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Shifting mosaics in semi-steppe rangelands driven by interactive effect of human made disturbances

Pejman tahmasebi Kohyani [1*] and Yousef askari [2]

[1]Assistant professor,Department of Range and Watershed Mangement,Faculty of Natural Resource and Earth Science, Shahrekord University, Po. Box 115, Shahrekord, Iran

[2]Ph.D student of forestry, Faculty of Natural Resources and Earth Science, University of Shahrekord, Shahrekord, Iran

ABSTRACT

Semi-steppe rangelands are a complex, highly dynamic and often multi-layered mosaic of grassland, shrubland, and intermediate communities. A few recent studies have explicitly or implicitly developed synthetic hypotheses about how interactive effects of human made disturbances initiate dynamic changes in plant community composition to cause a shifting mosaic of vegetation pattern across the landscape in rangeland ecosystems, yet to be tested in semi-steppe rangelands. The main goal of this study was to examine a conceptual model of plant community dynamic driven by the interactive effect of grazing and fire in semi-steppe rangelands in West-Iran. The study area includes shrubland, grassland and intermediate plant communities. Several patches within the study area were accidentally burned in 2006, 2008 and 2009. Burned patches were located along a gradient of animal grazing (from light to heavy grazing). We compared plant community composition and animal selections on burned and unburned patches (control) of each plant community. The results showed that if grazing intensity was low, a shift from shrublands to grasslands would be the observed pattern of community dynamics; otherwise with higher level of grazing intensity, change in vegetation structure caused by fire in shrublands was rather transient and this plant community returned to the former state of vegetation four years after the fire. We also observed a higher animal selection on recently burned areas compared to previously burned patches, a pattern that was the resulted of a series of positive and negative feedbacks in forage quality created by selective animal foraging behaviour. The results indicate that the effect of fire on plant community dynamics in semi-steppe rangeland is controlled by grazing intensity and the local changes in plant composition within each community. Both determinants cause a cyclical process of vegetation succession. Vegetation patterns represent the various states of recovery in vegetation and introduces a specific landscape composition in which each scrubland, grassland and intermediate vegetation patch can be described as part of a shifting mosaic process at landscape scale.

Key words: Cyclical process of succession, Plant community composition and dynamics, Semi-steppe rangelands, Shifting mosaics.

