

1 This manuscript contextually corresponds with the following paper:

2

3 Ónodi, G., Altbäcker, V., Aszalós, R., Botta-Dukát, Z., Hahn, I., Kertész, M., 2014. Long-  
4 term weather sensitivity of open sand grasslands of the Kiskunság Sand Ridge forest-steppe  
5 mosaic after wildfires. *Community Ecol.* 15, 121–129. doi: 10.1556/ComEc.15.2014.1.13.

6

7 Availability of the original paper and the electronic supplementary material:

8 <http://akademai.com/doi/abs/10.1556/ComEc.15.2014.1.13>

9

10

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

13

14 Running title: Long-term weather sensitivity after wildfires

15

16 Ónodi, Gábor<sup>1</sup>; Altbäcker, Vilmos<sup>2</sup>; Aszalós, Réka<sup>1</sup>; Botta-Dukát, Zoltán<sup>1</sup>; Hahn, István<sup>3</sup> and

17 Kertész, Miklós<sup>1</sup>

18 <sup>1</sup> Institute of Ecology and Botany, Centre for Ecological Research, Hungarian Academy of  
19 Sciences, Alkotmány 2-4, 2163 Vácrátót, Hungary

20 <sup>2</sup> Eötvös Loránd University, Department of Ethology, Jávorka 14, 2130 Göd, Hungary

21 <sup>3</sup> Eötvös Loránd University, Department of Plant Systematics, Ecology and Theoretical  
22 Biology, Pázmány Péter 1/C, 1117 Budapest, Hungary

23

24 Corresponding author: Ónodi, Gábor

25 Postal address: Alkotmány 2-4, 2163 Vácrátót, Hungary

26 E-mail: onodi.gabor@okologia.mta.hu

27 Fax: ++36-28-360-122/110

28

29 E-mail addresses

30 Altbäcker, Vilmos: altbac@gmail.com

31 Aszalós, Réka: aszalos.reka@okologia.mta.hu

32 Botta-Dukát, Zoltán: botta-dukát.zoltan@okologia.mta.hu

33 Hahn, István: hahn@ludens.elte.hu

34 Kertész, Miklós: kerteszmiklos@okologia.mta.hu

35

36

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

38

39 **Abstract**

40

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

58

59 Nomenclature: Simon 2000

60

61 **Introduction**

62

63 The impact of fire is one of the focal areas in the long-term ecological research on arid and  
64 semi-arid ecosystems (Bowman and Murphy 2010, Keeley 1986, Whelan 1995). The majority  
65 of the studies in Mediterranean shrublands (Capitaniao and Carcaillet 2008, Esposito et al.  
66 1999, Montenegro et al. 2004, Uys et al. 2004), tall-grass prairies (Collins 1992, Feldman and  
67 Lewis 2005), and tropical savannahs (Greenville et al. 2009, Langevelde et al. 2003, Lewis et  
68 al. 2010) focus on ecological processes of fire-adapted ecosystems (Keeley 1986, Lewis et al.  
69 2010). However, the impact of the fire is the most severe in ecosystems which are not adapted  
70 to fire (Engel and Abella 2011). Studying these ecosystems are particularly important if they  
71 have been recently exposed to more fire due to human activity and increasing aridity caused  
72 by climate change (Bowman and Murphy 2010). Fire is a primary disturbance factor of the  
73 grassland vegetation, which most often reduces the abundance of the woody elements (Belsky  
74 1992, Montenegro et al. 2004), but can also lead to invasion of bushes or trees (Franzese et al.  
75 2009).

76

77 We studied poplar-juniper-grassland vegetation complex belonging to the transitional forest-  
78 steppe biome in the Kiskunság Sand Ridge of Central Hungary (Kovács-Láng et al. 2000),  
79 which is particularly rich in endemic plant species (Molnár 2003). This is a two-phase system  
80 consisting poplar-juniper woods and sand grassland patches, forming a dynamic mosaic  
81 pattern. This pattern is sensitive to drought, wildfire, and changes in herbivory (Katona et al.  
82 2004, Kertész et al. 1993, Ónodi et al. 2006, Ónodi et al. 2008), thus particularly suitable for  
83 studying the impacts of these disturbances and stress factors.

84

85 The biodiversity of natural and semi-natural communities increasingly depends on human  
86 management (Chapin et al. 2010). Thus, the proper management, i.e. selection of wood  
87 species for plantation, forestry technology practices, regulation of grazing, alteration of the  
88 landscape pattern, and control of the water regime should mitigate the chance of ignition, fire  
89 propagation and fire severity in communities exposed to increasing fire risk. Despite this  
90 demand, a sort of management changes in the Kiskunság region has increased the fire risk for  
91 the Sand Ridge forest-steppe vegetation. Thus, as a combined effect of drainage, forest and  
92 orchard plantations, and increased water exploitation, the ground water level has decreased  
93 since the late 1970s (Pálfai 1994), and the subsequent decrease of soil moisture (Kertész and  
94 Mika 1999) may have also contributed to the larger extent of the fires. The grazing pressure  
95 has declined since the 1960s (Bíró 2003, Katona et al. 2004), increasing the hazard of wildfire  
96 (Ónodi et al. 2008). Similarly, after the sharp decrease of the animal stock in Southern Russia  
97 wildfires began to appear from the end of 1990s, and in 2006-07, wildfires spread over large  
98 areas (Dubinin et al. 2010). Since 1990, three out of the four large protected juniper-poplar  
99 forest grassland mosaics have been almost completely burnt in the Kiskunság Sand Ridge  
100 area. The extensive alien *Pinus nigra* plantations have invariably played major role in  
101 conducting the fire across the landscape (Kiskunság National Park, personal communication).  
102 So far, all the known wildfire events are man made in this region, thus the fire is not part of  
103 natural disturbance regime. According to climate change studies, the summer temperature and  
104 the inter-annual variation of the precipitation will keep increasing (Bartholy et al. 2007,  
105 Bartholy et al. 2009), thus we predict an increase of frequency and extension of wildfires,  
106 similarly to the Mediterranean areas (Bowman and Murphy 2010, Veblen 2003). In spite of  
107 these facts, there are very few well documented studies in Central-Europe concerning  
108 grassland burning (but see Ónodi et al. 2007, 2008; Deák et al. 2012, Valkó et al. 2012).  
109

