Cent. Eur. J. Biol. • 7(6) • 2012 • 1055-1065
DOI: 10.2478/s11535-012-0101-9

VERSITA

Central European Journal of **Biology**

Grazed Pannonian grassland beta-diversity changes due to C_4 yellow bluestem

Research Article

Szilárd Szentes[1], Zsuzsanna Sutyinszki[2], Gábor Szabó[2,3], Zita Zimmermann[2,3], Judit Házi[2], Barnabás Wichmann[2], Levente Hufnágel[4], Károly Penksza[2,*], Sándor Bartha[3]

[1]*Szent István University, Faculty of Agriculturale and Environmental Sciences, Institute of Plant Production, HU-2100 Gödöllő, Hungary*

[2]*Szent István University, Faculty of Agriculturale and Environmental Sciences, Department of Nature Conservation and Landscape Ecology, HU-2100 Gödöllő, Hungary*

[3]*Institute of Ecology and Botany, Centre for Ecological Research, Hungarian Academy of Sciences, HU-2163 Vácrátót, Hungary*

[4]*Corvinus University of Budapest, Department of Mathematics and Informatics, HU-1118 Budapest, Hungary*

Received 17 April 2012; Accepted 04 September 2012

Abstract: This study investigates how yellow bluestem affects biodiversity in a typical Pannonian grassland. Beta diversity (*i.e.* the fine-scale spatial variability of species compositions), was estimated by the realized number of species combinations sampled at various scales. Sampling was performed by a standard protocol. Presences of plant species were recorded along 52.2 m long belt transect of 1044 units of 0.05x0.05 m contiguous microquadrats. According to the results the massive presence of tested C_4 grass significantly reduced species richness of the grassland. Beta diversity assessment revealed that 90% of species combinations were lost due to yellow bluestem invasion. Fine-scale spatial pattern analyses showed complete local extinctions of other species from microsites dominated by yellow bluestem. This local extinction is enhanced by the specific clonal architecture of this species and by the accumulation of litter. Other dominant grasses had no effect on fine scale diversity, *i.e.* they could coexist well with other elements of the local flora. This study presents currently developed microhabitat types, forecasts and also draws attention to the danger that climate warming will probably enhance the spread of this detrimental C_4 species.

Keywords: *Dominant grass • Plant neighbourhood diversity • Litter • Spatial association • Climate change*

1. Introduction

Natural and seminatural grasslands are sources of biodiversity and provide important ecosystem services [1,2]. Improper grassland management often leads to decreasing diversity, threatens ecosystem health and the reliability of ecosystem services [3,4]. Marginal and transitional habitats are especially vulnerable to threatening factors [5,6]. In the Pannonian biogeographical region most of the natural and seminatural grasslands have been maintained in dry, nutrient poor environments or in secondary habitats after forest clearing and cropland abandonment [7-10].

Yellow bluestem (*Bothriochloa ischaemum* (L.) Keng) is one of the species which aggressively spread into transitional or degraded grassland habitats. This C_4 perennial bunchgrass is native in Hungary. Originally it is a subordinated component of slope steppe habitats living in small gaps of the grassland or appearing on nutrient poor eroded surfaces with drier and warmer micro-habitats [11,12]. However, it is also spreading into overgrazed and successional habitats where the plant coverage is low and the microclimatic conditions are extreme [13,14].

* *E-mail: wbarna@freemail.hu*

Grasslands on south-facing slopes are specially exposed to the invasion of C_4 grasses [12-15]. Studies reporting the spread of these species agree that climate change can strengthen this process worldwide [16]. On the other hand overgrazing and improper management can lead to the spread of C_3 grasses for example *Brachypodium genuense* [17,18]. Yellow bluestem as a typical C_4 grass appears invasive in several part of the world reducing biodiversity [19-21] and the economic value of grasslands [22]. Therefore, it is important to study and understand the patterns and mechanisms that regulate the spread of yellow bluestem and to recognize the related changes in plant community structures.

Grasslands dominated by invasive species have remarkable spatial heterogeneity in community structure [13,14,23]. This spatial heterogeneity is often represented by beta diversity and there is an ongoing debate on the relationship between beta diversity and invasibility [24,25]. Most of these studies investigated large-scale patterns of landscapes or continents [24,26] but little is known about community-level beta diversity patterns. We argue that alpha diversity, although routinely used in grassland monitoring [27-29], is less effective indicator of community changes than beta diversity. Therefore, we decided to use beta diversity for measuring the effect of yellow bluestem. Our preliminary studies showed that within-community patterns of species composition were good indicators of grassland succession and degradation [13,30-32]. In addition to be a good indicator, beta diversity reflects important constraints of the spatial organization of vegetation [31,33,34].

The aim of this study was to assess the changes in grassland community structure due to yellow bluestem invasion in mid-successional grassland communities developing on abandoned agricultural fields. We chose this type of community because it was more exposed to invasive species, and yellow bluestem typically developed large abundant stands in these grasslands. We compared stands with high and low yellow bluestem impacts and estimated the magnitude of alpha and beta diversity changes. We were also interested to compare the role of yellow bluestem to the role of other dominant grasses present in these grasslands.

We made the following hypotheses:

H1: Yellow bluestem is a strong competitor, it monopolizes resources and outcompetes other species. This effect is spatially restricted to patches colonized by yellow bluestem. Therefore, we expect decreasing alpha diversity but increasing beta diversity in communities invaded by yellow bluestem. As beta diversity appears due to the spatially heterogeneous distribution of yellow bluestem, beta diversity will be more pronounced at coarser scales.

