Long-term weather sensitivity of open sand grasslands of the Kiskunság Sand Ridge forest-steppe mosaic after wildfires

Running title: Long-term weather sensitivity after wildfires

Ónodi, Gábor[1]; Altbäcker, Vilmos[2]; Aszalós, Réka[1]; Botta-Dukát, Zoltán[1]; Hahn, István[3] and Kertész, Miklós[1]

[1] Institute of Ecology and Botany, Centre for Ecological Research, Hungarian Academy of Sciences, Alkotmány 2-4, 2163 Vácrátót, Hungary

[2] Eötvös Loránd University, Department of Ethology, Jávorka 14, 2130 Göd, Hungary

[3] Eötvös Loránd University, Department of Plant Systematics, Ecology and Theoretical Biology, Pázmány Péter 1/C, 1117 Budapest, Hungary

Corresponding author: Ónodi, Gábor
Postal address: Alkotmány 2-4, 2163 Vácrátót, Hungary
E-mail: onodi.gabor@okologia.mta.hu
Fax: ++36-28-360-122/110

E-mail addresses
Altbäcker, Vilmos: altbac@gmail.com
Aszalós, Réka: aszalos.reka@okologia.mta.hu
Botta-Dukát, Zoltán: botta-dukat.zoltan@okologia.mta.hu
Hahn, István: hahn@ludens.elte.hu
Kertész, Miklós: kertesz.miklos@okologia.mta.hu

Keywords: Disturbance; Drought; LTER; Post-fire succession; Resistance

Abstract

We studied the long-term impact of wildfire on the vegetation dynamics of sand grasslands in a forest-steppe vegetation mosaic in Central Hungary (Kiskunság). Long-term permanent quadrat monitoring was carried out from 1997 to 2008. We sampled the forest-steppe mosaic both in burnt and unburnt areas in 100 patches altogether using one by one meter quadrats. The effect of fire and precipitation on vegetation dynamics was characterized by patch type transitions between years. Patch types were defined by means of Cocktail method. Nine patch types of sand grasslands were altogether identified. The least productive patch types, bare soil and cryptogam dominance, did not occur in the burnt patches, while annual dominated patch type appeared only in burnt patches. The frequencies of patch type changes were significantly higher in burnt patches than in unburnt ones, independently on the time since fire. All the eight patch types found in the unburnt patches proved permanent, while in the burnt patches only four of seven were so. The relative frequency of patch type changes did not correlate to the precipitation in the vegetation period in the unburnt patches, while positively correlated in the burnt patches. It was concluded that the long-term difference in grassland dynamics between the unburnt and burnt patches, i.e. the excess of the patch type transitions in the burnt grasslands, are due to increased drought sensitivity of the grassland, which is the consequence of the elimination of the woody component of the forest-steppe vegetation.

Nomenclature: Simon 2000

Introduction

The impact of fire is one of the focal areas in the long-term ecological research on arid and semi-arid ecosystems (Bowman and Murphy 2010, Keeley 1986, Whelan 1995). The majority of the studies in Mediterranean shrublands (Capitanio and Carcaillet 2008, Esposito et al. 1999, Montenegro et al. 2004, Uys et al. 2004), tall-grass prairies (Collins 1992, Feldman and Lewis 2005), and tropical savannahs (Greenville et al. 2009, Langevelde et al. 2003, Lewis et al. 2010) focus on ecological processes of fire-adapted ecosystems (Keeley 1986, Lewis et al. 2010). However, the impact of the fire is the most severe in ecosystems which are not adapted to fire (Engel and Abella 2011). Studying these ecosystems are particularly important if they have been recently exposed to more fire due to human activity and increasing aridity caused by climate change (Bowman and Murphy 2010). Fire is a primary disturbance factor of the grassland vegetation, which most often reduces the abundance of the woody elements (Belsky 1992, Montenegro et al. 2004), but can also lead to invasion of bushes or trees (Franzese et al. 2009).

We studied poplar-juniper-grassland vegetation complex belonging to the transitional forest-steppe biome in the Kiskunság Sand Ridge of Central Hungary (Kovács-Láng et al. 2000), which is particularly rich in endemic plant species (Molnár 2003). This is a two-phase system consisting poplar-juniper woods and sand grassland patches, forming a dynamic mosaic pattern. This pattern is sensitive to drought, wildfire, and changes in herbivory (Katona et al. 2004, Kertész et al. 1993, Ónodi et al. 2006, Ónodi et al. 2008), thus particularly suitable for studying the impacts of these disturbances and stress factors.

The biodiversity of natural and semi-natural communities increasingly depends on human management (Chapin et al. 2010). Thus, the proper management, i.e. selection of wood species for plantation, forestry technology practices, regulation of grazing, alteration of the landscape pattern, and control of the water regime should mitigate the chance of ignition, fire propagation and fire severity in communities exposed to increasing fire risk. Despite this demand, a sort of management changes in the Kiskunság region has increased the fire risk for the Sand Ridge forest-steppe vegetation. Thus, as a combined effect of drainage, forest and orchard plantations, and increased water exploitation, the ground water level has decreased since the late 1970s (Pálfai 1994), and the subsequent decrease of soil moisture (Kertész and Mika 1999) may have also contributed to the larger extent of the fires. The grazing pressure has declined since the 1960s (Bíró 2003, Katona et al. 2004), increasing the hazard of wildfire (Ónodi et al. 2008). Similarly, after the sharp decrease of the animal stock in Southern Russia wildfires began to appear from the end of 1990s, and in 2006-07, wildfires spread over large areas (Dubinin et al. 2010). Since 1990, three out of the four large protected juniper-poplar forest grassland mosaics have been almost completely burnt in the Kiskunság Sand Ridge area. The extensive alien *Pinus nigra* plantations have invariably played major role in conducting the fire across the landscape (Kiskunság National Park, personal communication). So far, all the known wildfire events are man made in this region, thus the fire is not part of natural disturbance regime. According to climate change studies, the summer temperature and the inter-annual variation of the precipitation will keep increasing (Bartholy et al. 2007, Bartholy et al. 2009), thus we predict an increase of frequency and extension of wildfires, similarly to the Mediterranean areas (Bowman and Murphy 2010, Veblen 2003). In spite of these facts, there are very few well documented studies in Central-Europe concerning grassland burning (but see Ónodi et al. 2007, 2008; Deák et al. 2012, Valkó et al. 2012).

Hereinafter, we call “patch type” the clusters of the vegetation compositions of grassland patches, and “vegetation dynamics” the year to year changes of the patch types, and we consider “burnt” and “unburnt” states of the patches as natural treatments.

We aimed at studying the impact of wildfires on the vegetation dynamics in the grassland component of this transitional biome. Grasslands burnt by wildfires were compared with unburnt grasslands. The following questions were raised.1. Does the wildfire modify the sensitivity of vegetation dynamics of the grasslands to drought? 2. How long does wildfire affect the vegetation dynamics?

Our null-hypotheses were as follows: a) the frequency distributions of the patch types on the burnt and unburnt patches are not different; b) the distribution of year to year transitions of the patch types on the burnt and unburnt patches are not different; c) if there were differences in the distributions of transitions, these differences do not depend on the time since fire; d) the frequencies of transitions do not depend on the precipitation.