Corresponding Author E-mail: Pejman.Tahmasebi@nres.sku.ac.ir

INTRODUCTION

In rangeland ecosystems, such as steppe and semi-steppe, the frequency and intensity of disturbances such as grazing and fire are critical ecological features, that influence biological diversity, and temporal and spatial heterogeneity (Collins 1992, 2000; Hartnett *et al*. 1996). Historically, both are known as disturbances that play a critical role in shaping vegetative communities, altering community structure and causing shifts in vegetation dynamics (Fuhlendorf & Smeins 1997; Knight and Holt 2005; Tahmasebi *et al*. 2008). Steppe and semi-steppe rangeland systems are structurally diverse, exhibiting differences in woody plant canopy cover, stature, shrub functional form (evergreen vs. deciduous; broad-leaved vs. needle-leaved vs. succulent-leaved; shallow vs. deeply rooted), grass functional form (annual vs. perennial, C3 vs. C4 photosynthetic pathway) and spatial arrangement (random, regular, or clumped trees, bunch vs. rhizomatous grass) (Archer *et al*. 2001). In semi-steppe rangelands in Iran, the vegetation is dominated by a matrix of perennial grasses: *Bromus tomentellus, Agropyron repens, Agropyron intermedium, Stipa hohenckeriana,* and shrubs: *Astragalus* sp. (*A. adcenense, A. verus, A. susianus* and others). The relative temporal abundance of herbaceous and woody plants in these ecosystems can be highly dynamic due to changes in the competition balance between graminoids and shrubs (Tahmasebi Kohyani *et al*. 2011). Long-term observations show that a shift occurs from grasslands to shrublands due to high grazing intensity by domestic animals during a century ago (Van Auken 2000, House et al. 2003; Tahmasebi Kohyani 2009), leading to a alarming situation, in which grasslands composed of native species are rapidly disappearing due to this shrubland expansion. Available studies showed that fire can alter the spatial effects of grazing (Noy-Meir 1995; Hartnett *et al*. 1996; Fuhlendorf and Smeins 1997; Kerby *et al*. 2007). In the long run, the interactions of burning and grazing may restore native grasslands and create a shifting mosaic landscape of grazed and ungrazed patches (Olff *et al.* 1999), whereas in the absence of fire a more stable mosaic of shrubland communities may exist (Adler et al. 2001; Fuhlendorf and Engle 2004). Most previous research on the effects of fire and grazing on spatial heterogeneity of plant communities focused on either the impact of fire (e.g. Collins 1992; Shokri *et al*. 2002; Ghermandi *et al*. 2004; Eiswerth and Shonkwiler, 2006; Haubensak *et al*. 2009) or grazing (e.g. Milchunas and Lauenroth 1993, Adler *et al*. 2001;; McIntyre *et al*. 2003; Tahmasebi Kohyani *et al*. 2008). Only a few studies assessed shifting mosaics of vegetation through the interactive effect of grazing and fire (e.g. Hobbs *et al*. 1991 and Fuhlendorf and Engle 2004 on North-American prairie systems; Belskey 1992 on a Kenyan savannah system and Noy-Meir 1995 on Meditteranean grassland). None of these deal with semi-steppe rangelands. Here we present and then test a conceptual model of the fire–grazing interaction (Fig 1), which predicts a shifting mosaic of vegetation pattern across the landscape caused by grazing and fire, through interacting a series of positive and negative feedbacks in response of plant community composition to fire and grazing. Disturbances caused by physical processes such as fire and grazing create open space necessary for plant colonization and initiate a cycle of succession by species adapted to colonizing disturbed sites (Ricklefs 1990). At a moderate level of disturbance, the community becomes a mosaic of patches of habitat at different stages of regeneration; together these patches contain the full variety of species characteristics of the successional sere (Ricklefs 1990). Over time, various vegetative communities have evolved in close association with fire, forcing many species to develop traits to deal with the stress of the event (Whelan, 1995). According to our model, the cover of perennial grasses decrease due to high grazing intensity, which result in a shift in plant community from grassland to shrubland. Fire in semi-steppe rangelands in Iran, largely fueled by shrub species such as *Astragalus adcenense, A. verus, A. susianus* and annual grasses such as *Bromus tectorum* and *Heterranthelium piliferum,* has become an important structuring force altering vegetation composition (Tahmasebi Kohyani 2009). According to Briggs *et al*. (2002), fire causes shrublands to convert into grassland with palatable species. In recently burned areas, a positive feedback appears when this grassland attracts grazing animals (Ritchie *et al.* 1998), which further disturb the site. However, this depends on grazing intensity: if grazing intensity maintains low, tall and short graminoid species eventually recover dominance. On the other hand, if recently burned areas are heavily grazed by animals, a shift from grasslands to shrublands can be expected. The objective of the present study was to gain insight in the effects of fire, grazing and their interaction on plant species composition and to test the conceptual model presented in fig (1).