H2: The phenological optimum of yellow bluestem is in late summer - early autumn, much later than the phenological optimum of most other species in the grassland community. Therefore, we expect strong seasonality of yellow bluestem effects, with minor influence on the spring aspect but with considerable influence on the autumn aspect of the community.

H3: The typical dominant species of these grasslands (*Elymus repens*, *Poa angustifolia*, *Bromus inermis*, *Festuca* spp.) also form distinct patches during their colonization and establishment. Therefore, we asked if diversity loss during grass invasion is a general phenomenon and we hypothesize that all mid-successional perennial grasses will show similar phenomenon at the stage of their invasion.

2. Experimental Procedures

2.1 Description of sample areas

The experiments were carried out on a sheep pasture (150 ha) situated in a northwest-southeast valley near Kisfüzes in the Mátra which is part of the North Hungarian Mountains. The average annual temperature is 9°C, while the average temperature in the vegetation period is 16°C. The average annual rainfall is 560 mm and the average rainfall is 360 mm in the vegetation period. The soil of the sample area is degraded brown forest soil. The steep south-western slope under investigation creates dry and warm conditions for the vegetation. The erosion is also considerable, which delays natural succession. Our study was carried out in a south-western (20 ha) paddock, at 200-210 m altitude. The sample area was a vineyard 40 years ago, so it can be considered an old field. The pasture was grazed all year round by 150 texel ewe and their lambs. Rotational grazing system was used and the whole pasture area was divided into five paddocks. Shredding was accomplished every October. No chemicals were used and the area was not overseeded, so the actual vegetation is the result of natural succession. The most common perennial species of the grassland are *Poa angustifolia*, *Bromus inermis*, *Achillea nobilis*, *Plantago lanceolata*, *Verbascum phoeniceum* and *Bothriochloa ischaemum*.

2.2 Standardized sampling protocol

Fine-scale (*i.e.*, high resolution) vegetation analysis was used for measuring the effect of yellow bluestem on the beta diversity of grassland community. There were 6 large plots marked – each 23×3 m – in the appointed grassland during spring of 2011. Three of them were dominated by yellow bluestem while this critical species

was very rare (<10% frequency) in the three remaining plots. In each plot, the presence of plant species were recorded along 52.2 m long belt transect of 1044 units of 0.05x0.05 m contiguous microquadrats. The transects were permanently marked. Two surveys were taken, one on 12-13th May 2011 and another on 12-13th Septebmer 2011.

This sampling protocol has been tested and applied successfully in many grasslands ecosystems [32,33,35-37]. The large number and small size of microquadrats ensure the precise estimation of frequency and spatial patterns of species and species combinations. Comparing with other sampling designs (e.g. recording two-dimensional spatial coordinates of individuals or presences in high-resolution grids), transect sampling is much faster and less destructive. Therefore it can be applied in extensive vegetation surveys and long-term monitoring as well [32,36].

2.3 Data processing

We applied an established methodology of spatial scaling and analyses [30-33,37,38]. For representing beta diversity (*i.e*. the fine-scale spatial variability of species compositions), we estimated the number of species combinations at increasing plot sizes. With high resolution sampling and large sample sizes (N=1044), we efficiently could estimate all realized species combinations (as structural modules) in the community, receiving a very detailed, high resolution picture about the spatial variability and complexity of within-stand coexistence relationships. Species combinations were measured across a range of scales from 0.05×0.05 m to 0.05×25 m by merging two, then three, then four, …*etc*. consecutive microquadrats by subsequent computerised samplings from the baseline transect data sets (spatial series analysis). This computerized sampling and the calculation of species combinations was performed by the PRIMPRO program [31].

The pairwise spatial associations between the spatial pattern of subordinate species richness, the patterns of rooting ramets of dominant grasses (*Bothriochloa ishaemum*, *Elymus repens*, *Poa angustifolia*, *Bromus inermis*, *Festuca rupicola* and *Festuca pseudovina*), and the pattern of local litter accumulations were also calculated. Litter was marked in a microquadrat if its cover was more than 80%. The number of subordinate species (*i.e*. the number of species other than the dominant grass species listed above) was counted in each microquadrat. Microquadrats with S=0, *i.e*. where no subordinate species were present was marked, then the spatial pattern of this low diversity microsites was correlated with the spatial patterns of other variables. Interspecific association was estimated in space series analysis using 2x2 contingency tables, according to the methods of Juhász-Nagy and Podani [30]. The significance of associations was detected by Monte-Carlo randomization tests. 999 „random shifts" of the individual patterns of variables were used for testing the null hypotheses that patterns are spatially independent. Adjusted p-values were used for the multiple tests. We used „random shifts" as a neutral model to avoid the artifacts due to aggregated patterns of clonal grasses or due to the large sizes of individual ramets (see [39] for further explanations, [31,35] for the softwares).

3. Results

The number of species was lower in both spring and autumn in transects dominated by yellow bluestem (Table 1). The average difference between the two sample areas (yellow bluestem dominated and control field) was 21 species in spring and 17 species in autumn. In general, species number was lower in both sample areas during autumn.

The control transects represent typical mid-successional grasslands (Table 2). The target C_3

Code of transects	Species richness in transects		Presence of yellow bluestem		Presence of litter	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Bi1	43	39	34%	33%	67%	65%
Bi2	42	38	39%	36%	82%	87%
Bi3	42	33	43%	47%	90%	82%
C1	62	56	6%	9%	27%	14%
C2	60	51	6%	8%	29%	20%
C3	66	55	2%	2%	18%	8%

Table 1. Total number of species and abundances (frequency%) of yellow bluestem and plant litter in sample transects.