Materials and methods

The study sites are in the Kiskunság National Park in Central Hungary, in vegetation mosaics consisting juniper-poplar woods and open sand grasslands. This two-component vegetation type can be found in the western edge of the Eurasian forest-steppe zone (Kovács-Láng et al. 2000). The two-phase character is enhanced by the extreme moisture regime of the soil caused by the high hydraulic conductivity of the calcareous sand soil of low (<1%) humus content (Calcaric Arenosol) (Várallyay 2005). The precipitation quickly infiltrates through the root zone of the grassland, while remains available for woody vegetation (Molnár 2003). The climate is moderately continental with sub-Mediterranean effects (Zólyomi et al. 1997). Annual mean precipitation is around 500–550 mm and mean monthly temperatures range from -1,8 °C in January to 21 °C in July (Kovács-Láng et al. 2000). The main growing season in the open sand grassland is the late spring.

Long-term monitoring on three partially burnt sand dune areas have been carried out since 1997, combining space-for-time substitution (Pickett 1989) with long-term permanent plot observations (Bakker et al. 1996). The study is part of the KISKUN LTER project (Kovács-Láng et al. 2008). The Bugac site was burnt in 1976, the Bócsa site in 1993. On these sites the vegetation changes have been recorded since 1997. The Orgovány site was burnt in 2000, and we started the monitoring in 2002. In all three sites, the burnt area ranged several square-kilometers, affecting planted forests as well as forest-steppe stands. We consider the unburnt areas reference vegetation for the burnt areas before the fire. Both unburnt and burnt areas are covered by a mosaic of woods and grassland patches. On the unburnt areas, the woods are dominated by either juniper (*Juniperus communis*), or poplar species (*Populus alba, P. canescens, and P. nigra*) and juniper. On the burnt areas junipers can not regenerate, but poplar species resprout after the wildfire.

Our sampling unit were 1 by 1 m quadrats. Five quadrats were placed in each selected grassland patches of the open sand grassland component of the mosaic, both in burnt and unburnt areas (Fig. 1). Samples were taken from 100 patches, 46 burnt and 54 unburnt, from ten groups of patches in three sites. Groups of patches were fenced in order to control the previously very high grazing pressure; this resulted in spatially aggregated patch distribution (Fig. 2). In the Bugac site (Fig. 2c) patches were grouped in two partially burnt (N 46˚ 39,30', E 19˚ 36,49'; N 46˚ 39,20', E 19˚ 36,48') and two unburnt (N 46˚ 38,91', E 19˚ 36,43'; N 46˚

38,88’, E 19˚ 36,21’) areas. From 1997 to 2001 we took samples in ten burnt and 26 unburnt patches, and in 2002 we enlarged the sample to 12 burnt and 28 unburnt patches (Table 1). In the two partially burnt areas (N 46˚ 38,68’, E 19˚ 28,08’; N 46˚ 38,60’, E 19˚ 28,03’) of the Bócsa site (Fig. 2b) ten burnt and six unburnt patches were sampled from 1997 to 2001. In 2002 we enlarged the sample to 14 burnt and six unburnt patches. In the Orgovány site (Fig. 2a) 20 burnt from two burnt areas and 20 unburnt patches from two unburnt ones were sampled.

In the quadrats, we visually estimated the cover of the vascular plants as well as the cover of the mosses, lichens, litter, and exposed soil surface twice a year. Visual estimation has low expected errors at the scale of our sampling, especially in nutrient deficient habitats (Klimeš 2003), like in open sand grasslands. The first sampling was carried out each year in late May or early June, at the time of the biomass peak before the summer drought, and the second in late September or early October, at the secondary biomass peak.

Vegetation dynamics was studied at the spatial scale of the patches, represented by five quadrats. We associated a patch type to each patch in each year, applying the Cocktail method (Bruelheide 2000). First, the spring and autumn data were pooled within years and within quadrats choosing the higher score, then cover in the five quadrats were averaged, and these patch level cover values were used in the subsequent analysis. Species groups were formed based on the positive associations among species (Bruelheide and Chytrý 2000). The interspecific associations were measured by hypergeometric u-value (Chytrý et al. 2002) calculated from binary data. Group forming started with the pair of ungrouped species that had the highest interspecific association. It stopped when the u-value of the new candidate species to the group was below 5. We modified the original Cocktail algorithm, and instead of presence of species groups we used their total cover to define the patch types. If the cover of vascular plants exceeded 5%, the patch was classified according to the vascular species group which has the highest cover. Otherwise, it was classified either into cryptogam patch type, if cover of cryptogams was at least 50%, or bare soil patch type. We choose the above method in order to get of patch types which provide us opportunity (1) to compare the patch type distributions of burnt and unburnt patches, (2) to calculate the frequency of year to year transitions between patch types.

Originally, the Cocktail method (Bruelheide 2000) was developed for finding groups of species, which then define plant associations in databases of preferentially selected relevés. We looked for all species groups which define an exhaustive classification of the sample. The application of this method, to define patch types, allows describing the vegetation dynamics by means of analysis of transitions between a few discrete states, which provides a general picture of the changes in the composition. The species abundance data themselves are loaded with high noise because of the effect of the weather immediately previous to the sampling, while patch types are less affected by this noise.

The type associated to a patch could change from year to year. The changes between consecutive years were summarized in transition matrices for burnt and unburnt patches, separately. The transition matrices calculated from the pooled data were compared with a null-model in which transition probabilities depended on the proportion of vegetation types before and after the transition only. First, the global difference was tested by chi-square test, and if it proved to be significant, Freeman-Tukey deviates were used to find the significantly over- and under-represented transitions. For each site, we calculated the proportion of values in the diagonal of transition matrices (i.e. no-change between consecutive years) and compared it between burnt and unburnt areas applying u-test for proportions (Zar 1999). The complement of this proportion (i.e. the proportion of changes) was calculated from the pooled data set and it was correlated with precipitation in the vegetation period from April to September when the new vegetation type appeared. Separate correlations were calculated for burnt and unburnt patches. We interpret the significantly over-represented year to year transitions from a patch type to the same one, as resistance, and from one patch type to another, as sensitivity.

Results

Nine patch types were identified: bare soil, cryptogam dominance, annual dominance, *Festuca vaginata* group dominance, *Stipa borysthenica* group dominance, *Carex liparicarpos* group dominance, *Poa bulbosa* group dominance, *Calamagrostis epigeios* group dominance, and *Poa angustifolia* group dominance. (Henceforth, we refer the patch types without the notion 'group dominance'). Fig. 3a and 3b show the relative frequency of the patch types in each year, for burnt and unburnt patches separately.

The patch types 'bare soil' and 'cryptogam' occurred only in the unburnt patches, while the patch type 'annual' only in burnt patches. Of the characteristic patch types of the open perennial sand grasslands, the patch type '*Festuca vaginata*' was frequent in both burnt and unburnt patches, while patch type '*Stipa borysthenica*' gradually spread in burnt patches, together with the disappearance of the more closed '*Calamagrostis epigeios*' and '*Poa angustifolia*' patch types.

All the patch types found in the unburnt patches were permanent, i.e. the frequencies of the transitions into themselves proved significantly higher than expected, based on the frequencies of their occurrences (Freeman-Tuckey deviates; $p<5\%$). On the contrary, in the burnt patches only the patch types '*Festuca vaginata*', '*Stipa borysthenica*', '*Carex liparicarpos*', and '*Calamagrostis epigeios*' were permanent, and we got transitions of significantly higher frequency than expected, namely, between '*Calamagrostis epigeios*' and 'annual' and between '*Calamagrostis epigeios*' and '*Poa bulbosa*' (Fig. 4a and 4b).

By means of two-sample u-test we found that the frequency of patch type changes were significantly higher in burnt than in unburnt patches in Bugac ($Z=2.52$, $p=0.012$) and Bócsa ($Z =2.06$, $p=0.039$) sites (Fig. 5). The most recently burnt Orgovány site the same tendency was found close to be significant ($Z =1.89$, $p=0.059$).