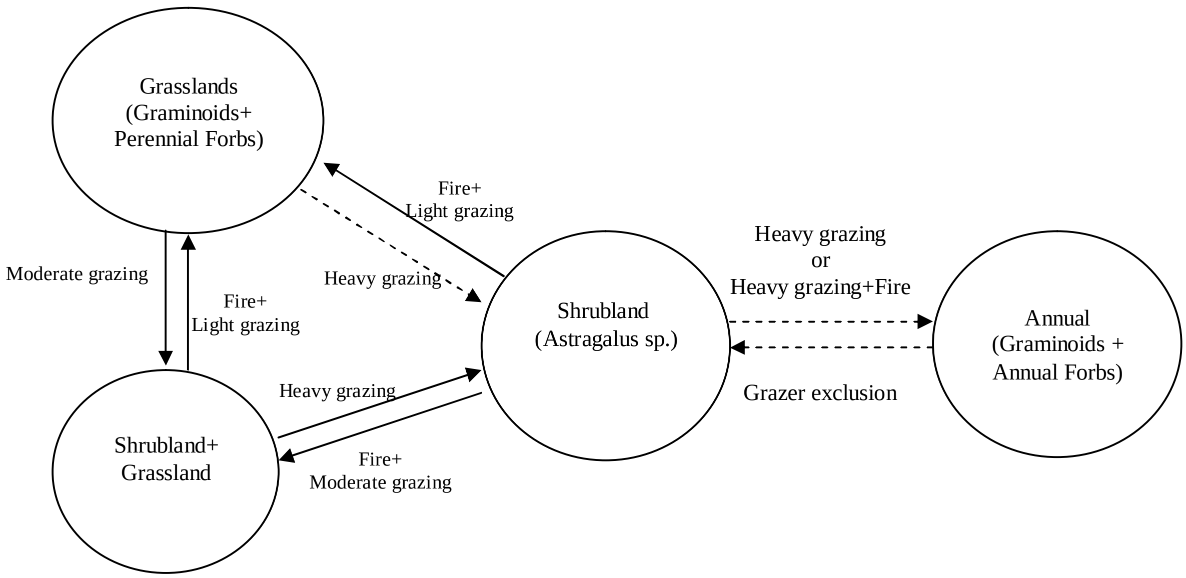

Fig. 1. The conceptual model of plant community dynamics resulting from the interactive effect of fire and different levels of grazing intensity in semi-steppe rangelands. Circles and arrows respectively show vegetation states and transitions. Transitions indicated by dotted arrows were designated as the potential states, which were not investigated in this study.

MATERIALS AND METHODS

Study area

The study was conducted in the semi-steppe rangelands (32° 30' N, 50° 26' E, area 800ha), Chahar Mahaal-Bakhtiari province in Iran. This region is characterized by a transitional situation between arid and temperate climate, with hot summers and cool winters and 600 mm annual rainfall, mostly in winter and early spring. Differences in geological substrate and topography further contribute to diversity of vegetation types in the region. The natural vegetation in the study area presents itself as grassland-shrubland mosaics, including shrubland (*Astragalus adscendense*), shrubland-grassland (*Agropyron repens-Astragalus adscendense*) and grassland (*Bromus tomentelus-Agropyron repens*). A further distinction can be made according to (co-)dominance of shrubs alone, perennial grasses and shrubs, annual grasses and shrubs and perennial grasses alone. The quantity of fire events has increased dramatically in this semi-steppe rangeland system and results in patches of burned (with areas up to 100 ha) and unburned areas. They are generally followed by scrub encroachment and a strongly increasing human population during the last 50 years. Next to fire frequency differences, the study area also shows grazing intensity differentiation with several local patches with different grazing intensity and fire events. We selected different parts of the study area with known differences in grazing intensity and dates since the last fire event. They were located along an ordinal scale gradient of animal grazing (grazing intensity from light to moderate), and time since the last fire event (2006, 2008 and 2009). The study area is grazed by domestic animals, including sheep and goat. Grazing starts from mid spring to late summer in a herding system. Native people believe that fire increases forage quality and in order to increase animal performances, they start grazing from recently burned areas and keep animals in the burned patches until the forage quantity constrains animal maintenance. This indicates that grazing intensity is maintained higher in burned patches as compared to unburned patches.

