in four cases (Table 1). It was noticeable that the frequency of Bromus hordeaceus, a drought tolerant species, greatly increased at both sites in 2014 (with no differences between sites). Most probably it was the results of drought in the previous years. This showed the adaptive capability of grasslands to changing climatic conditions and highlighted the need for species rich grasslands (as there could be years which favour some species better than others).
Besides temporal variability we found that both the grazed and the mowed grassland sites were highly heterogeneous (patchy) spatially. This is also characteristic for species-rich grasslands, especially for grasslands under long-term grazing, as grazing usually leads to patchy vegetation due to differences in grazing intensity as well as to selective grazing by livestock in contrast to mowing (Bakker et al., 1983). Heterogeneous vegetation could contribute to functional stability (Loreau et al., 2003; Wilcox et al., 2017). For example at our site the spatial pattern of soil respiration and nitrous oxide fluxes become spatially more homogenous but temporally more variable due to mowing in contrast to grazing (Fóti et al., 2018).

4.3. Carbon uptake and vegetation composition

In the studied grassland parallel to the vegetation (microcoenological) survey we investigated the C uptake and the net ecosystem carbon exchange as well. We observed large differences in the net C uptake between the grazed and mowed sites (Koncz et al., 2017). Mowed site was a source for C in dry years, while the grazed site remained C sink. Loss of C was due to high herbage use intensity in the mowed site, which resulted in a low gross primary production and high rates of ecosystem respiration after mowing. Based on the yearly course of C fluxes there was a sudden drop in C uptake and a large loss of C after mowing due to the respiration of the ecosystem. Vegetation composition did not change, thus differences in C uptake between the grazed and mowed sites could not be attributed to the expected differences in the vegetation composition. We assumed that the effect of contrasting managements affected the functionality of the grassland (mowed site became a source for C), without vegetation composition changes. Although functional changes may have an effect on the structure in the long run. In our study the vegetation patches remained stable and spatially heterogeneous also at the mowed site even at the finest scale. Therefore, we can conclude that functional
differences can occur independently of composition changes. This showed the stability of the vegetation composition to contrasting managements. We found evidence for fast functional degradation, a phenomenon in which mowed site turns to be a C source. However, we assume that it could be restored provided that grazing will be reintroduced because the vegetation structure remained the same. It was shown in a study that differences in the vegetation due to difference in stocking rates influenced net C uptake of the ecosystem (Klumpp et al., 2011), thus vegetation differences played a key role in carbon balance. However, according to other researches, changing plant community structure induced by grazing did not lead to changes in soil C storage (Frank et al., 1995), thus it is the question of what role vegetation changes play in maintaining C balance.

4.4. Management recommendations

Grazing or mowing alone does not necessarily secure that the management regime will favourably affect vegetation composition i.e. to sustain or increase diversity, stability. However, managing semi-natural grasslands is usually better than no management at all (i.e. abandonment) as it was found that species were more frequent in grazed sites compared to abandoned ones (Pykälä 2005). Management is recommended in Hungary as large grasslands became abandoned, however it could be utilized to support livestock (Koncz et al 2017). Depending on the timing and intensity both grazing and mowing could alter vegetation composition but, in general, extensive grazing and extensive mowing were found to maintain or increase plant diversity (Házi et al., 2012; Jantunen, 2003; Fritch et al., 2011; Socher et al., 2012; Török et al., 2018). Based on our study we also recommend that extensive grazing should be supported and extended in space and time (where possible). Annually grazed and mowed plots were found to have higher species number compared to untreated (abandoned) plots in semi-natural grasslands of Southern Sweden after 28 years of experiment (Wahlman
Grazing has proved to be a successful management tool in terms of maintenance and restoration of biodiversity (Benthien et al. 2018; Vadász et al., 2016). In a 22-year-long experiment with different management types of dry limestone grasslands it was found that a mixture of varying cutting regimes is required to sustain high species diversity (Köhler et al., 2005). Long-lived forbs (Trifolium medium, Salvia pratensis, Primula veris) tended to be favoured by annual mowing in October and by controlled annual burning at the end of winter in contrast to annual mowing in July (as in the latter case no nutrients were stored) (Köhler et al., 2005). In general, to improve vegetation composition and species richness mowing date, stocking rate, grazing period should be tailored to specific local conditions (Smith et al., 2000), keeping in mind that management alone is just one of the many other driving factors (climate, soil, topography, hydrology) shaping vegetation composition (Wellstein et al., 2007). It is recommended to design agri-environmental measures that will encourage alternating mowing and grazing, because this promotes the coexistence of multiple forbs and grasses, balances the nutrient limitation and ensures stable biomass production (Mládková et al., 2015).

In summary, our study shows that a species rich, well preserved, closed steppe grassland could turn to be a C source when changing the management from grazing to mowing. However, it is important to emphasize that vegetation composition and diversity of the grassland remained stable, thus changing the management regime back from mowing to extensive grazing could potentially recover the C sink activity of grassland.

5. Conclusion

We compared the effect of grazing and mowing on fine-scale diversity of sandy grasslands in Hungary. We found that both grassland sites were heterogeneous and the vegetation diversity indices and compositional parameters showed large inter-annual variability. We found no
differences in the fine-scale vegetation composition between the two management regimes analysed by mixed effect model, information theory model and PERMANOVA. The studied grassland sites had been grazed with traditional extensive methods in the last 150 years thus we expected to find some significant changes in the vegetation patterns in response to changing the management regime from grazing to mowing after five years (the mowed site was fenced in 2011). The stand-scale composition stability might be attributed to the spatiotemporal heterogeneity of the grasslands. On the other hand, C uptake showed large differences between grazed vs. mowed site unrelated to vegetation composition. The reintroduction of grazing at the mowed site would probably restore C uptake capacity of the mowed site as the vegetation composition remained unchanged.

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