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

113

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

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

124

125

## 126 **Materials and methods**

127

128 The study sites are in the Kiskunság National Park in Central Hungary, in vegetation mosaics  
129 consisting juniper-poplar woods and open sand grasslands. This two-component vegetation  
130 type can be found in the western edge of the Eurasian forest-steppe zone (Kovács-Láng et al.  
131 2000). The two-phase character is enhanced by the extreme moisture regime of the soil caused  
132 by the high hydraulic conductivity of the calcareous sand soil of low (<1%) humus content  
133 (Calcaric Arenosol) (Várallyay 2005). The precipitation quickly infiltrates through the root  
134 zone of the grassland, while remains available for woody vegetation (Molnár 2003). The

135 climate is moderately continental with sub-Mediterranean effects (Zólyomi et al. 1997).  
136 Annual mean precipitation is around 500–550 mm and mean monthly temperatures range  
137 from -1,8 °C in January to 21 °C in July (Kovács-Láng et al. 2000). The main growing season  
138 in the open sand grassland is the late spring.

139

140 Long-term monitoring on three partially burnt sand dune areas have been carried out since  
141 1997, combining space-for-time substitution (Pickett 1989) with long-term permanent plot  
142 observations (Bakker et al. 1996). The study is part of the KISKUN LTER project (Kovács-  
143 Láng et al. 2008). The Bugac site was burnt in 1976, the Bócsa site in 1993. On these sites the  
144 vegetation changes have been recorded since 1997. The Orgovány site was burnt in 2000, and  
145 we started the monitoring in 2002. In all three sites, the burnt area ranged several square-  
146 kilometers, affecting planted forests as well as forest-steppe stands. We consider the unburnt  
147 areas reference vegetation for the burnt areas before the fire. Both unburnt and burnt areas are  
148 covered by a mosaic of woods and grassland patches. On the unburnt areas, the woods are  
149 dominated by either juniper (*Juniperus communis*), or poplar species (*Populus alba*, *P.*  
150 *canescens*, and *P. nigra*) and juniper. On the burnt areas junipers can not regenerate, but  
151 poplar species resprout after the wildfire.

152

153 Our sampling unit were 1 by 1 m quadrats. Five quadrats were placed in each selected  
154 grassland patches of the open sand grassland component of the mosaic, both in burnt and  
155 unburnt areas (Fig. 1). Samples were taken from 100 patches, 46 burnt and 54 unburnt, from  
156 ten groups of patches in three sites. Groups of patches were fenced in order to control the  
157 previously very high grazing pressure; this resulted in spatially aggregated patch distribution  
158 (Fig. 2). In the Bugac site (Fig. 2c) patches were grouped in two partially burnt (N 46° 39,30',  
159 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°

160 38,88', E 19° 36,21') areas. From 1997 to 2001 we took samples in ten burnt and 26 unburnt  
161 patches, and in 2002 we enlarged the sample to 12 burnt and 28 unburnt patches (Table 1). In  
162 the two partially burnt areas (N 46° 38,68', E 19° 28,08'; N 46° 38,60', E 19° 28,03') of the  
163 Bócsa site (Fig. 2b) ten burnt and six unburnt patches were sampled from 1997 to 2001. In  
164 2002 we enlarged the sample to 14 burnt and six unburnt patches. In the Orgovány site (Fig.  
165 2a) 20 burnt from two burnt areas and 20 unburnt patches from two unburnt ones were  
166 sampled.

167

168 In the quadrats, we visually estimated the cover of the vascular plants as well as the cover of  
169 the mosses, lichens, litter, and exposed soil surface twice a year. Visual estimation has low  
170 expected errors at the scale of our sampling, especially in nutrient deficient habitats (Klimeš  
171 2003), like in open sand grasslands. The first sampling was carried out each year in late May  
172 or early June, at the time of the biomass peak before the summer drought, and the second in  
173 late September or early October, at the secondary biomass peak.

174

175 Vegetation dynamics was studied at the spatial scale of the patches, represented by five  
176 quadrats. We associated a patch type to each patch in each year, applying the Cocktail method  
177 (Bruehlheide 2000). First, the spring and autumn data were pooled within years and within  
178 quadrats choosing the higher score, then cover in the five quadrats were averaged, and these  
179 patch level cover values were used in the subsequent analysis. Species groups were formed  
180 based on the positive associations among species (Bruehlheide and Chytrý 2000). The  
181 interspecific associations were measured by hypergeometric u-value (Chytrý et al. 2002)  
182 calculated from binary data. Group forming started with the pair of ungrouped species that  
183 had the highest interspecific association. It stopped when the u-value of the new candidate  
184 species to the group was below 5. We modified the original Cocktail algorithm, and instead of



185 presence of species groups we used their total cover to define the patch types. If the cover of  
186 vascular plants exceeded 5%, the patch was classified according to the vascular species group  
187 which has the highest cover. Otherwise, it was classified either into cryptogam patch type, if  
188 cover of cryptogams was at least 50%, or bare soil patch type. We choose the above method  
189 in order to get of patch types which provide us opportunity (1) to compare the patch type  
190 distributions of burnt and unburnt patches, (2) to calculate the frequency of year to year  
191 transitions between patch types.