Abundant species	C1		C2		C3	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Veronica arvensis	41,00%	0,10%	38,30%	0,00%	48,80%	0,00%
Achillea nobilis	25,70%	28,00%	23,90%	23,20%	23,30%	21,40%
Bromus inermis	20,10%	32,10%	21,30%	27,30%	54,50%	57,40%
Bromus japonicus	14,20%	0,40%	20,30%	2,20%	4,20%	0,80%
Poa angustifolia	14,10%	17,80%	16,00%	20,60%	18,50%	16,80%
Arenaria serpyllifolia	13,10%	0,50%	8,20%	0,20%	6,00%	0,30%
Achillea collina	11,90%	14,60%	17,30%	21,60%	6,60%	7,80%
Inula britannica	11,60%	16,00%	7,30%	11,30%	7,10%	5,70%
Plantago lanceolata	11,30%	12,10%	12,30%	12,30%	7,00%	8,30%
Medicago minima	8,90%	0,10%	9,10%	0,00%	3,40%	0,00%
Erigeron annuus	8,00%	1,90%	6,80%	2,00%	21,00%	14,80%
Verbascum phoeniceum	7,60%	7,50%	8,40%	6,40%	8,10%	4,00%
Festuca rupicola	6,80%	9,20%	1,40%	5,50%	0,10%	0,10%
Bothriochloa ischaemum	6,20%	8,80%	5,90%	8,00%	1,90%	1,90%
Hieracium bauchinii	5,70%	7,80%	4,60%	4,00%	3,80%	5,70%
Fragaria viridis	4,80%	6,40%	2,20%	2,70%	1,10%	1,30%
Cerastium tenoreanum	4,10%	0,00%	5,40%	0,00%	9,50%	0,00%
Galium verum	2,80%	3,00%	4,20%	4,50%	8,80%	7,10%
Clinopodium vulgare	0,40%	0,30%	0,10%	0,10%	8,60%	9,40%
Alyssum alyssoides	0,00%	0,00%	0,00%	0,00%	5,90%	0,00%
Conyza canadensis	0,00%	5,90%	0,00%	4,70%	0,00%	3,00%
Setaria pumila	0,00%	27,40%	0,00%	22,20%	0,00%	22,30%

Table 2. Frequency (%) of the most abundant species in the control transects (species with frequency >5% at least in one transect were selected) C: control transect.

perennial grass, *Festuca rupicola* is already present, but still subordinate. The most frequent species are *Bromus inermis* and *Poa angustufolia*, two grasses which are characteristic to degraded grasslands and to the middle stage of oldfield succession. Typical subordinate dicots are mostly creeping and decumbent perennial forbs (e.g. *Hieracium bauchinii*, *Fragaria viridis*, *Achillea* spp.) and few perennial erect forbs (e.g. *Galium verum*, *Verbascum phoniceum* and *Inula britannica*). Besides the high proportion of perennial grasses and dicotyledonous species, the frequency of three annual species was over 10% in the control transects. These include *Arenaria serpyllifolia* (6.0-13.0%) and Veronica arvensis (41.0-48.8%) in spring, while *Setaria pumila* (22.2-27.4%) in autumn. The number of species with frequency >5% was much higher in the control transects. *Bothriochloa ischaemum* was present but only sporadic in control transects.

The presence of annual species was negligible in transects dominated by yellow bluestem while their number and frequency was higher in the control transects. *Setaria pumila*, which is an annual species flowering from August to October, appeared in the yellow bluestem transects but with significantly lower frequency than in the control transects due to the high coverage of the yellow bluestem. In most cases the frequency of perennial species decreased in the yellow bluestem dominated transects. At the same time these species, including important grass species like *Bromus inermis*, *Poa angustifolia* or *Festuca rupicola*, became more frequent in the control transects in autumn. There were only five species with frequency >10% in transects dominated by yellow bluestem (Table 3). *Bothriochloa ischaemum* was the most frequent of all of them with a frequency ranging from 33.0 to 47.2%. The second and third most common species were *Bromus inermis* (15.6-31.1%) and *Poa angustifolia* (10.0-16.6%), respectively.

Beta diversity was scale dependent. We scaled compositional variability between 0.05 m and 25 m (Figure 1). Most variability (the highest beta diversity)

Abundant species	Bi1		Bi2		Bi3	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
Bothriochloa ischaemum	33,80%	33,00%	39,30%	36,30%	42,70%	47,20%
Bromus inermis	31,10%	27,50%	17,10%	24,10%	15,60%	13,00%
Poa angustifolia	13,40%	10,00%	13,00%	14,20%	13,10%	16,60%
Erigeron annuus	10,60%	10,00%	5,30%	2,30%	6,90%	4,00%
Veronica arvensis	10,20%	0,00%	9,50%	0,00%	5,20%	0,00%
Verbascum phoeniceum	8,40%	3,80%	5,70%	4,00%	4,00%	1,60%
Hieracium bauchinii	3,10%	1,40%	8,90%	7,10%	3,90%	1,60%
Hieracium pilosella	2,40%	6,10%	2,20%	1,80%	0,00%	1,70%
Galium verum	2,20%	2,30%	2,90%	2,00%	5,70%	5,00%
Clinopodium vulgare	0,20%	0,00%	0,90%	1,40%	5,70%	5,20%
Setaria pumila	0,00%	6,70%	0,00%	7,10%	0,00%	1,20%

Table 3. Frequency% of the most abundant species in transects dominated by yellow bluestem (species with frequency >5% at least in one transect were selected) Bi: transect dominated by *Bothriochloa ischaemum*, C: control transect.