In the unburnt patches, the relative frequency of patch type changes proved to be independent from the precipitation in the vegetation period ($R^2_{adj} = 6.4*10^{-7}$, $p=0,998$, Fig. 6a), while positively correlated in the burnt patches ($R^2_{adj} = 0,406$, $p=0,035$, Fig. 6b). The driest year was 2003, and we found the less patch type changes in that year, while we found the most changes in the next, wet year. In case of the burnt patches, the 2008 data (in the lower right part of Fig. 6b) proved to be a leverage point as Cook's $D>1$ (Cook 1979, Reiczigel et al. 2007). Without this point $R^2_{adj}= 0.72$, $p=0.0019$.

Discussion

General pattern of post-fire regeneration

Both patch type data (Fig. 3b) and our field experience show that the patch types dominated by perennials are the starting stages of the post-fire succession. Those patch types were the most frequent on the non-burnt areas too, and they were also present before the fire. We observed that the perennial plant species of the sand grassland were persistent; i.e. they re-sprouted after the fire from their buds, in accordance with ‘regeneration’ type post-fire succession of Ghermandi et al. (2004). This ability of fast regeneration is indicative to fire adaptation of the vegetation (Lewis et al. 2010). The same fast regeneration was found in fire-adapted grasslands in South Africa (Uys et al. 2004), where the grass species tolerated the four-year burning cycle, while most of the dicots tolerated even the yearly burning.

However, the post-fire regeneration of plant species in our grasslands highly varied by life forms. Most of the drought tolerant perennial vascular plants have high below-ground/above-ground biomass ratio, and the below-ground parts easily survive the fast spreading fire. On contrary, we did not find 'cryptogam' patch type on the burnt areas (Fig. 3b). This result is in contradiction with our first null-hypothesis and shows that fire has long-term effect on grassland composition. The fire reduces the cover of cryptogams, especially the abundance of lichens (Johansson and Reich 2005). Esposito et al. (1999) found quick establishment of pioneer moss species in burnt macchia vegetation. In our case, the regeneration process of *Tortella* and *Tortula* species was very slow, while lichens could not re-establish in the timescale of our study.

Another characteristic difference between unburnt and burnt areas was that the 'annual' patch type appeared only in the latter ones (Fig. 3a and 3b). Similar increase in the abundance of annuals can be observed in wet years after dry years. All of those annuals live in the studied grasslands, and they are generally prolific after disturbance. Thus we consider the ‘annual’ patch type an expected ordinary response of the annual species of the open grasslands.

The woody perennial species were variously affected by the fire. The fire induced intensive re-sprouting of poplar species, together with spreading of other clonal species like *Calamagrostis epigeios*, in accordance with the findings of Marozas et al. (2007). We observed the spreading of poplar species (*Populus alba* and *P. nigra*) which have resprouter and clonal spreading strategy (Menges and Kohfeldt 1995). Szujkó-Lacza and Komáromy (1986) also detected the fast spreading of the poplar two years after the Bugac wildfire. On contrary, the common juniper (*Juniperus communis*) does not regenerate after fire (Marozas et al. 2007, Wink and Wright 1973). According to our observations, even the partially burnt specimens died in a year. The lack of junipers (the darkest element of the vegetation) is noticeable around the burnt patches in Fig. 2. The sensitivity of the juniper to the fire causes major change in the structure of the vegetation, where it was dominant before. Consequently, the whole vegetation mosaic cannot be considered fire-adapted, as both the dominant juniper and the widespread cryptogams do not recover after the fire.

The long-term effect of wildfire

According to the observed patch type transitions (Fig. 4) the vegetation is more dynamic after fire than in unburnt areas: contrary to our second null-hypothesis, less patch types are significantly permanent and statistically significant transitions from one patch type into another appear in burnt areas. The long-term effect of fire, which we found in all of our sites in the Kiskunság Sand Ridge, shows the lack of fire adaptation based on Engel and Abella (2011). According to our third null-hypothesis, application of space-for-time-substitution (Pickett 1989) for the patch type transitions (Fig. 5) shows that the excess of dynamics in the burnt areas does not disappear even in longer time. Engel and Abella (2011) also found dynamics independent from time since fire and high long-term post-fire variability in *Coleogyne ramosissima* dominated community of Mojave.

The changes of patch types show a network-like pattern of transitions. Thus, most of the patch types, except the rare ones, have more than one connection, and most of the connections are bidirectional (Fig. 4). This pattern of transitions differs from the Clementian directional succession (Clements 1916), and rather corresponds to Egler's (1954) concept of initial floristic composition which he applied to secondary succession. In accordance to our results, Capitanio and Carcaillet (2008) also found Egler's concept applicable to post-fire succession of Mediterranean vegetation mosaic of Aleppo pine forest and sclerophyll shrubs (*garrigue*). The regeneration was quick, and in both studies, the species of the post-fire vegetation had been present in the pre-fire vegetation. These findings put the question, if the post-fire vegetation dynamics could be considered secondary succession, or rather a quick development towards a patchwork of metastable stages which could also be built up without fire (Trabaud 1987).

Factors influencing the dynamics

The vegetation dynamics in our study sites is regulated at two levels: locally in short term, and at landscape scale in longer terms. Locally, the resistance of the patch types is different. By 2007 and 2008, the *Festuca vaginata* and *Stipa borysthenica* patch types reached a combined frequency of more than 90 % in the burnt patches (Fig. 3b). Fewer transitions can be found between these years, which we interpret as the impact of the high resistance of those patch types (Fig. 4). The contradiction between the impact of precipitation and spreading of permanent patch types might result in the leverage point of 2008 in the precipitation-transition relation (Fig. 6b).

Despite our fourth null-hypothesis, the burnt state of the landscape resulted in precipitation dependent vegetation dynamics, however, the dynamics of control patches were independent from precipitation. Fire increased the dynamics of the grassland vegetation of the wood-grassland mosaic on the long run as less patch types were found permanent in the bunt areas (Fig. 4). We found this in the sites which had burnt two to eight, four to fourteen, and twenty to thirty years before the study. The independence of the increased dynamics from the time passed from the fire implies to long-term indirect effect of the fire. The most conspicuous impact of the fire is the disappearance of the juniper, which is a long-term change of habitat structure (Bond and Keeley 2005). This disappearance leads to less shade in the grasslands. The different reaction (Fig. 6) to the precipitation of the partially shaded unburnt patches and the open burnt patches is a result of higher resistance due to the presence of woody vegetation or the shades (Bartha et al. 2008). In our opinion, this buffering effect of the shades is the major factor reducing the impact of droughts in the more woody areas. We observed the dynamics by means of year to year transitions of patch types. Thus, the impact of drought can be observed in the subsequent wet years when the damaged vegetation regenerates.

We propose a conceptual scheme on the changing dynamics after fire (Fig. 7). The same wet years, in which there are higher biomass production and more opportunity to change in composition, lead to transitions of patch types only after the fire which made the vegetation more open.

Our main finding is that the grassland patches of the juniper-poplar-grassland mosaic is more dynamic after wildfire, and remain more dynamic even for decades. We observed that the changes mostly occurred in wet years; however, we suppose that the cause of the changes is the increased vulnerability of the grassland species for the drought in the bunt sites, where the shadows of the junipers does not reduce the effect of drought. As the wildfire is not part of the natural disturbance regime of the juniper-poplar stands, we think that they should be saved from wildfire more effectively than in the past. We should add that the largest remaining unburnt juniper-poplar stand in Bugac region burnt down in 2012, ignited by the surrounding *Pinus nigra* plantations.