192

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

201

202 The type associated to a patch could change from year to year. The changes between  
203 consecutive years were summarized in transition matrices for burnt and unburnt patches,  
204 separately. The transition matrices calculated from the pooled data were compared with a  
205 null-model in which transition probabilities depended on the proportion of vegetation types  
206 before and after the transition only. First, the global difference was tested by chi-square test,  
207 and if it proved to be significant, Freeman-Tukey deviates were used to find the significantly  
208 over- and under-represented transitions. For each site, we calculated the proportion of values  
209 in the diagonal of transition matrices (i.e. no-change between consecutive years) and

210 compared it between burnt and unburnt areas applying u-test for proportions (Zar 1999). The  
211 complement of this proportion (i.e. the proportion of changes) was calculated from the pooled  
212 data set and it was correlated with precipitation in the vegetation period from April to  
213 September when the new vegetation type appeared. Separate correlations were calculated for  
214 burnt and unburnt patches. We interpret the significantly over-represented year to year  
215 transitions from a patch type to the same one, as resistance, and from one patch type to  
216 another, as sensitivity.

217

218

## 219 **Results**

220

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

227

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

234

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

242

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

247

248 In the unburnt patches, the relative frequency of patch type changes proved to be independent  
249 from the precipitation in the vegetation period ( $R^2_{\text{adj}} = 6.4 \cdot 10^{-7}$ ,  $p = 0.998$ , Fig. 6a), while  
250 positively correlated in the burnt patches ( $R^2_{\text{adj}} = 0.406$ ,  $p = 0.035$ , Fig. 6b). The driest year  
251 was 2003, and we found the less patch type changes in that year, while we found the most  
252 changes in the next, wet year. In case of the burnt patches, the 2008 data (in the lower right  
253 part of Fig. 6b) proved to be a leverage point as Cook's  $D > 1$  (Cook 1979, Reiczigel et al.  
254 2007). Without this point  $R^2_{\text{adj}} = 0.72$ ,  $p = 0.0019$ .

255

256

## 257 **Discussion**

258

259 *General pattern of post-fire regeneration*

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

269

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

280

281 Another characteristic difference between unburnt and burnt areas was that the 'annual' patch  
282 type appeared only in the latter ones (Fig. 3a and 3b). Similar increase in the abundance of  
283 annuals can be observed in wet years after dry years. All of those annuals live in the studied

284 grasslands, and they are generally prolific after disturbance. Thus we consider the ‘annual’  
285 patch type an expected ordinary response of the annual species of the open grasslands.  
286  
287 The woody perennial species were variously affected by the fire. The fire induced intensive  
288 re-sprouting of poplar species, together with spreading of other clonal species like  
289 *Calamagrostis epigeios*, in accordance with the findings of Marozas et al. (2007). We  
290 observed the spreading of poplar species (*Populus alba* and *P. nigra*) which have resprouter  
291 and clonal spreading strategy (Menges and Kohfeldt 1995). Szujkó-Lacza and Komáromy  
292 (1986) also detected the fast spreading of the poplar two years after the Bugac wildfire. On  
293 contrary, the common juniper (*Juniperus communis*) does not regenerate after fire (Marozas et  
294 al. 2007, Wink and Wright 1973). According to our observations, even the partially burnt  
295 specimens died in a year. The lack of junipers (the darkest element of the vegetation) is  
296 noticeable around the burnt patches in Fig. 2. The sensitivity of the juniper to the fire causes  
297 major change in the structure of the vegetation, where it was dominant before. Consequently,  
298 the whole vegetation mosaic cannot be considered fire-adapted, as both the dominant juniper  
299 and the widespread cryptogams do not recover after the fire.

300

### 301 *The long-term effect of wildfire*

302 According to the observed patch type transitions (Fig. 4) the vegetation is more dynamic after  
303 fire than in unburnt areas: contrary to our second null-hypothesis, less patch types are  
304 significantly permanent and statistically significant transitions from one patch type into  
305 another appear in burnt areas. The long-term effect of fire, which we found in all of our sites  
306 in the Kiskunság Sand Ridge, shows the lack of fire adaptation based on Engel and Abella  
307 (2011). According to our third null-hypothesis, application of space-for-time-substitution  
308 (Pickett 1989) for the patch type transitions (Fig. 5) shows that the excess of dynamics in the

309 burnt areas does not disappear even in longer time. Engel and Abella (2011) also found  
310 dynamics independent from time since fire and high long-term post-fire variability in  
311 *Coleogyne ramosissima* dominated community of Mojave.

312

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

325

### 326 *Factors influencing the dynamics*

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

333 permanent patch types might result in the leverage point of 2008 in the precipitation-transition  
334 relation (Fig. 6b).

335

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

351

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

356

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

366

### 367 **Acknowledgements**

368

369 We thank Sándor Bartha and György Kröel-Dulay for their advice. We are grateful to Tibor  
370 Tóth, Katalin Szitár and Piroska Kucs for their contribution to the field work. We thank the  
371 Kiskunság National Park (Hungary) for the support of our field experiments. This study was  
372 funded by the Hungarian Scientific Research Found (OTKA F5254, T29703, and A08-1-  
373 2009-0051) and by the National Research and Development Program (NKFP 3B-0008/2002,  
374 NKFP 6-0013/2005).