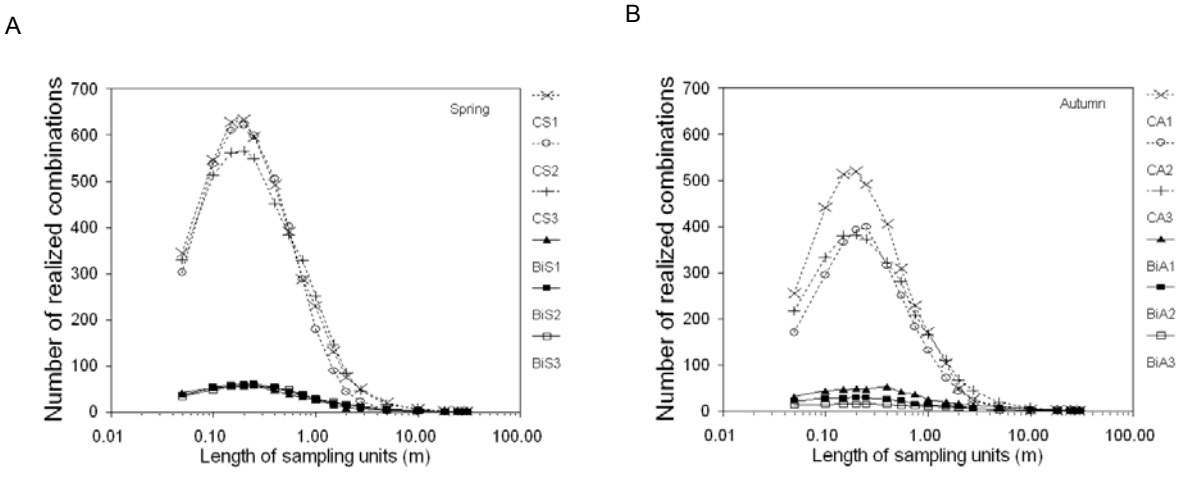

Figure 1. Beta diversity as a function of sampling scale. At each resolution (sampling unit length) beta diversity was represented by the number of realized species combinations found in 1044 overlapping sampling units. (CS1, CS2, CS3, CA1, CA2 CA3 denote the control transects sampled in spring (S) or autumn (A), while the transects dominated by yellow bluestem are denoted by BiS1, BiS2, BiS3, and BiA1, BiA2, BiA3.).

appeared between 0.1 m and 0.5 m. This maximum scale was similar among all transets and seasons. In spring the maximum number of species combinations was higher in the control transects (C1: 634, C2: 622, C3: 565) than in the yellow bluestem dominated transects (Bi1: 58, Bi2: 61, Bi3: 58). According to the results the maximum number of species combinations in the yellow bluestem dominated sample area was only one-tenth of the value measured in the control area. There was seasonal difference between the results of autumn and spring surveys. The values of both sample areas decreased by autumn (C1: 520, C2: 400, C3: 382, Bi1: 53, Bi2: 30, Bi3: 16).

Significant positive spatial associations were found between the low diversity microsites (*i.e.* microsites without subordinate species (S=0)) and the local presence of yellow bluestem and litter (Table 4). Tests with other grass species (*Elymus repens*, *Poa angustifolia*, *Bromus inermis*, *Festuca pseudovina* and *Festuca rupicola*) were not significant (not shown here), *i.e.* these grasses were not associated to the low diversity microsites. The associations were scale dependent, most significant associations appeared between 0.05 m and 0.5 m. No significant associations were found above 1 m scale.

Pairs of variables		C1	C2	C3	C1	C2	C3	Bi1	Bi2	Bi3	Bi1	Bi2	Bi3
		Spring			Autumn			Spring			Autumn		
S0	Bothriochloa ischaemum	0	0	0	1	1	1	1	1	1	1	1	1
S0	litter	0	0	0	1	1	1	0	1	0	1	1	1
litter	Bothriochloa ischaemum	0	1	0	1	1	1	1	1	1	1	1	1

Table 4. Fine-scale spatial associations between low diversity microsites (S0) and the spatial patterns of yellow bluestem and litter (critical value for significance $P<0.006$) (0 independence, 1 positive association).

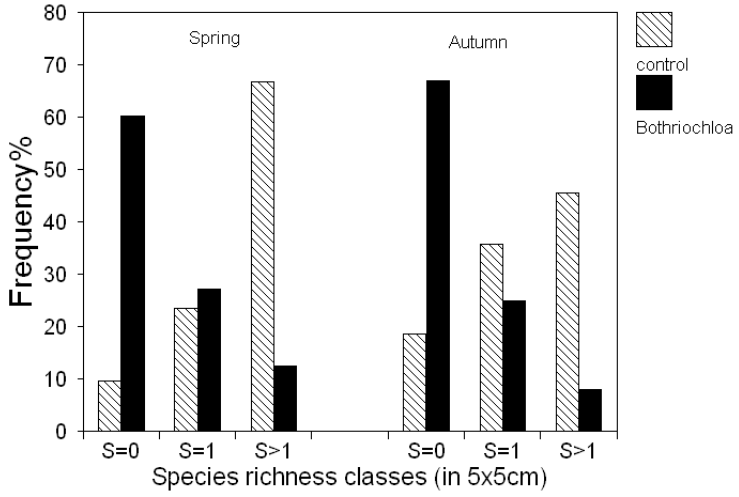

Figure 2. The effect of yellow bluestem on the fine-scale distribution of subordinated species richness. For simplicity we distinguished only 0.05x0.05 m micro-quadrats with zero, one or more subordinated species, and data from the three replicated transects (with same season and treatment) were pooled.

This positive associations between low diversity microsites and yellow bluestem were consistent over transects and seasons in yellow bluestem dominated transects. Seasonality appeared in the control transects, where positive spatial associations were found in autumn, but independence in spring. It can be explained by the low number of low diversity microsites in spring (Figure 2). Positive associations were found between yellow bluestem and litter in almost all case (except 2 control transects in spring).