Methods

Sampling was performed in June and July 2010. We first selected suitable patches (area more than 50 ha) with treatments mentioned in the conceptual model (figure 1), including fire+light grazing, fire+moderate grazing, no fire+moderate grazing and no fire+light grazing. These treatments were distributed among different plant communities: In shrublands, treatments were fire+light grazing, fire+moderate grazing. In grasslands, the treatment moderate grazing was included and finally in shrubland-grasslands, fire+light grazing and heavy grazing were the main treatments. In order to inspect the shifts in plant communities, unburned areas in close proximity to each treatment were chosen. For grazing control of each plant community, we chose the sites that no grazing occurred, where was far from watering points. Ten plots (2×2m) were randomly installed along a 200m transect therein each treatment and its control in which the cover of plant species was estimated. Furthermore, the cover of different life forms including perennial grass, annual grass, annual forb, perennial forb and shrub were measured in each plot. In order to investigate the effect of fire on animal selection, within each plot the number of grazed plants were counted and compared to control plots. Whether plants were grazed or not was established by visual inspection of any signs of animal bites or plant phytomass being harvested by animals. Grazing intensity was monitored based on distance to watering points (Landsberg et al. 2003). Previous studies in this area showed that grazing intensity decreased with distance to drinking facilities (Payranj 2010).

Statistical analysis

First, we extracted two matrices of life form-plant communities and plot-plant species. Then None-Metric Multidimentional Scaling (NMS) was used to inspect variation in plant community composition between burned and control areas using matrix of life form-plant communities. A Multi-Response Permutation Procedure (MRPP) was used to examine statistical differences between burned and control areas (McCune and Grace 2002). Here we aimed to test if there was a significant difference in plant community composition between burned and control areas in each plant community. Moreover, we measured the cover of life forms in each treatments and used Mann-Whitney test for examining differences in life form spectrum between burned and control areas. By integrating the results of MRPP and Mann-Whitney test, we were able to test hypothesis presented in figure (1). For example, if the results of MRPP on shrubland community showed a significant difference between burned and control areas and Mann-Whitney test showed a higher abundance of graminoids in burned area, the hypothesis on conversion of shrubland into grassland would be accepted. The same expectations would be correct for other hypothesis in figure (1). The Mann-Whitney test was also used to compare animal selection between burned patches and control areas for each year. NMS and MRPP were executed in Pc-Ord 4.2 and Mann-Whitney in SPSS17.

RESULTS

69 percent of variation was explained by the first and second axis of NMS (Mont-Carlo test; Axis1: %42 $p=0.032$, Axis2: %27 $p= 0.032$). The results of NMS showed that grazing and fire both had a significant effect on plant community composition in the study area (figure 2). Plant community conversions can be revealed on Axis one of NMS: Shrubland communities and those communities that were converted to shrublands were placed on the right hand side of axis 1. Grasslands and also those communities that were converted to grassland were placed at the left hand side of axis 1. The NMS diagram in fig (2) also showed that if fire occurred in a shrubland and grazing intensity was held moderate, shrubland would convert into shrubland-grassland. However, if grazing intensity was light, shrubland would convert to

grassland (figure 2). The results of MRPP showed the significant shifts in plant community composition comparing testaments and control areas in each plant community (Table 1).