375

376

### 377 **Refereces**

378

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



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

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

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

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

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

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

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

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

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

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

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

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

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

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

415 Cook, R.D. 1979. Influential Observations in Linear Regression. *J. Am. Statist. Assoc.* 74:  
416 169–174.

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

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

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

425 Engel, E.C. and S.R. Abella. 2011. Vegetation recovery in a desert landscape after wildfires:  
426 influences of community type, time since fire and contingency effects. *J. Appl. Ecol.*  
427 48: 1401–1410.

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

- 430 Feldman, S.R. and J.P. Lewis. 2005. Effects of fire on the structure and diversity of a *Spartina*  
431 *argentinensis* tall grassland. *Appl. Veg. Sci.* 8: 77–84.
- 432 Franzese, J., L. Ghermandi and B. Donaldo. 2009. Post - fire shrub recruitment in a  
433 semi - arid grassland: the role of microsites. *J. Veg. Sci.* 20: 251–259.
- 434 Ghermandi, L., N. Guthmann and D. Bran. 2004. Early post-fire succession in northwestern  
435 Patagonia grasslands. *J. Veg. Sci.* 15: 67–76.
- 436 Greenville, A.C., C.R. Dickman, G.M. Wardle and M. Letnic. 2009. The fire history of an  
437 arid grassland: the influence of antecedent rainfall and ENSO. *Int. J. Wildland Fire*  
438 18: 631–639.
- 439 Johansson, P. and P.B. Reich. 2005. Population size and fire intensity determine post-fire  
440 abundance in grassland lichens. *Appl. Veg. Sci.* 8: 193–198.
- 441 Katona, K., Z. Bíró, I. Hahn and V. Altbäcker. 2004. Competition between European hare and  
442 European rabbit in a lowland area, Hungary: a long-term ecological study in the period  
443 of rabbit extinction. *Folia Zool.* 53: 255–268.
- 444 Keeley, J.E. 1986. Resilience of Mediterranean shrub communities to fires. In: B. Dell,  
445 A.J.M. Hopkins and B.B. Lamont (eds.), *Resilience in Mediterranean-Type*  
446 *Ecosystems*. Dr. W. Junk, Dordrecht, The Netherlands, pp. 95-112.
- 447 Kertész, Á. and J. Mika. 1999. Aridification-Climate change in South-Eastern Europe. *Phys.*  
448 *Chem. Earth* 24: 913–920.
- 449 Kertész, M., J. Szabó and V. Altbäcker. 1993. The Bugac Rabbit Project. Part I.: Description  
450 of the study site and vegetation map. *Abstr. Bot.* 17: 187–196.
- 451 Klimeš, L. 2003. Scale - dependent variation in visual estimates of grassland plant cover. *J.*  
452 *Veg. Sci.* 14: 815–821.
- 453 Kovács-Láng, E., Gy. Kröel-Dulay, M. Kertész, G. Fekete, J. Mika, I. Dobi-Wantuch, T.  
454 Rédei, K. Rajkai, I. Hahn and S. Bartha. 2000. Changes in the composition of sand

455 grasslands along a climatic gradient in Hungary and implications for climate change.  
456 *Phytocoenologia* 30: 385–408.

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

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

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

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

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

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

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

- 478 Montenegro, G., R. Ginocchio, A. Segura, J.E. Keely and M. Gómez. 2004. Fire regimes and  
479 vegetation responses in two Mediterranean-climate regions. *Rev. Chil. Hist. Nat.* 77:  
480 455–464.
- 481 Ónodi, G., M. Kertész and Z. Botta-Dukát. 2006. Effects of simulated grazing on open  
482 perennial sand grassland. *Comm. Ecol.* 7: 133–141.
- 483 Ónodi, G., Csatádi, K., Németh, I., Váczi, O., Botta-Dukát, Z., Kertész, M., Altbäcker, V.,  
484 2007. Birka (*Ovis aries*, L.)- és nyúllegelés (*Oryctolagus cuniculus*, L.) hatásainak  
485 vizsgálata az égésre homokpusztagyepen. *Természetvédelmi Közlemények* 14, 117-  
486 129.
- 487 Ónodi, G., M. Kertész, Z. Botta-Dukat and V. Altbäcker. 2008. Grazing Effects on Vegetation  
488 Composition and on the Spread of Fire on Open Sand Grasslands. *Arid Land Res.*  
489 *Manag.* 22: 273–285.
- 490 Pálfai, I. 1994. *Összefoglaló Tanulmány a Duna–Tisza közti Talajvízszint-süllyedés Okairól és*  
491 *a Vízhiányos Helyzet Javításának Lehetőségeiről. A Duna–Tisza közti hátság*  
492 *vízgazdálkodási problémái.*(The Problems of Water Management in Cisdanubia).  
493 Nagyalföld Alapítvány, Békéscsaba, pp. 111–125.
- 494 Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In:  
495 Likens GE (ed.), *Long-term Studies in Ecology: Approaches and Alternatives.*  
496 Springer-Verlag, New York, pp. 110–135.
- 497 Reiczigel, J., A. Harnos and N. Solymosi. 2007. *Biostatisztika - Nem Statisztikusoknak*  
498 (Biostatistics). Pars Kft.
- 499 Simon, T. 2000. *A Magyarországi Edényes Flóra Határozója* (Identification hand-book of the  
500 Hungarian vascular plants). Nemzeti Tankönyvkiadó, Budapest.
- 501 Szujko-Lacza, J. and Z. Komaromy. 1986. Postfire resuccessional process in Juniper-Poplar  
502 wood in Bugac, Kiskunság National Park, Hungary. *Bull. Bot. Surv. India* 28: 89–110.
- 503 Trabaud, L. 1987. Dynamics after fire of sclerophyllous plant communities in the  
504 mediterranean basin. *Ecol. Medit.* 13: 25–37.