4. Discussion

Dominant species usually exert strong competitive effects on subordinate species [40-42]. Our results provide additional evidence to this finding. Alpha diversity was lower in all transects dominated by yellow bluestem. This is consistent with previous studies on *Bothriochloa ischaemum* [22,43] and other grasses [44-46]. As an unexpected result, we found significant decrease in beta diversity as well. While *ca*. 30% of alpha diversity was lost due to yellow bluestem, beta diversity differences were much higher, 90% of compositional variability was lost due to yellow bluestem invasion. These results show that traditional statistics recording only alpha diversity may seriously underestimate the changes that appeared due to yellow bluestem invasion. Sites invaded by yellow bluestem are virtually more heterogeneous showing remarkable physiognomic differences. They virtually appear as a two-phase mosaic of yellow bluestem dominated patches and non-invaded vegetation. Contrary to our expectation, this mosaic had lower beta diversity than the physiognomically more uniform control vegetation when beta diversity was quantified with precise methodology [33]. Bassett *et al.* [25] found higher beta-diversity in the presence of an invasive species [25]. However, they worked in an aquatic system where the diversities of invaded and non-invaded patches did not differ. Because most research links beta diversity and plant invasion at landscape scale [24] further studies

are necessary to clarify this relationship at community level.

In our study, beta diversity was represented by the number of realized species combinations [33]. This methodology (cf. [30,31] has been proposed recently for vegetation monitoring [32,36,37]. By distinguishing all realized species combinations (instead of using mean composition) we receive a very detailed record about local coexistence relations. When it is calculated in space series, it actually reports how species live together at different scales. The sizes of individuals in plant communities vary considerably, from a few centimetres (seedlings and short-lived annuals) to several meters (large aggregates of clonal perennials) (cf. [35,47]). To understand how individuals of different sizes interact, we used the space series analysis, *i.e.* we applied a series of increasing sampling unit sizes which fit to all sizes of plants and provided an account of plant neighbourhood relationships at various relevant scales. We scaled compositional variability between 0.05 m and 25 m and found that most of the compositional variability appears between 0.1 m and 0.5 m. This magnitude of scales corresponds to the magnitude of sizes of most abundant plant species in this grassland. Most studies in plant community ecology use 2x2 m or larger sampling unit sizes for evaluating vegetation [48]. Our results show clearly that traditional sampling designs - used routinely in vegetation science - probably underestimate diversity changes. This bias in pattern recognition might have important consequences for detecting and managing environmental problems.

Differences between *Bothriochloa* dominated and control transects showed a seasonal effect, because alpha and beta diversity were slightly lower in autumn. However, the negative effect of yellow bluestem on diversity was apparent in both seasons. Fine scale analyses of spatial associations between yellow bluestem and the low diversity (S=0, where no subordinate species were present) microsites revealed significant spatial dependence. We found positive spatial association between the microsites without subordinate species (S=0) and the local presence of yellow bluestem. This positive association was consistent over the replicated transects and over seasons in yellow bluestem dominated vegetation patches. Interestingly, this positive spatial association also appeared in all control transects in autumn, *i.e.* the negative effect of yellow bluestem was already present in the early stage of invasion at low abundances of yellow bluestem (2-9% frequency). No effects were found in control transects in spring. So seasonality was important only in the control transects. What mechanisms are responsible for the spring effect of yellow bluestem? Our results showed that yellow bluestem was frequent in spring in the yellow bluestem dominated transects, but the size of ramets was small and its effect could be minor. However, we also found positive association between the rooting yellow bluestem and the micro-scale presence of plant litter. Therefore, we assume that the effect of yellow bluestem is mediated by litter. Similar effects have been reported from several ecosystems [49]. Yellow bluestem produces considerable amount of litter that remains persistent around the individuals. Litter is known to have strong effect on vegetation diversity [50,51]. In most cases the effect is negative on local plant diversity [46,49,52,53].

Our fine-scale analyses revealed a tendency for the competitive exclusion of other species from microsites occupied by yellow bluestem. Figure 3 illustrates these fine-scale changes in the spatial organization of plant community during the process of yellow bluestem invasion. It shows the stochastic processes of filter-effects resulting in low diversity. Experimental evidences confirm the competitive superiority of *Bothriochloa ishaemum* [21]. There are several traits (e.g. bunchgrass architecture; reproduction by rhizomes, stolons, and seeds *via* apomixis; small seed sizes; good dispersal ability; very plastic morphological traits; rapid growth to sexual maturity) that explain the competitive advantage of *Bothriochloa ishaemum* [21,54-57].

It is a general phenomenon that grass species become excessively dominant shortly after establishment [40,41]. Therefore we asked the question if other grass species that are co-dominant in the studied grassland would have similar effect on local diversity. Therefore we repeated the same fine scale spatial association analyses for all abundant grassland species (*Elymus repens*, *Poa angustifolia*, *Bromus inermis*, *Festuca pseudovina* and *Festuca rupicola*), however, no significant associations found. This means that these species do not hinder the colonization of subordinate species. The influence of existing vegetation on the immigration of new species is an important issue in vegetation succession [44,45]. The rate of immigration is the highest in early succession then it decreases exponentially. Immigration rate also varies spatially due to the identity of dominants, *i.e.* due to the characters of the vegetation matrix [42]. The concept of „plant successional window" [58-60] has been developed for describing this phenomenon. Our findings suggest that „plant successional window" is closed in patches dominated by yellow bluestem but it remain open in other vegetation patches.