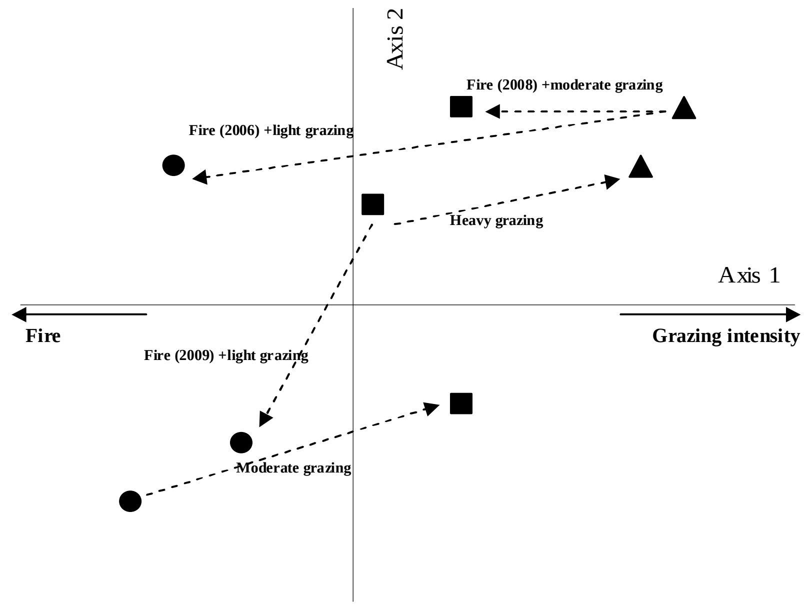

Fig. 2. Diagram of Non-Metric multidimensional scaling on plant community types: shrublands (Triangles), shrubland-grasslands (squares), and grasslands (circles). Dotted and solid arrows respectively show transitions of plant communities and gradients along axis 1.

Table 1. Results on Multi-Response Permutation Procedures testing statistical differences between burned and control areas in each plant community.

	Treatment							
	Fire +light grazing		Fire +moderate grazing		Moderate grazing		Heavy grazing	
Plant community type	T	*p*	T	*p*	T	*p*	T	*p*
Shrubland	-28.35	0.000	-28.25	0.000	-	-	-	-
Shrubland-grassland	-25.42	0.000	-	-	-	-	-34.68	0.000
Grassland	-	-	-	-	17.58	0.0	-	-

These results were also confirmed by the Mann-Whitney test, examining variations in life form compositions between treatments and control areas. The outcomes for different plant communities were not the same and fire and grazing and the interactive effect of them replaced a specific vegetation state for each plant community. In shrublands with fire+light grazing, the cover of perennial grasses and forbs were significantly higher than control areas, meanwhile the cover of shrub species significantly decreased by 35 percent (Fig. 3a). Within this community, fire+moderate grazing also resulted in significant changes in the cover of perennial grasses and shrubs (increase in perennial grasses and decrease in shrubs). However, lower changes were observed compared to fire+light grazing (Fig. 3b).