Acknowledgements

We thank Sándor Bartha and György Kröel-Dulay for their advice. We are grateful to Tibor Tóth, Katalin Szitár and Piroska Kucs for their contribution to the field work. We thank the Kiskunság National Park (Hungary) for the support of our field experiments. This study was funded by the Hungarian Scientific Research Found (OTKA F5254, T29703, and A08-1-2009-0051) and by the National Research and Development Program (NKFP 3B-0008/2002, NKFP 6-0013/2005).

Refereces

Bakker, J.P., H. Olff, J.H. Willems and M. Zobel. 1996. Why do we need permanent plots in the study of long‐term vegetation dynamics? *J. Veg. Sci.* 7: 147–156.

Bartha, S., G. Campetella, E. Ruprecht, A. Kun, J. Házi, A. Horváth, K. Virágh and Zs. Molnár. 2008. Will interannual variability in sand grassland communities increase with climate change? *Comm. Ecol.* 9: 13–21.

Bartholy, J., R. Pongrácz, and G. Gelybói. 2007. Regional climate change expected in Hungary for 2071-2100. *Appl. Ecol. Env. Res.* 5: 1–17.

Bartholy, J., R. Pongracz, C. Torma, I. Pieczka, P. Kardos and A. Hunyady. 2009. Analysis of regional climate change modelling experiments for the Carpathian basin. *Int. J. Global. Warm.* 1: 238–252.

Belsky, A.J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *J. Veg. Sci.* 3: 187–200.

Bíró, M. 2003. Pillantás a múltba: a Duna–Tisza közi homokbuckások tájtörténete az elmúlt kétszázötven évben. In: Zs. Molnár (ed.), *Sanddunes in Hungary (Kiskunság).* TermészetBÚVÁR Alapítvány Kiadó, Budapest. pp. 71–82.

Bond, W.J. and J.E. Keeley. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends Ecol. Evol.* 20: 387–394.

Bowman D.M.J.S. and B.P. Murphy. 2010. Fire and biodiversity. In: N.S. Sodhi and P.R. Ehrlich (eds.), *Conservation Biology for All*. Oxford University Press, pp. 163–181.

Bruelheide, H. 2000. A new measure of fidelity and its application to defining species groups. *J. Veg. Sci.* 11: 167–178.

Bruelheide, H. and M. Chytrý. 2000. Towards unification of national vegetation classifications: A comparison of two methods for analysis of large data sets. *J. Veg. Sci.* 11: 295–306.

Capitanio, R. and C. Carcaillet. 2008. Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. *Forest. Ecol. Manag.* 255: 431–439.

Chapin, F.S., S.R. Carpenter, G.P. Kofinas, C. Folke, N. Abel, W.C. Clark, P. Olsson, D.M.S. Smith, B. Walker, O.R. Young, F. Berkes, R. Biggs, J.M. Grove, R.L. Naylor, E. Pinkerton, W. Steffen and F.J. Swanson. 2010. Ecosystem stewardship: sustainability strategies for a rapidly changing planet. *Trends. Ecol. Evol.* 25: 241–249.

Chytrý, M., L. Tichý, J. Holt and Z. Botta Dukát. 2002. Determination of diagnostic species with statistical fidelity measures. *J. Veg. Sci.* 13: 79–90.

Clements, F.E. 1916. *Plant Succession: an Analysis of the Development of Vegetation*. Carnegie Institution of Washington. Washington.

Collins, S.L. 1992. Fire Frequency and Community Heterogeneity in Tallgrass Prairie Vegetation. *Ecology* 73: 2001–2006.

Cook, R.D. 1979. Influential Observations in Linear Regression. *J. Am. Statist. Assoc.* 74: 169–174.

Deák B., Valkó O., Schmotzer A., Kapocsi I., Tóthmérész B., Török P. (2012): Gyepek égetésének természetvédelmi megítélése Magyarországon: Problémák és pozitív tapasztalatok. *Tájökológiai Lapok* 10: 287-303

Dubinin, M., P. Potapov, A. Lushchekina and V.C. Radeloff. 2010. Reconstructing long time series of burned areas in arid grasslands of southern Russia by satellite remote sensing. *Remote. Sens. Environ.* 114: 1638–1648.

Egler, F.E. 1954. Vegetation Science Concepts I. Initial Floristic Composition, a Factor in Old-Field Vegetation Development. *Vegetatio* 4: 412–417.

Engel, E.C. and S.R. Abella. 2011. Vegetation recovery in a desert landscape after wildfires: influences of community type, time since fire and contingency effects. *J. Appl. Ecol.* 48: 1401–1410.

Esposito, A., S. Mazzoleni and S. Strumia. 1999. Post-fire bryophyte dynamics in Mediterranean vegetation. *J. Veg. Sci.* 10: 261–268.

Feldman, S.R. and J.P. Lewis. 2005. Effects of fire on the structure and diversity of a Spartina argentinensis tall grassland. *Appl. Veg. Sci.* 8: 77–84.

Franzese, J., L. Ghermandi and B. Donaldo. 2009. Post‑fire shrub recruitment in a semi‑arid grassland: the role of microsites. *J. Veg. Sci.* 20: 251–259.

Ghermandi, L., N. Guthmann and D. Bran. 2004. Early post-fire succession in northwestern Patagonia grasslands. *J. Veg. Sci.* 15: 67–76.

Greenville, A.C., C.R. Dickman, G.M. Wardle and M. Letnic. 2009. The fire history of an arid grassland: the influence of antecedent rainfall and ENSO. *Int. J. Wildland Fire* 18: 631–639.

Johansson, P. and P.B. Reich. 2005. Population size and fire intensity determine post-fire abundance in grassland lichens. *Appl. Veg. Sci.* 8: 193–198.

Katona, K., Z. Bíró, I. Hahn and V. Altbäcker. 2004. Competition between European hare and European rabbit in a lowland area, Hungary: a long-term ecological study in the period of rabbit extinction. *Folia Zool.* 53: 255–268.

Keeley, J.E. 1986. Resilience of Mediterranean shrub communities to fires. In: B. Dell, A.J.M. Hopkins and B.B. Lamont (eds.), *Resilience in Mediterranean-Type Ecosystems*. Dr. W. Junk, Dordrecht, The Netherlands, pp. 95-112.

Kertész, Á. and J. Mika. 1999. Aridification-Climate change in South-Eastern Europe. *Phys. Chem. Earth* 24: 913–920.

Kertész, M., J. Szabó and V. Altbäcker. 1993. The Bugac Rabbit Project. Part I.: Description of the study site and vegetation map. *Abstr. Bot.* 17: 187–196.

Klimeš, L. 2003. Scale‑dependent variation in visual estimates of grassland plant cover. *J. Veg. Sci.* 14: 815–821.

Kovács-Láng, E., Gy. Kröel-Dulay, M. Kertész, G. Fekete, J. Mika, I. Dobi-Wantuch, T. Rédei, K. Rajkai, I. Hahn and S. Bartha. 2000. Changes in the composition of sand grasslands along a climatic gradient in Hungary and implications for climate change. *Phytocoenologia* 30: 385–408.

Kovács-Láng, E., E. Molnár, Gy. Kröel-Dulay and S. Barabás. 2008. *The KISKUN LTER: Long-term Ecological Research in the Kiskunság, Hungary*. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót.

Langevelde van, F., C.A.D.M. Vijver van de, L. Kumar, J. Koppel van de, N. Ridder, J. Andel van de, A.K. Skidmore, J.W. Hearne, L. Stroosnijder, W.J. Bond, H.H.T. Prins and M. Rietkerk. 2003. Effects of Fire and Herbivory on the Stability of Savanna Ecosystems. *Ecology* 84: 337–350.