The suppressive role of yellow bluestem calls for some restoration management option. Prescribed fire would be a solution against the accumulating litter. However, burning is known to promote the growth of

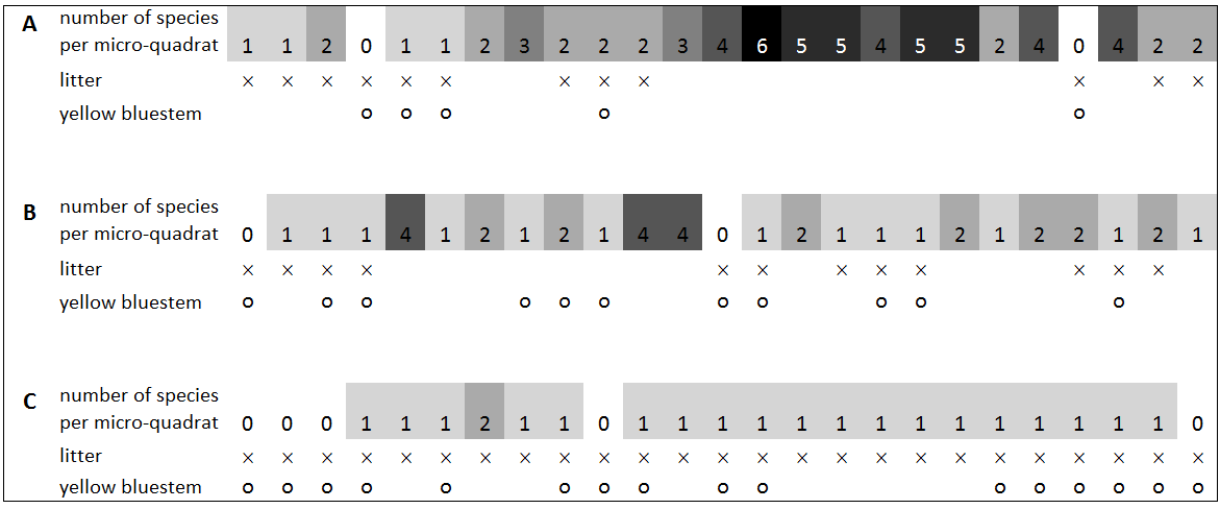

Figure 3. Graphical representation of fine-scale diversity patterns of subordinate species as they appeared in our sampling. A, B, and C, denote typical stages of yellow bluestem invasion.

C_4 grasses [61], therefore it cannot be recommended. Mowing is not feasible because of the low productivity. Grazing is not feasible as well because of the low nutritional value of yellow bluestem. Still we propose early spring sheep grazing and related trampling to force back the spread of this species.

Bothriochloa ischaemum is known in Hungary to be related to grazing intensity. Its abundance is considered as an indicator of grassland degradation due to overgrazing [14,22,43]. This role will probably change due to climate warming. According to a recent assessment in Inner Mongolia, the distributions of C_4 grasses were determined by growing season temperature while the effect of stocking rate was not significant [62]. The coenological role of yellow bluestem will probably change as climate change disturbs the present balance of C_3/C_4 species. Therefore, studying the ecological behaviour of invasive species remains a hot topic in community ecology [63,64].

5. Conclusions

Our study shows that the spread and local dominance of yellow bluestem result in considerable loss of biodiversity in mid-succesional grasslands. Beta diversity assessment revealed much larger effects (90% diversity loss) than was previously thought. Fine-scale spatial pattern analyses showed the mechanism behind diversity loss as the local extinction of other species by yellow bluestem. This local extinction is enhanced by the clonal architecture of yellow bluestem and by the accumulation of its litter. Its negative effect on diversity appears in very early stage of yellow bluestem colonization, even in young stands with very low abundance of yellow bluestem. Although yellow bluestem is a typical late summer – early autumn species its negative effect is apparent also in spring. The positive correlation found between yellow bluestem and litter suggests that the unexpected negative effect of yellow bluestem in spring can be explained by the accumulation and persistence of its litter. As a consequence of climate change, the abundance of C_4 grasses will probably increase in the future, and the threat of yellow bluestem remains a great challenge for grassland managers.

Acknowledgements

The research was supported by the Hungarian National Science Foundation (OTKA K 72561). We thank János Dietrich, the owner of the pasture, for his help.

References

[1] Pärtel M., Bruun H.H., Sammul M., Biodiversity in temperate European grasslands: origin and conservation, Grassl. Sci. Eur., 2005, 10, 1-14

[2] Hopkins A., Del Prado A., Implications of climate change for grassland in Europe: impacts, adaptations and mitigation options: a review, Grass Forage Sci., 2007, 62, 118-126

[3] Conant R.T., Paustian K., Elliott E.T., Grassland management and conversion into grassland: effect on soil carbon, Ecol. Appl., 2001, 11, 343-355