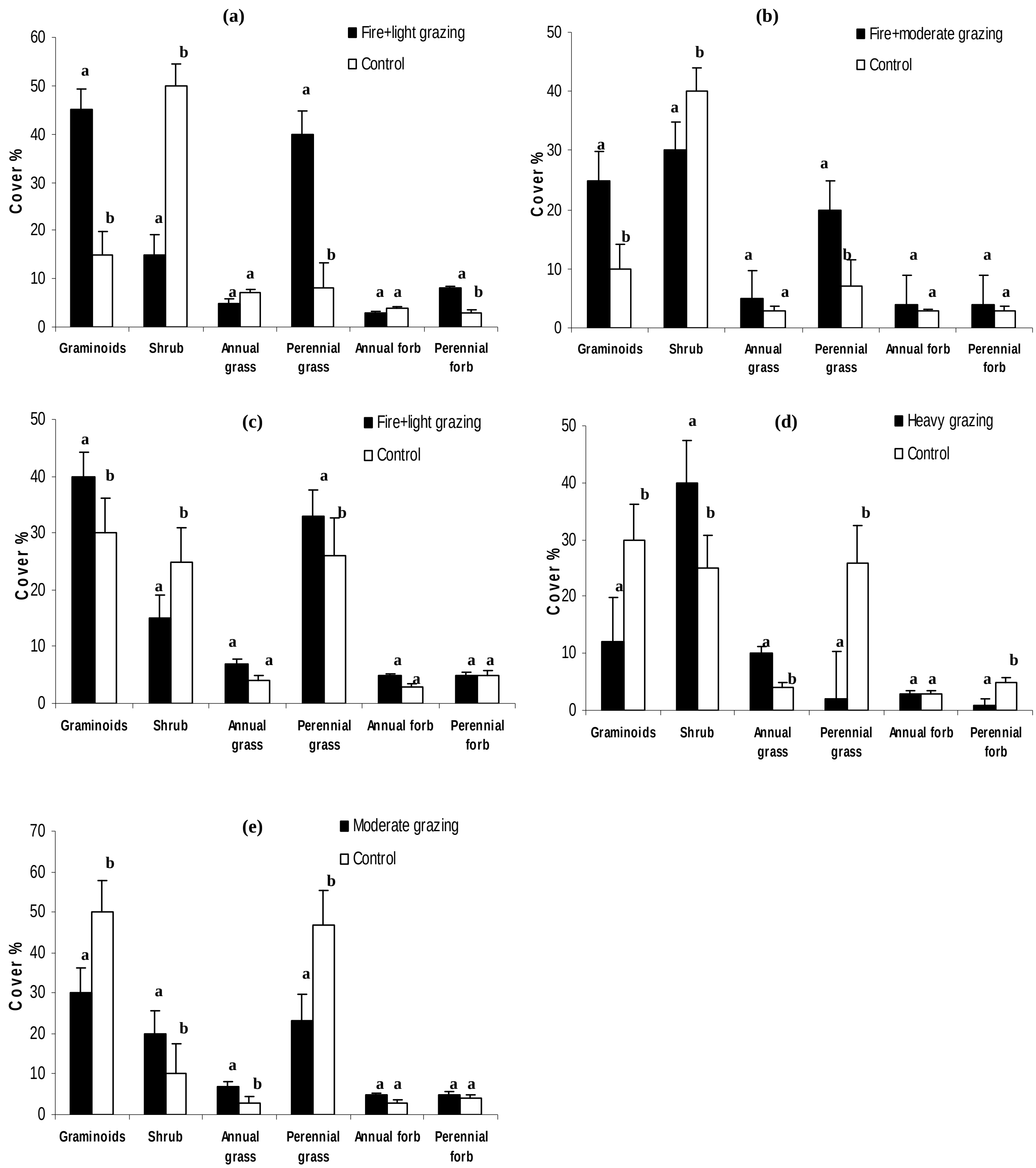

Fig. 3. Shifts in life forms by grazing and fire in different plant communities, (a): shrublands, burned in 2006; (b): shrubland, burned in 2008; (c): shrubland-grassland, burned in 2009; (d): heavily grazed shrubland-grassland; (e): moderately grazed grassland.

The same effect was observed for Shrubland-grassland community (Fig. 3c). In Shrubland-grassland community, the effect of heavy grazing on Shrubland-grassland community resulted in a significant decrease in the cover of perennial grass and forbs and an increase in the cover of shrub and annual grasses and forbs (Fig. 3d). Additionally, although the cover of perennial grass and forbs did not change with moderate grazing in grassland community, shrubs, annual grasses and forbs was significantly higher at this level of grazing (Fig. 3 e). The number of animal bite traces on plants was different between burned patches and control areas and between years (Fig 4). For recently burned patches (2008 and 2009), animal bite traces within burned patches were significantly higher than in non-burned control areas. For example, plants in burned areas in 2009 were grazed three times more than in non-burned control areas. However, there was no significant difference in animal selection between patches that were burned in 2005 and non-burned control areas (Fig. 4).