Lewis, T., N. Reid, P.J. Clarke and R.D.B. Whalley. 2010. Resilience of a high conservation value, semi-arid grassland on fertile clay soils to burning, mowing and ploughing. *Austral Ecol.* 35: 464–481.

Markó, G., G. Ónodi, K. Csatádi, I. Németh, O. Váczi, J. Bernáth, Z. Botta-Dukát, M. Kertész and V. Altbäcker. 2008. The effects of herbivory and grazing on vegetation. In: Kovács-Láng E, Molnár E, Kröel-Dulay G and Barabás S (eds.), *The KISKUN LTER: Long-term Ecological Research in the Kiskunság, Hungary*. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, pp. 61-63.

Marozas, V., J. Racinskas and E. Bartkevicius. 2007. Dynamics of ground vegetation after surface fires in hemiboreal Pinus sylvestris forests. *Forest Ecol. Manag.* 250: 47–55.

Menges, E.S. and N. Kohfeldt. 1995. Life History Strategies of Florida Scrub Plants in Relation to Fire. *Bull. Torrey Bot. Club.* 122: 282–297.

Molnár, Zs. 2003. *Sanddunes in Hungary (Kiskunság).* TermészetBÚVÁR Alapítvány Kiadó, Budapest.

Montenegro, G., R. Ginocchio, A. Segura, J.E. Keely and M. Gómez. 2004. Fire regimes and vegetation responses in two Mediterranean-climate regions. *Rev. Chil. Hist. Nat.* 77: 455–464.

Ónodi, G., M. Kertész and Z. Botta-Dukát. 2006. Effects of simulated grazing on open perennial sand grassland. *Comm. Ecol.* 7: 133–141.

Ónodi, G., Csatádi, K., Németh, I., Váczi, O., Botta-Dukát, Z., Kertész, M., Altbäcker, V., 2007. Birka (Ovis aries, L.)- és nyúllegelés (Oryctolagus cuniculus, L.) hatásainak vizsgálata az égésre homokpusztagyepen. *Természetvédelmi Közlemények* 14, 117-129.

Ónodi, G., M. Kertész, Z. Botta-Dukat and V. Altbäcker. 2008. Grazing Effects on Vegetation Composition and on the Spread of Fire on Open Sand Grasslands. *Arid Land Res. Manag.* 22: 273–285.

Pálfai, I. 1994. *Összefoglaló Tanulmány a Duna–Tisza közi Talajvízszint-süllyedés Okairól és a Vízhiányos Helyzet Javításának Lehetőségeiről.* A Duna–Tisza közi hátság vízgazdálkodási problémái.(The Problems of Water Management in Cisdanubia). Nagyalföld Alapítvány, Békéscsaba, pp. 111–125.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed.), *Long-term Studies in Ecology: Approaches and Alternatives*. Springer-Verlag, New York, pp. 110–135.

Reiczigel, J., A. Harnos and N. Solymosi. 2007. *Biostatisztika - Nem Statisztikusoknak* (Biostatistics). Pars Kft.

Simon, T. 2000. *A Magyarországi Edényes Flóra Határozója* (Identification hand-book of the Hungarian vascular plants). Nemzeti Tankönyvkiadó, Budapest.

Szujko-Lacza, J. and Z. Komaromy. 1986. Postfire resuccessional process in Juniper-Poplar wood in Bugac, Kiskunság National Park, Hungary. *Bull. Bot. Surv. India* 28: 89–110.

Trabaud, L. 1987. Dynamics after fire of sclerophyllous plant communities in the mediterranean basin. *Ecol. Medit.* 13: 25–37.

Uys, R.G., W.J. Bond and T.M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biol. Conserv.* 118: 489–499.

Valkó O., Deák B., Kapocsi I., Tóthmérész B., Török P. (2012): Gyepek kontrollált égetése, mint természetvédelmi kezelés – Alkalmazási lehet?ségek és korlátok. *Természetvédelmi Közlemények 18*: 517-526.

Várallyay, G. 2005. Magyarország talajainak vízraktározó képessége (Water storage capacity of Hungarian soils). *Agrokem.Talajtan.* 54: 5–24.

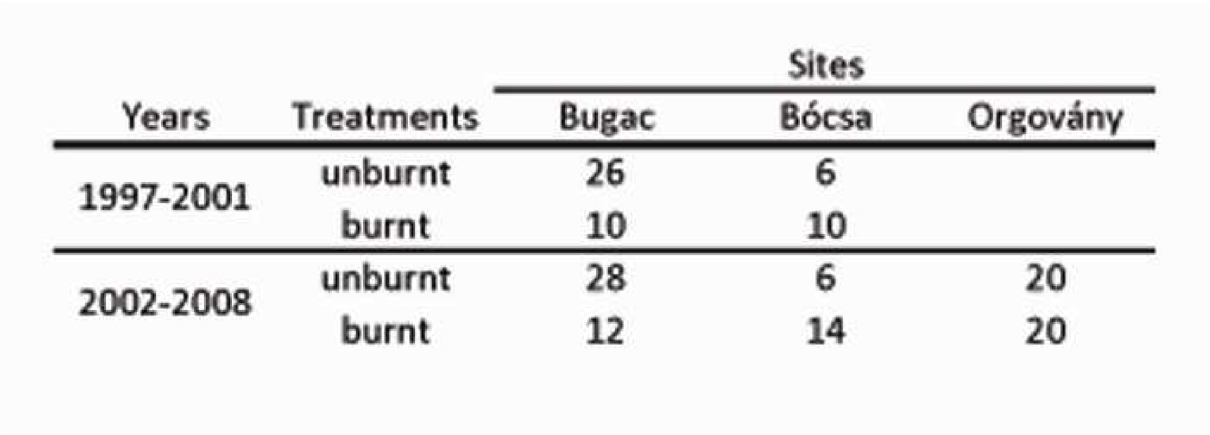
Veblen, T.T. 2003. *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*. Springer.

Whelan, R.J. 1995. *The Ecology of Fire*. Cambridge University Press, Cambridge.

Wink RL and Wright HA. 1973. Effects of Fire on an Ashe Juniper Community. *J. Range. Manage.* 26: 326–329.

Zar, J.H. 1999*. Biostatistical Analysis*. Prentice hall Upper Saddle River, NJ.

Zólyomi, B., M. Kéri and F. Horváth. 1997. Spatial and temporal changes in the frequency of climatic year types in the Carpathian Basin. *Coenoses* 12: 33–41.