[4] Zimmermann Z., Szabó G., Bartha S., Szentes Sz., Penksza K., Effects of sheep grazing on the nature conservation value of grazed and abandoned grasslands, AWETH, 2012, 7, 234-262, (in Hungarian)
[5] Borhidi A., (Ed.), Plant associations of Hungary, Akadémiai Kiadó, Budapest, 2003 (in Hungarian)
[6] Hobbs R.J., Arico S., Aronson J., Baron JS., Bridgewater P., Cramer V.A., et al., Novel ecosystems: theoretical and management aspects of the new ecological world order, Glob. Ecol. Biogeogr., 2006, 15, 1–7
[7] Illyés E., Bölöni J., (Eds,). Slope steppes, loess steppes and forest steppe meadows in Hungary, MTA ÖBKI, Budapest, 2007
[8] Kiss T., Lévai P., Ferencz Á., Szentes Sz., Hufnagel L., Nagy A., et al., Change of composition and diversity of species and grassland management between different grazing intensity in pannonian dry and wet grasslands, Appl. Ecol. Env. Res., 2011, 9, 197-230
[9] Szentes Sz., Dannhauser C., Coetzee R., Penksza K, Biomass productivity, nutrition content and botanical investigation of Hungarian Grey cattle pasture in Tapolca basin, AWETH, 2011, 7, 180-198 (in Hungarian)
[10] Szentes Sz., Penksza K., Orosz Sz., Dannhauser C., Forage managed investivagation on the Hungarian grey cattle pasture near Balaton Uplands, AWETH, 2011, 7, 180-198, (in Hungarian)
[11] Zólyomi B, The natural vegetation of Budapest and its surrounding. Loess vegetation. In: Pécsi M., (Ed.), Geography and biogeography of Budapest, Akadémiai Kiadó, Budapest, 1958, (in Hungarian)
[12] Zólyomi B., Fekete G., The Pannonian loess steppe: differentiation in space and time, Abstr. Bot., 1994, 18, 29-41
[13] Horváth A., The spatial organization of loess vegetation at Mezőföld, Hungary, Scientia Kiadó, Budapest, 2002 (in Hungarian)
[14] Bartha S.,Composition, differentiation and dynamics of the grasslands in the forest steppe biome, In: Illyés E., Bölöni J., (Eds.), Slope steppes, loess steppes and forest steppe meadows in Hungary, MTA ÖBKI, Vácrátót, 2007
[15] Illyés E., Molnár Z., Csathó A., I., Bothriochloa ischaemum dominated steppes, In: Illyés E., Bölöni J., (Eds.), Slope steppes, loess steppes and forest steppe meadows in Hungary, MTA ÖBKI, Budapest, 2007
[16] Wittmer M.H.O.M., Auerswald K., Bai Y.F., Schaufele R., Schnyder H., Changes in the abundance of C3/C4 species of Inner Mongolia grassland: evidence from isotopic composition of soil and vegetation, Global Change Biol., 2010, 16, 605-616
[17] Catorci A., Ottaviani G., Cesaretti S., Functional and coenological changes under different long-term management conditions in Apennine meadows (central Italy), Phytocoenologia, 2011, 41, 45-58
[18] Catorci A., Cesaretti S., Gatti R., Ottaviani G., Abiotic and biotic changes due to spread of Brachypodium genuense (DC.) Roem. & Schult. in sub-Mediterranean meadows, Community Ecol., 2011, 12, 117-125
[19] Harlen J, Celarier R., Richardson W., Studies on Old World Bluestem II, Oklahoma Agr. Exp. Sta. Tech. Bull.T-72, 1958
[20] Gabbard B.L., Fowler N.L., Wide ecological amplitude of diversity-reducing invasive grass, Biol. Invasions., 2007, 9, 149-160
[21] Schmidt C.D., Hickman K.R., Channell R., Harmoney K., Stark W., Competitive abilities of native grasses and non-native (Bothriochloa spp.) grasses, Plant Ecol., 2008, 197, 69–80
[22] Szabó I., Kercsmár V., Hársvölgyiné Szőnyi É., Comparative study of loess steppe pastures with/without domination of bluegrass (Bothriochloa ischaemum), Grassl. Stud., 2008, 6, 55-61 (in Hungarian)
[23] Pickett S.T.A., Cadenasso M.L., Bartha S., Implications from the Buell-Small Succession Study for vegetation restoration, Appl. Veg. Sci., 2001, 4, 41-52
[24] Davies K.F., Chesson P., Harrison S., Inouye B.D., Melbourne B.A., Rice K.J., Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship, Ecology, 2005, 86, 1602-0610
[25] Bassett I., Paynter Q., Hankin R., Beggs J.R., Characterising alligator weed (Alternanthera philoxeroides; Amaranthaceae) invasion at a northern New Zealand lake, New Zeal. J. Ecol., 2012, 36, 216-222
[26] Stohlgren T.J., Jarnevich C., Geneva W., Ching G.W., Evangelista P.H.E., Scale and plant invasions: a theory of biotic acceptance, Preslia, 2006, 78, 405-426
[27] During H.J., Willems J.H., Diversity models applied to a chalk grassland, Vegetatio, 1984, 57, 103–114
[28] Willems J.H., Peet R.K., Bik L., Changes in chalk-grassland structure and species richness resulting from selective nutrient additions, J. Veg. Sci., 1993, 4, 203–212
[29] Canals R.-M., Sebastiá M.-T., Analyzing mechanisms regulating diversity in rangelands

through comparative studies: a case in the southwestern Pyrennees, Biodivers. Conserv., 2000, 9, 965–984

[30] Juhász-Nagy P., Podani J., Information theory methods for the study of spatial processes and succession, Vegetatio, 1983, 51, 129-140

[31] Bartha S., Czárán T., Podani J., Exploring plant community dynamics in abstract coenostate spaces, Abstr. Bot., 1998, 22, 49-66

[32] Virágh K., Horváth A., Bartha S., Somodi I., A multiscale methodological approach novel in monitoring the effectiveness of grassland management, Community Ecol., 2008, 9, 237-246

[33] Bartha S., Campetella G., Kertész M., Hanh I., Kröel-Dulay Gy., RédeiT., et al., Beta diversity and community differentiation in dry perennial sand grassland, Ann. di Bot., 2011, 1, 9–18

[34] Erdős L., Gallé R., Bátori Z., Papp M., Körmöczi L., Properties of shrubforest edges:a case study from South Hungary, Cent. Eur. J. Biol., 2011, 6, 639-658

[35] Bartha S., Kertész M., The importance of neutral-models in detecting interspecific spatial associations from 'trainsect' data, Tiscia, 1998, 31, 85-98