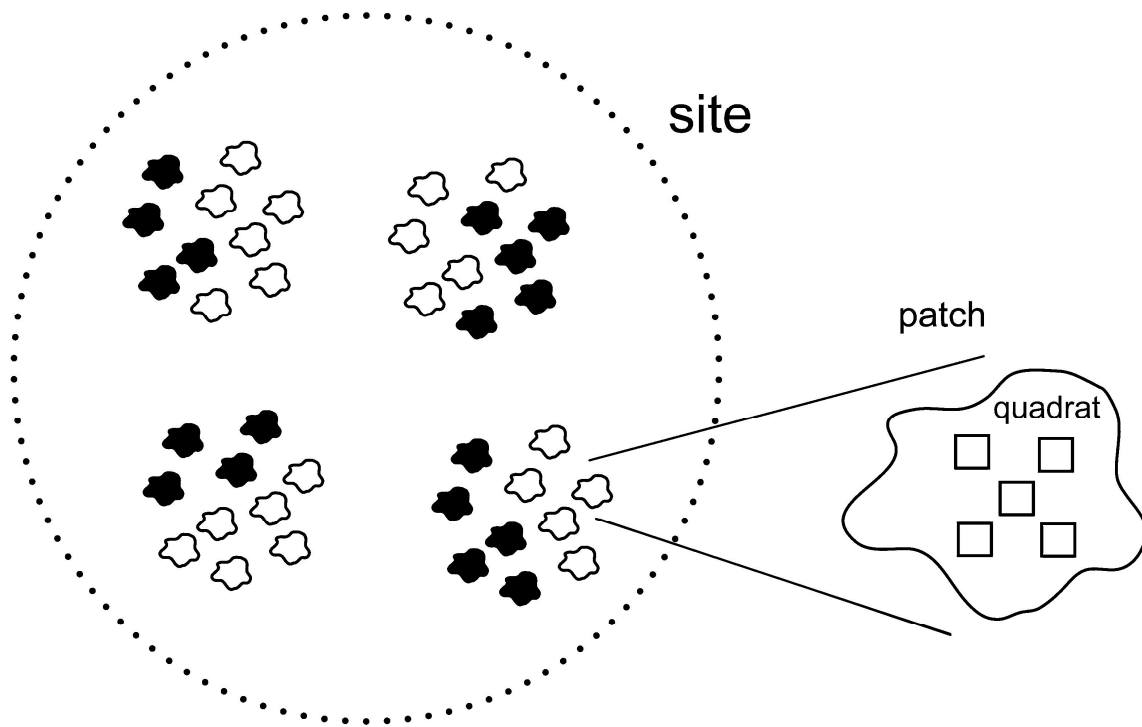
- 505 Uys, R.G., W.J. Bond and T.M. Everson. 2004. The effect of different fire regimes on plant  
506 diversity in southern African grasslands. *Biol. Conserv.* 118: 489–499.
- 507 Valkó O., Deák B., Kapocsi I., Tóthmérész B., Török P. (2012): Gyepek kontrollált égetése,  
508 mint természetvédelmi kezelés – Alkalmazási lehetőségek és korlátok.  
509 *Természetvédelmi Közlemények* 18: 517-526.
- 510 Várallyay, G. 2005. Magyarország talajainak vízraktározó képessége (Water storage capacity  
511 of Hungarian soils). *Agrokém.Talajtan.* 54: 5–24.
- 512 Veblen, T.T. 2003. *Fire and Climatic Change in Temperate Ecosystems of the Western*  
513 *Americas.* Springer.
- 514 Whelan, R.J. 1995. *The Ecology of Fire.* Cambridge University Press, Cambridge.
- 515 Wink RL and Wright HA. 1973. Effects of Fire on an Ashe Juniper Community. *J. Range.*  
516 *Manage.* 26: 326–329.
- 517 Zar, J.H. 1999. *Biostatistical Analysis.* Prentice hall Upper Saddle River, NJ.
- 518 Zólyomi, B., M. Kéri and F. Horváth. 1997. Spatial and temporal changes in the frequency of  
519 climatic year types in the Carpathian Basin. *Coenoses* 12: 33–41.
- 520