Years	Treatments	Sites		
		Bugac	Bócsa	Orgovány
1997-2001	unburnt	26	6	
	burnt	10	10	
2002-2008	unburnt	28	6	20
	burnt	12	14	20

Table 1 Number of unburnt and burnt grassland patches in the experimental sites

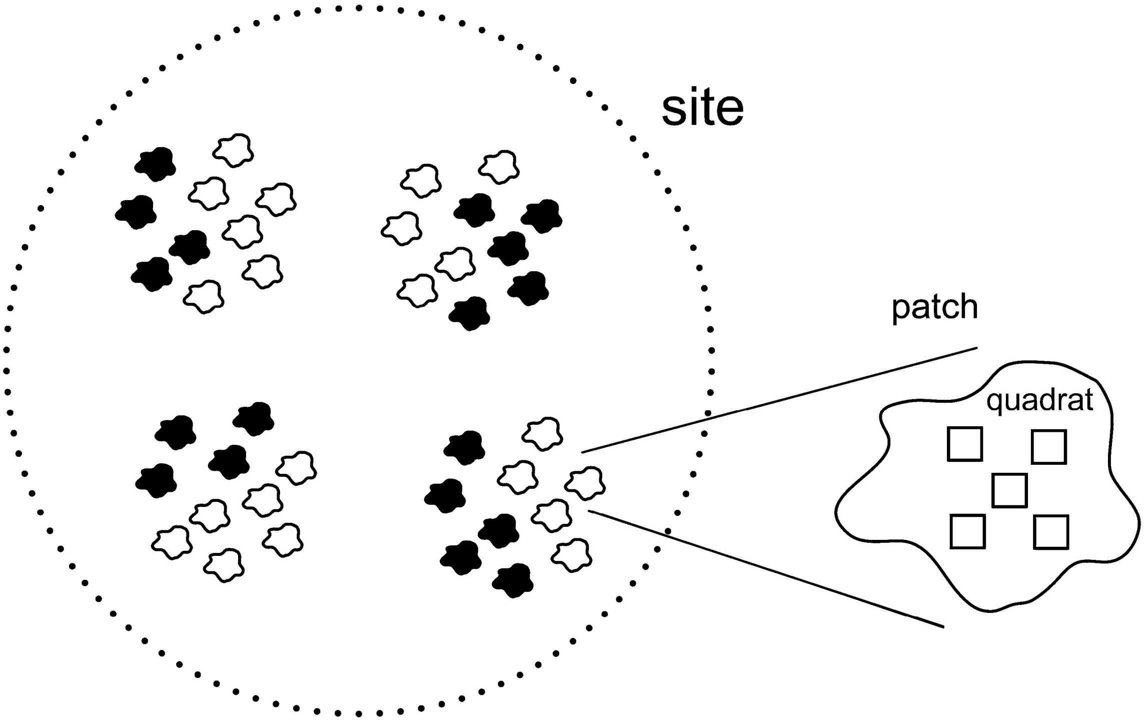


Fig 1 Levels of the sampling design: (1) 1 by 1 meter quadrats; (2) five quadrats are grouped in one grassland patch; (3) burnt (black filled) and unburnt (white filled) patches are arranged in the burnt and unburnt areas of the sites (dotted line)

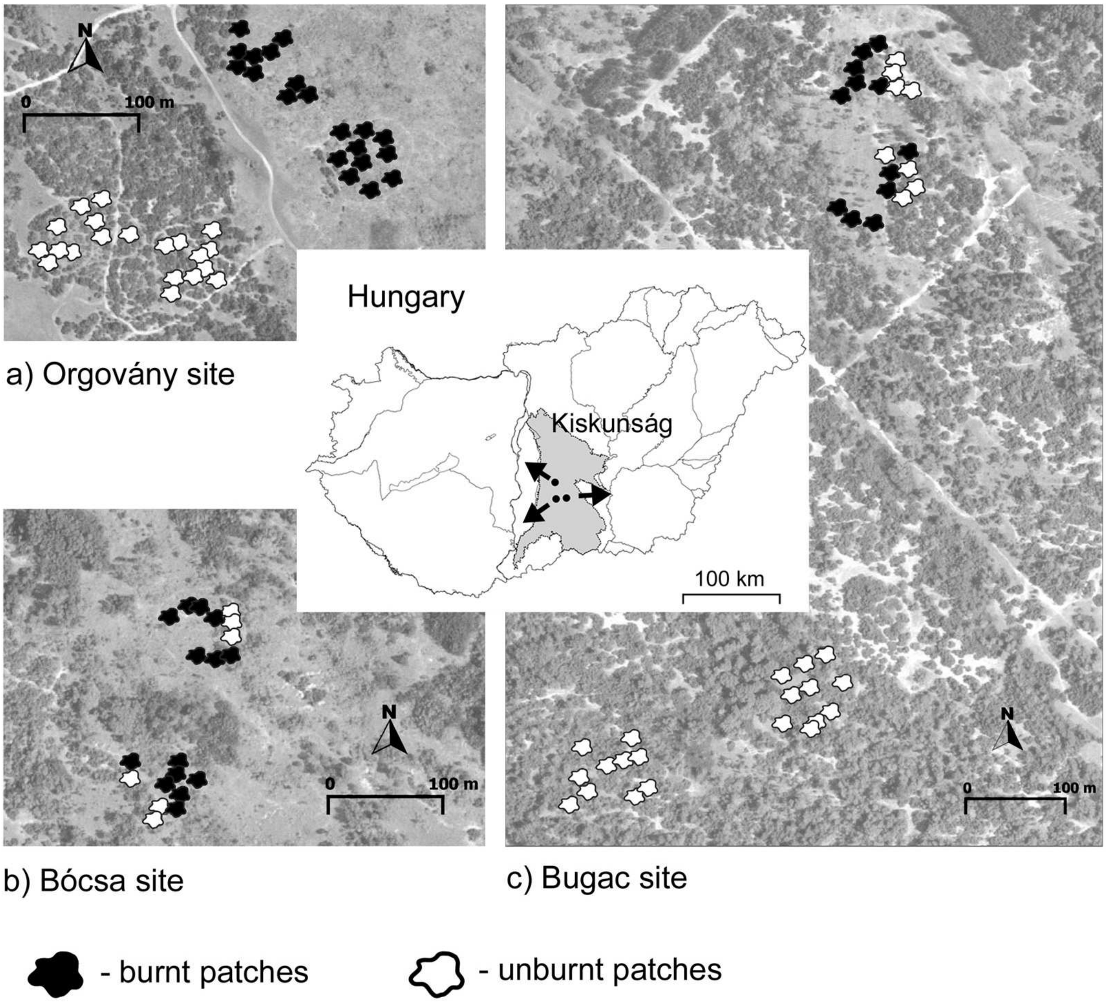


Fig 2 The study area: (a) the Orgovány site, (b) the Bócsa site, (c) the Bugac site. The sampled burnt (black filled) and unburnt (white filled) grassland patches of juniper-poplar forest-steppe mosaics are shown on aerial photographs in 2005.