[36] Bartha S., Campetella G., Canullo R., Bódis J., Mucina L., On the Importance of Fine-Scale Spatial Complexity in Vegetation Restoration Studies, Int. J. Ecol. Environ. Sci., 2004, 30, 101-116

[37] Bartha S., Zimmermann Z., Horváth A., Szentes Sz, Sutyinszki Zs., Szabó G., et al., High resolution vegetation assessment with beta-diversity - a moving window approach, Agr. Informat., 2011, 2, 1-9

[38] Juhász-Nagy P., Notes on compositional divesity, Hydrobiologia, 1993, 249, 173-182

[39] Roxburgh S.H., Chesson P., A new method for detecting species associations with spatially autocorrelated data, Ecology, 1998, 79, 2180-2192

[40] Baer S.G., Blair J.M., Collins S.L., Knapp A.K., Plant community responses to resource availability and heterogeneity during restoration, Oecologia, 2004, 139, 617-629

[41] McCain K.N.S., Baer S.G., Blair J.M., Wilson G.W.T., Dominant Grasses Suppress Local Diversity in Restored Tallgrass Prairie, Restor. Ecol., 2010, 18, 40-49

[42] Wilsey B.J., Productivity and subordinate species response to dominant grass species and seed source during restoration, Restor. Ecol., 2010, 18, 628-637

[43] Virágh K., Horváth F., Bokros S., Modelling the regeneration dynamics of a Hungarian loess steppe community, In: Demeter A., Peregovits L., (Eds.), 'Ecological processes: Current status and Perspectives', Abstracts of EURECO'95, 7th European Ecological Congress, Budapest, August 20–25, 1995, Hungary

[44] Török P., Deák B., Vida E., Valkó O., Lengyel S., Tóthmérész B., Restoring grassland biodiversity: sowing low-diversity seed mixtures can lead to rapid favourable changes, Biol. Conserv., 2010, 143, 806–812

[45] Török P., Vida E., Deák B., Lengyel S., Tóthmérész B., Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs, Biodiv. Conserv., 2011, 20, 2311–2332

[46] Házi J., Bartha S., Szentes Sz., Penksza K., Seminatural grassland management by mowing of Calamagrostis epigeios in Hungary, Plant Biosyst, 2011, 145, 699–707

[47] Oborny B., Bartha S., Clonality in plant community - an overview, Abstr. Bot., 1995, 19, 115-127

[48] van der Maarel E., (Ed.), Vegetation ecology, Blackwell, Oxford, 2005

[49] Holdredge C., Bertness M.D., Litter legacy increases the competitive advantage of invasive Phragmites australis in New England wetlands, Biol. Invasions, 2011, 13, 423-433

[50] Facelli J.M., Pickett S.T.A., Plant litter: its dynamics and effects on plant community structure, Bot. Rev., 1991, 57, 1-32

[51] Xiong S., Nilsson C., The effects of plant litter on vegetation: a meta-analysis, J. Ecol., 1999, 87, 984-994

[52] Ruprecht E., Enyedi M.Z., Eckstein R.L., Donath T.W., Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation, Biol. Conserv., 2010, 143, 449–456

[53] Deák B., Valkó O., Kelemen A., Török P., Miglécz T., Ölvedi T., et al., Litter and graminoid biomass accumulation suppresses weedy forbs in grassland restoration, Plant Biosyst, 2011, 145, 730-737

[54] Kalapos T., C3 and C4 grasses of Hungary: their environmental requirements, phenology and role in the vegetation, Abstr. Bot., 1991, 15, 83-88

[55] Szente K, Nagy Z, Tuba Z., Fekete G., Photosynthesis of Festuca rupicola and Bothriochloa ischaemum under degradation and cutting pressure in a semiarid loess grassland, Photosynthetica, 1996, 32, 399–407

[56] Kalapos T., Mojzes A., What is the future of C4 grasses in temperate grasses during glocal changes?, In: Kröel-Dulay Gy., Kalapos T., Mojzes A., (Eds.), Soil-vegetation-climate interactions, ÖBKI, Vácrátót, 2008, (in Hungarian)

[57] Mojzes A., Kalapos T., Leaf gas exchange responses to abrupt changes in light intensity for two invasive and two non-invasive C4 grass species, Environ. Exp. Bot., 2008, 64, 232–238
[58] Johnstone I.M., Plant invasion windows: A time-based classification of invasion potential, Biol. Rev., 1986, 61, 369-394
[59] Kollmann J., Regeneration window for fleshy-fruited plants during scrub development on abandoned grassland, EcoScience, 1995, 2, 213-222
[60] Bartha S., Meiners S.J., Pickett S.T.A., Cadenasso M.L., Plant colonization windows in a mesic old field succession, Appl Veg Sci, 2003, 6, 205–212
[61] Knapp A.K., Briggs J.M., Hartnett D.C., Collins S.L. (Eds.), Grassland dynamics. Long-term ecological research in tallgrass prairie, Oxford Univ. Press, N.Y, 1998
[62] Auerswald K., Wittmer M.H.O.M., Bai Y., Yang H., Taube F., Susenbeth A., et al., C4 abundance in an Inner Mongolia grassland system is driven by temperature–moisture interaction, not grazing pressure, Basic Appl. Ecol., 2012, 13, 67–75
[63] Follak S., Potential distribution and environmental threat of Pueraria lobata, Cent. Eur. J. Biol., 2011, 6, 457-469
[64] Šilc U., Vrbničanin S., Božić D., Čarni A., Stevanović Z.D., Alien plant species and factors of invasiveness of anthropogenic vegetation in the Northwestern Balkans – a phytosociological approach, Cent. Eur. J. Biol., 2012, 7, 720-730