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

521

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

523

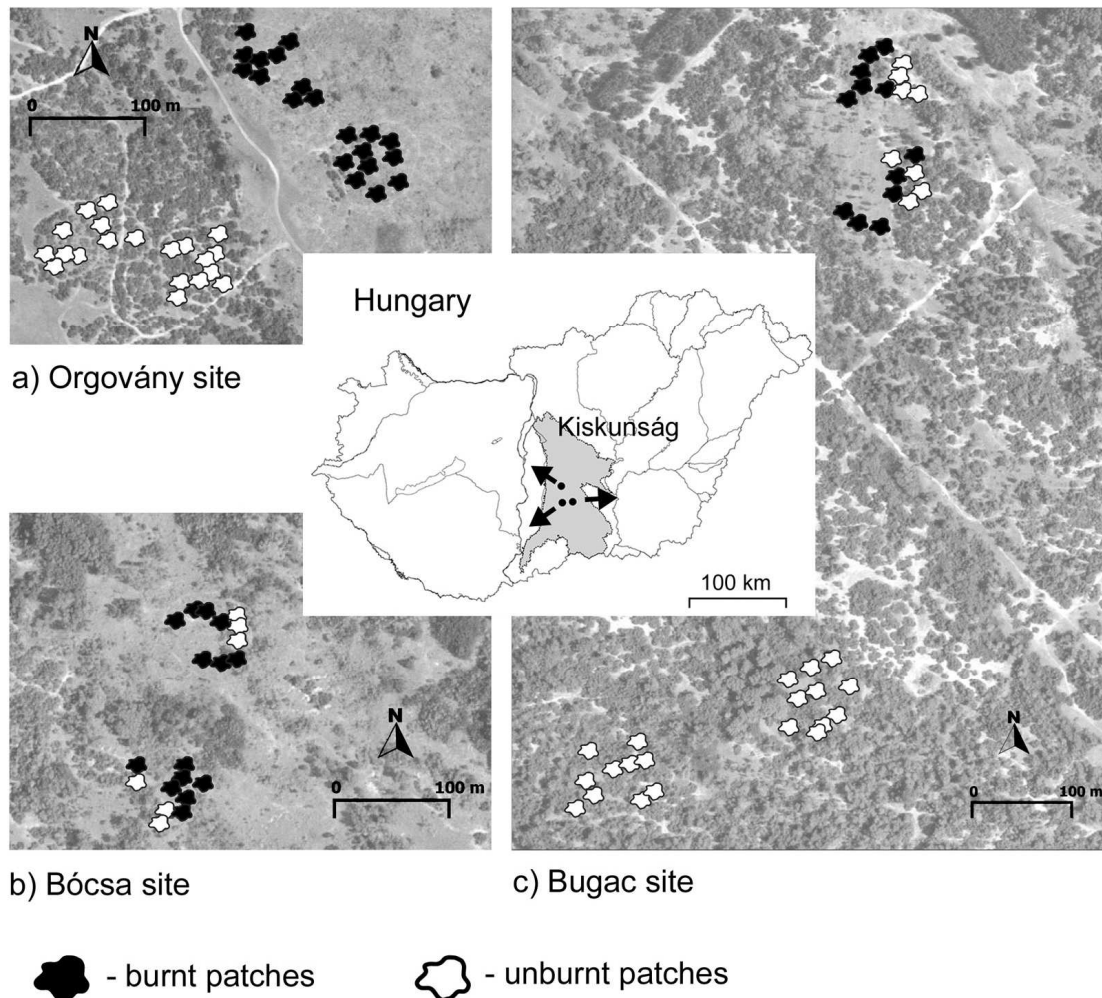


524

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

528

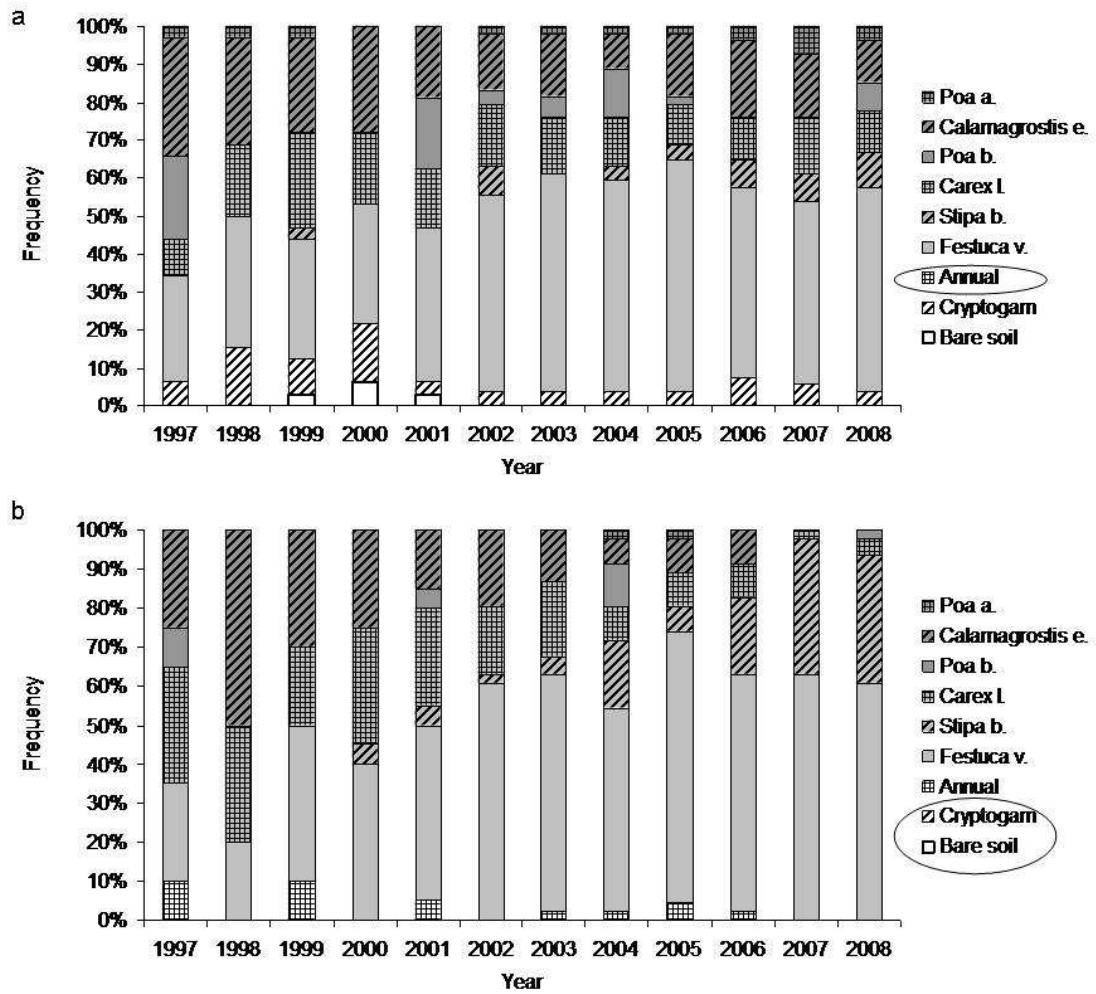




529

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

533



534

535 **Fig 3** Relative frequency of the patch types in the unburnt (a) and burnt (b) grassland patches.