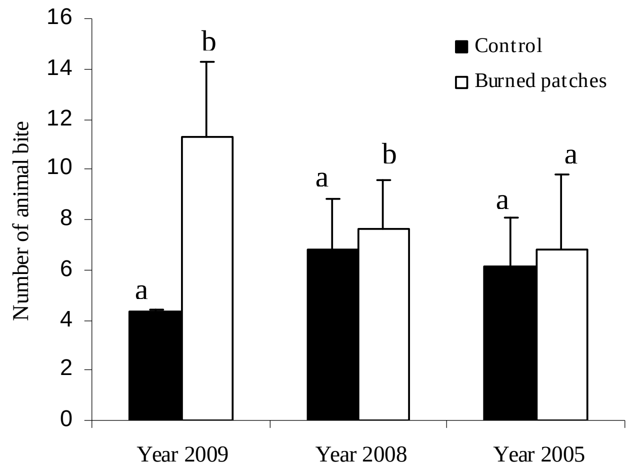

Fig. 4. Animal selection on burned patches and control areas monitored by the number of animal bites on plants.

DISCUSSION

The overall results suggest that plant communities followed a cyclical pattern of succession through the positive, negative and interactive effect of fire and grazing in semi-steppe rangelands, consistent with the hypothesis presented in the conceptual model (figure 1). Semi-steppe rangelands can be viewed as lying within a continuum between grassland and shrubland, where ground shrub coverage ranges from absence non-existent to complete coverage (Pickett and Cadenasso 1995**;** Van Auken 2000; Archer *et al*. 2001; House *et al*. 2003). The results showed that fire replaced shrubland by grassland which may then promote grazing intensity in recently burned areas. Dominant unpalatable shrub species such as *Astragalus adcendense, A. susianus* and *A. verus* (fig. 3a) reduced animal selectivity in shrublands (Payranj 2010). Their cover decreased with fire and opened space, enabling perennial palatable grass species such as *Agropyron repens* and *Bromus tomentellus* to colonize (fig. 3a) the area, and encouraging nomad people to keep animals in these areas. As we expected the results showed that animals selected the burned areas more than non-burned control areas. This is consistent with the results in North American prairies, where grazing animals spend more than 70% of their grazing time on recently burned areas that provide relatively higher forage quality (Vinton et al. 1993; Coppedge & Shaw, 1998, Ritchie *et al*. 1998). Similarly, in subalpine tussock grassland in New Zealand, fire increased the palatability of the dominant grasses and hence their vulnerability to sheep grazing in the following growing season (Mark, 1994). This fire-induced phenomenon of increased presence of palatable grass species, promoted initial overgrazing of grass species and in the end into shrub encroachment within a couple of years (fig 3d. and 3e) (Ramos-Neto and Pivello, 2000). We may interprete these changes as a result of preferential grazing of the palatable dominant grasses and decrease in their cover, concomitant competitive release and increased abundance of unpalatable shrub species with prolongation or severe grazing (Belskey 1992; Noy-Meir 1995; Whelan, 1995; House *et al*. 2003). By decreasing forage quantity and quality, animals may be forced to abandon or set aside the sites. This is consistent with our results as we found that four years after burning (Fig. 4), animal selectivity for grass species decreased and became the same as in unburned control sites. This suggests that the positive and negative feedbacks created by fire and grazing in animal behaviors may induce cyclical changes in vegetation composition and structure (Briggs *et al*. 2002). But burning not always led to intensive grazing. There were burned areas where grazing intensity was maintained low due to a large distance to watering points. In areas far from watering points, tall grass species gained dominance. In these areas after fire, grass species can gain dominance (fig 3c) and a stable state may exist until disturbance such as fire or grazing occurs again (Archer *et al*. 2001; Briggs *et al*. 2002). As a consequence, if animals were excluded throughout the landscape, tall grass species would reduce the abundance and diversity of early and mid successional species which leads to a homogenous landscape (Adler *et al*. 2001; Tahmasebi *et al*. 2008). Suppose that either extensive fire or homogenous grazing occurred in the region, this also creates homogenous vegetation at the landscape scale (Callaway, and Davis, 1993; Knight and Holt 2005). However, when fire occurred within different patches in different years, temporary changes in plant community composition make local sites more attractive for grazing animals. By reducing site productivity and inducing the plant community shift into unpalatable shrubland, animals leave these sites for new burned sites (Vinton et al. 1993; Coppedge & Shaw 1998). With the accumulation of shrubs and annual grasses in previously burned sites, patches that have recently been burned and grazed are the most diverse in terms of structure and composition. Nevertheless, the amount of changes in plant community composition in burned areas that are moderately grazed is different from burned areas that are lightly grazed (compare fig 3b with 3c). In the former, although the cover of grasses significantly increased with fire, shrub species were still dominant (fig 3b) and shrublands were replaced by a shrubland-grassland community. This result indicates that the effect of fire on plant community dynamics in semi-steppe rangeland is controlled by grazing intensity. Additionally, this interactive effect of grazing and fire may promote heterogeneity at the landscape scale by the fact that patches with different burning history and grazing intensity introduce specific differences in plant community composition and hence in landscape mosaic pattern (Callaway and Davis, 1993; Kerby *et al*. 