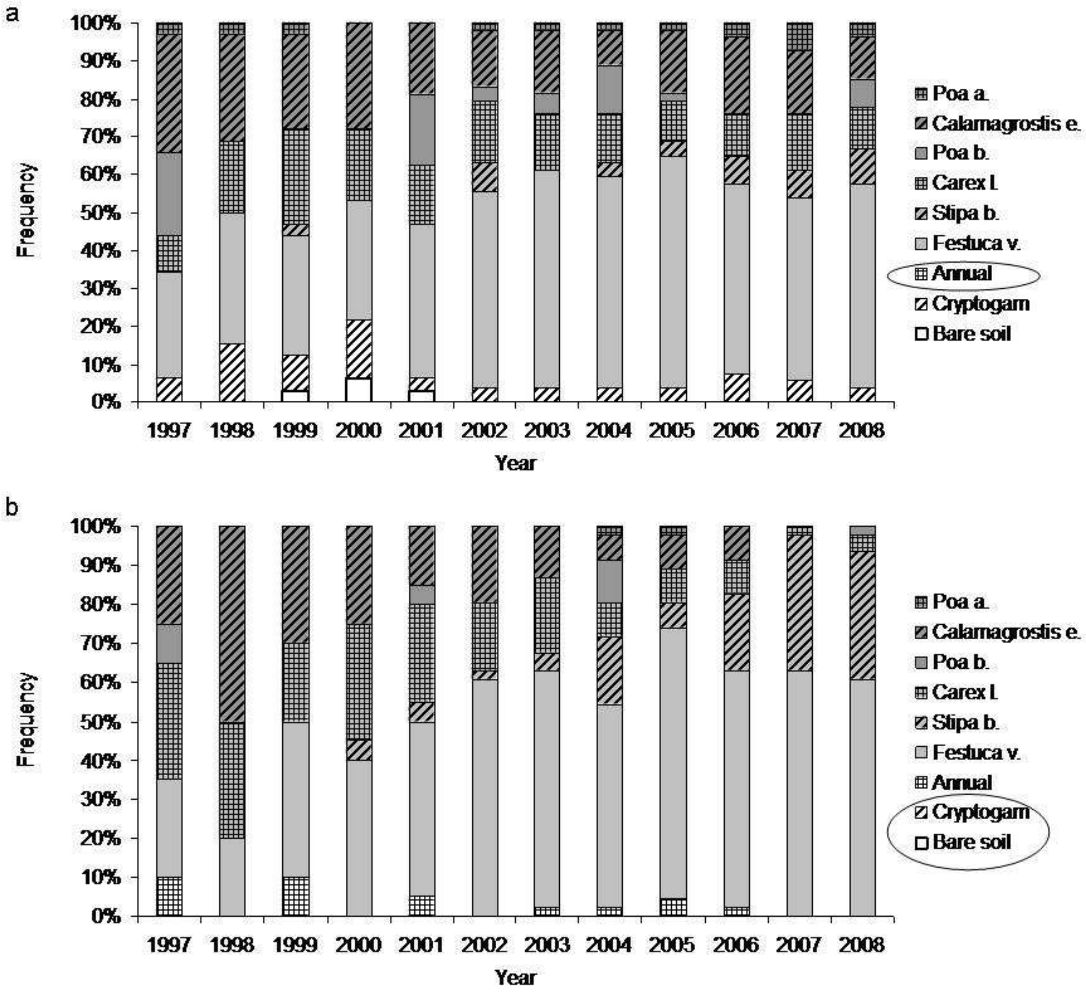
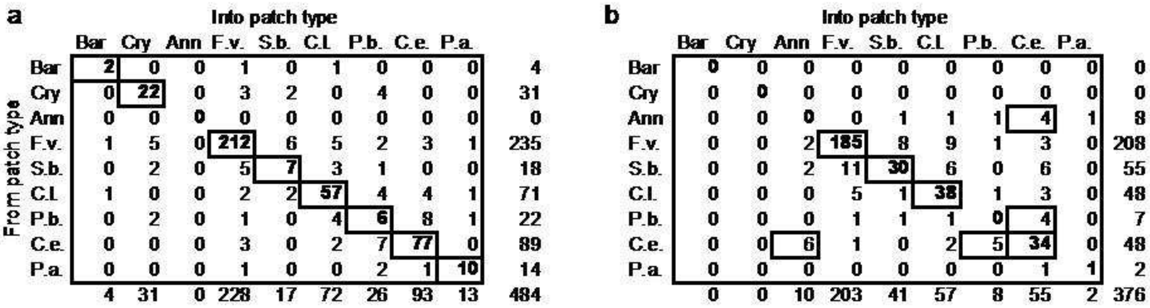


Fig 3 Relative frequency of the patch types in the unburnt (a) and burnt (b) grassland patches. Unobserved patch types are marked by circles



a

Into patch type

From patch type	Bar	Cry	Ann	F.v.	S.b.	C.l.	P.b.	C.e.	P.a.	
Bar	2	0	0	1	0	1	0	0	0	4
Cry	0	22	0	3	2	0	4	0	0	31
Ann	0	0	0	0	0	0	0	0	0	0
F.v.	1	5	0	212	6	5	2	3	1	235
S.b.	0	2	0	5	7	3	1	0	0	18
C.l.	1	0	0	2	2	57	4	4	1	71
P.b.	0	2	0	1	0	4	6	8	1	22
C.e.	0	0	0	3	0	2	7	77	0	89
P.a.	0	0	0	1	0	0	2	1	10	14
	4	31	0	228	17	72	26	93	13	484

b

Into patch type

	Bar	Cry	Ann	F.v.	S.b.	C.l.	P.b.	C.e.	P.a.	
Bar	0	0	0	0	0	0	0	0	0	0
Cry	0	0	0	0	0	0	0	0	0	0
Ann	0	0	0	0	1	1	1	4	1	8
F.v.	0	0	2	185	8	9	1	3	0	208
S.b.	0	0	2	11	30	6	0	6	0	55
C.l.	0	0	0	5	1	38	1	3	0	48
P.b.	0	0	0	1	1	1	0	4	0	7
C.e.	0	0	6	1	0	2	5	34	0	48
P.a.	0	0	0	0	0	0	0	1	1	2
	0	0	10	203	41	57	8	55	2	376

Fig 4 Transition matrix (a) for unburnt patches and (b) for burnt patches. Bold frames denote transitions which significantly higher than the expected values based on the frequencies of the patch types. The marked significant deviations are positive ones. Abbreviations: Bar - bare soil, Cry - cryptogam, Ann - annual, F.v. - *Festuca vaginata* group, S.b. - *Stipa borysthenica* group, C.l. - *Carex liparicarpos* group, P.b. - *Poa bulbosa* group, C.e. - *Calamagrostis epigeios* group, P.a. - *Poa angustifolia* group

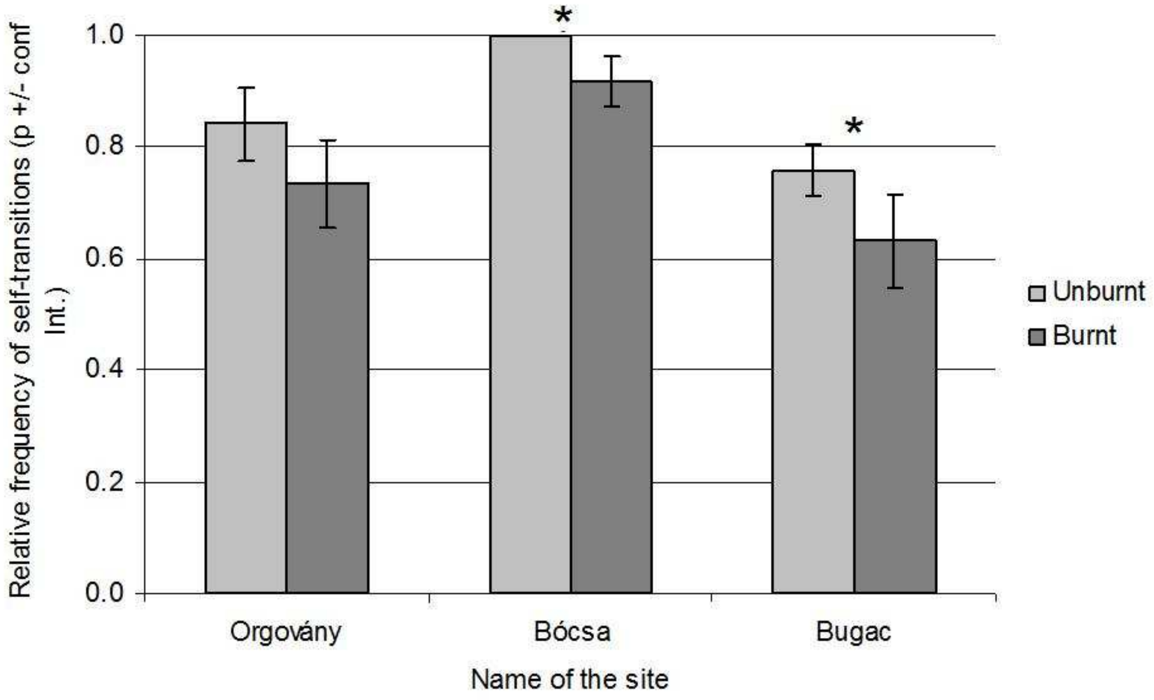


Fig 5 Self-transitions of unburnt and burnt open sand grassland patches. Asterisks indicate significantly decreased self-transitions in the burnt patches