536 Unobserved patch types are marked by circles

537

**a**

		Into patch type									
		Bar	Cry	Ann	F.v.	S.b.	C.L.	P.b.	C.e.	P.a.	
From patch type	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

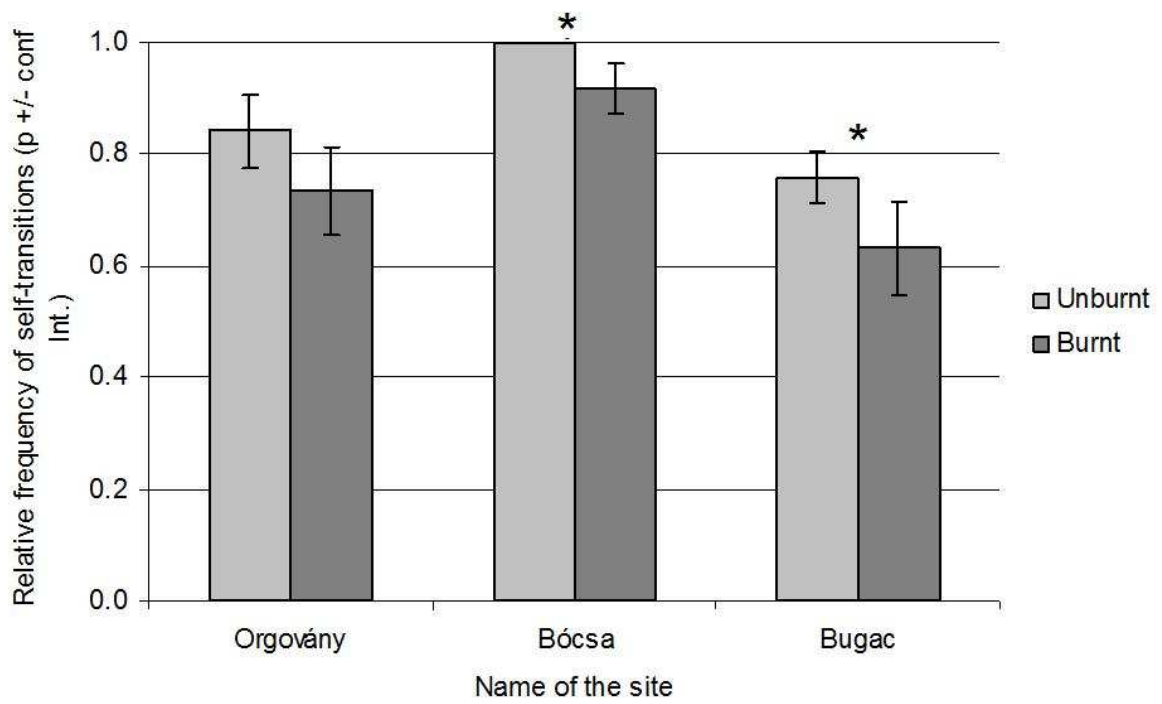
**b**

		Into patch type									
		Bar	Cry	Ann	F.v.	S.b.	C.L.	P.b.	C.e.	P.a.	
From patch type	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