2007). For example, there can be a pattern of burned and unburned patches with different grazing intensity, each may have a given vegetation composition such that they increase landscape heterogeneity. However, it depends on fire extension and severity. If fires were so extensive, it would induce less heterogeneity in burned landscapes than existed in the previous plant mosaic (Fuhlendorf and Engle 2004). In the present study, fire occurred in spatially discrete patches with areas of about 10-100 ha and observations demonstrated the pattern of focal grazing in burned patches. This may finally cause local changes in the plant community and increase patch-level heterogeneity across landscapes (Adler *et al*. 2001). Furthermore fire is shifted to other patches over time in the study area, making animals to graze new patches and to release previously burned patches. This may lead to cyclical successional processes within the burned patches that are moderately to intensively grazed (Fuhlendorf and Engle 2004; Kerby *et al*. 2007). The effect observed here is also reported in North American Great Plains grasslands (Fuhlendorf and Engle 2004) and in tall-grass prairie (Hobbs *et al*. 1991, Coppedge *et al*. 1998). Fuhlendorf and Engle (2004) found that fire increased nutritional value of herbage over grazed landscapes and obliterated a pattern of preferential re-grazing of previously grazed patches, present in unburned grasslands. Our results are consistent with their study as they also predicted that interactive effects of grazing and fire led to shifting mosaics in vegetation composition, increasing heterogeneity of the landscape of tall grass prairie grazed by bison. However this study is somehow different from their's, since they did not consider grazing intensity as one of the main factor in creating shifting mosaics. They also noted that by introducing free ranging animals in spatially discrete burned patches, heterogeneity in vegetation would increase. Differences in management may also contribute to differences in vegetation responses to fire (Hartnett, *et al*. 1996). In semi-steppe rangelands managed for livestock production, grazing is often seasonal, whereas systems managed with native ungulates typically involve year-round grazing with minimal grazing management. Here we showed that domestic animals can also create this landscape heterogeneity, since the shepherd actively steered animals into recently burned areas and excluded them from previously burned patches with lower forage quantity and quality, as they assume increased forage quality after burning. This study presents evidence that shifts in vegetation composition are caused by separate and interactive effects of fire and grazing and that both contribute to the mechanism of cyclical succession in semi-steppe rangelands. There were apparent shifts from shrublands into grasslands after fire and shifts from grasslands to shrublands induced by grazing. The results indicate that the change in vegetation structure caused by fire is rather transient and suggest that four years after fire, burned sites returned to their earlier state of vegetation. However, this depends on grazing intensity; with low grazing intensity, fire may create a stable state of grasslands where the site is far from watering points. With moderately and high grazing intensity on burned areas, negative and positive feedbacks between plant community composition (forage quantity and quality) and grazing, vegetation characterized as various stages of recovery and consequently this leads to a heterogeneous vegetation at the landscape scale. Thus, this interactive effect of fire and native and domestic ungulate grazers has important potential implications for grassland ecosystems grassland biodiversity and rangeland management (Pickett and Cadenasso 1995).

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