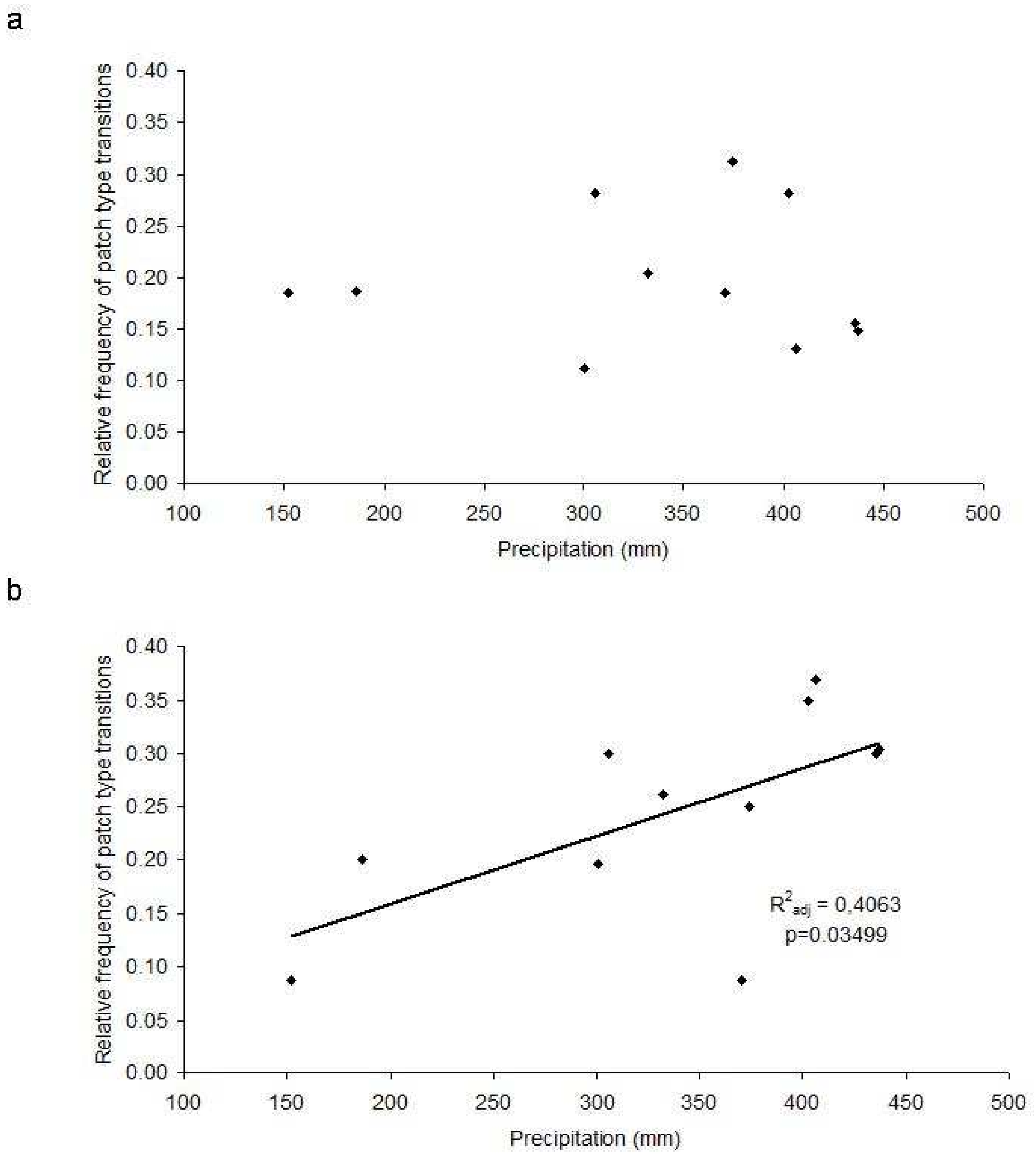
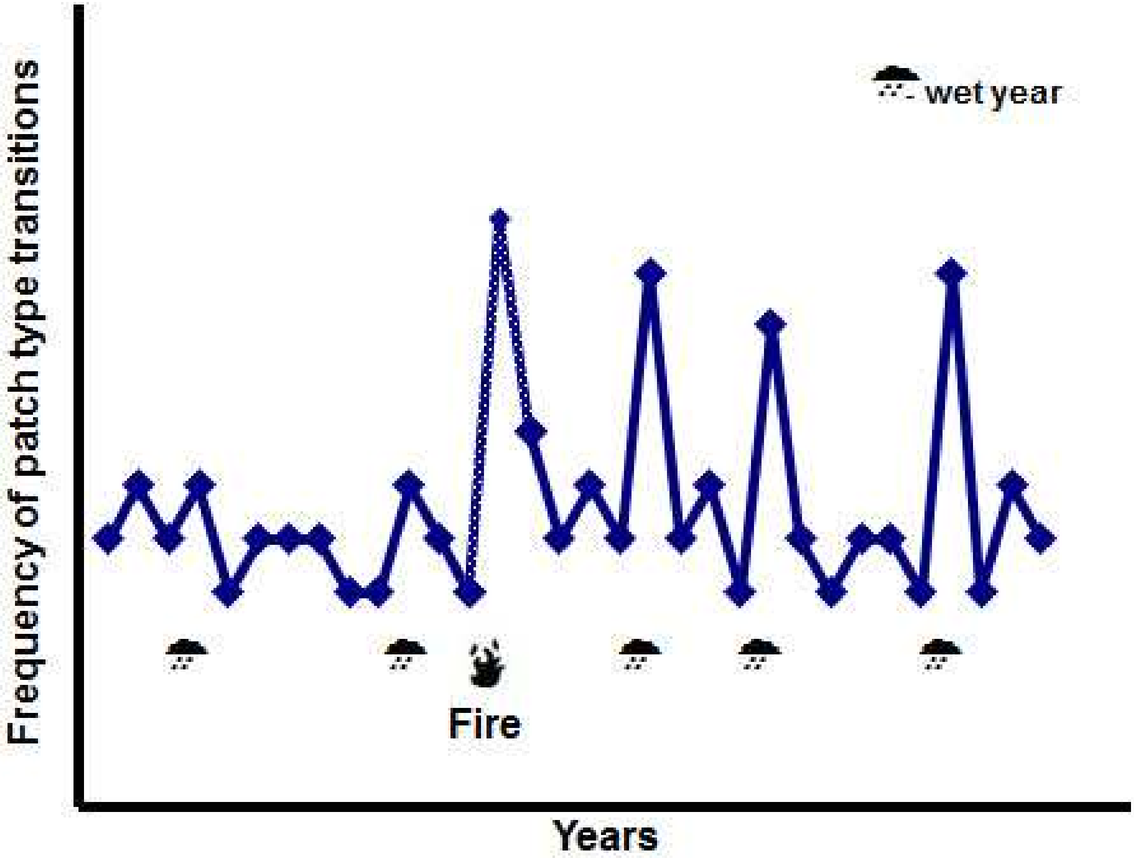


Fig 6 The relationship between the precipitation (from April to September) and the relative frequency of the patch type changes (the ratio is calculated by dividing the number of the changed patches compared to the former year by the total number of the patches) in the unburnt (a) and burnt (b) patches



536

537 **Fig 7** Conceptual scheme of the impact of wet years on vegetation dynamics before and after

538 fire