538

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

545

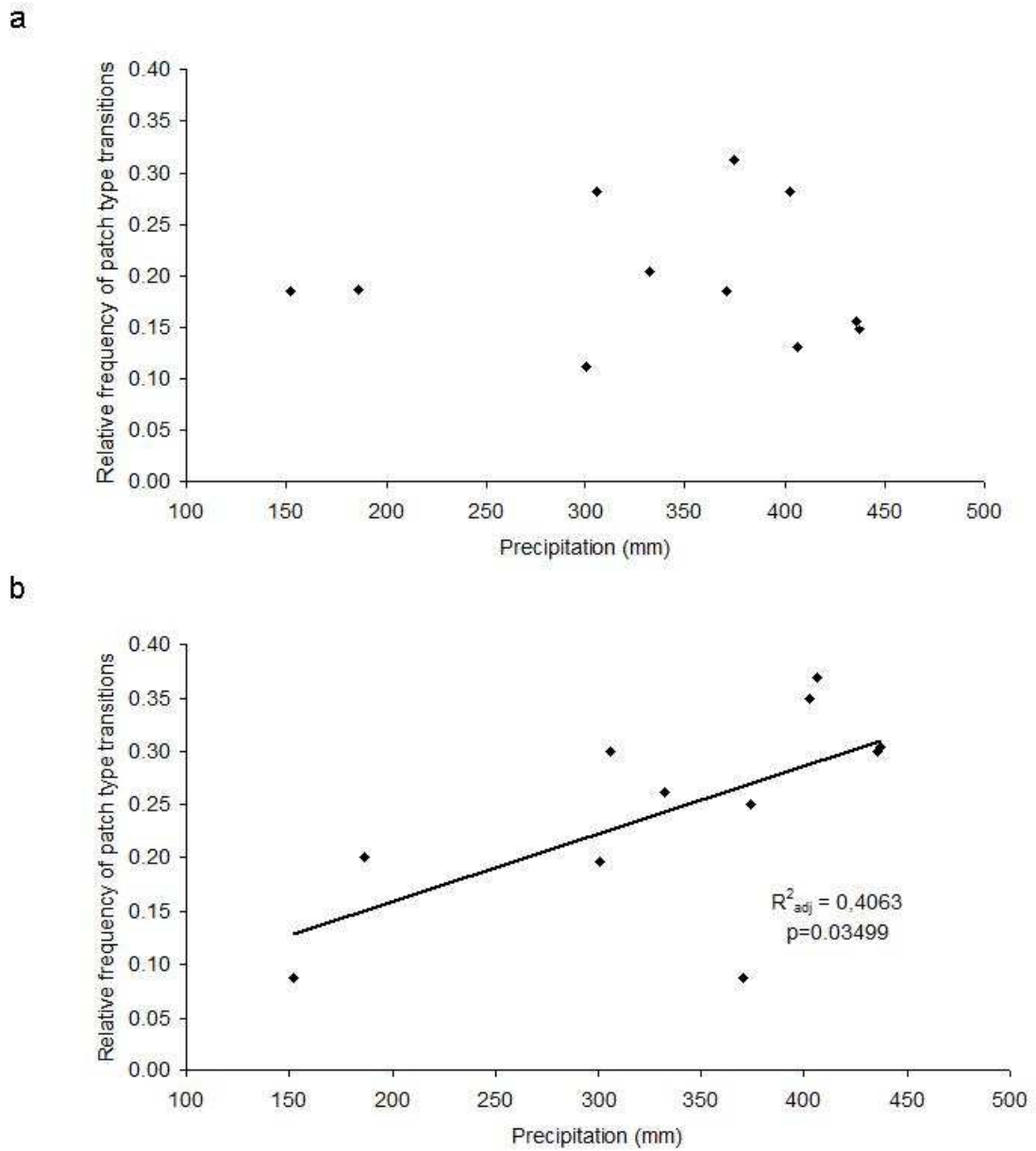


546

547 **Fig 5** Self-transitions of unburnt and burnt open sand grassland patches. Asterisks indicate

548 significantly decreased self-transitions in the burnt patches

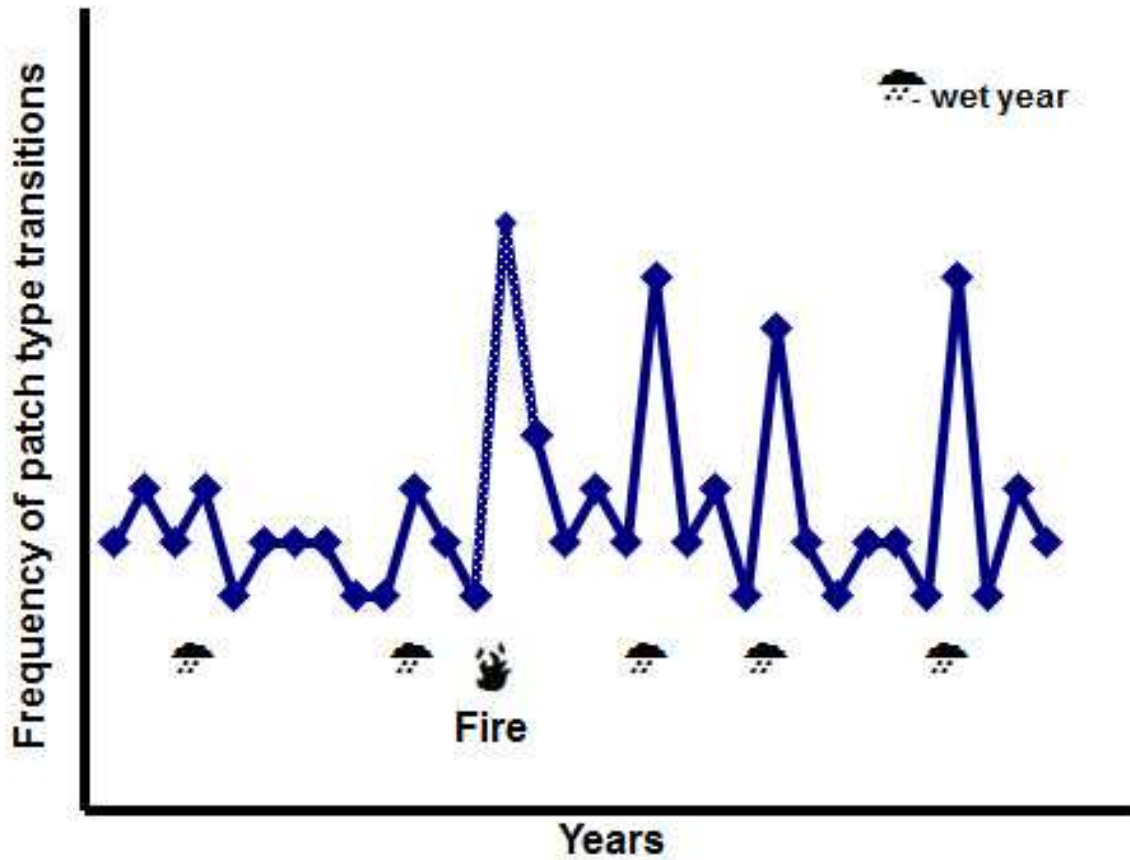
549



550

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

555



556

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

558 fire