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Post-burn species richness patterns of vascular plants and Orthoptera (Insecta) in a steppe grassland[1]

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A b s t r a c t : The effects of fire on species richness patterns of vascular plants and Orthoptera were assessed in a 1500 ha dry grassland area in Eastern Austria. Using a stratified random sampling design, 25 sampling points with a postburn age of one to >20 years after burning were considered. Burning significantly reduced competition exerted by the dominant grass species *Bromus erectus* and thus played an important role in maintaining species richness. Plant species richness and forb biomass were both highest in the first few years after burning and significantly decreased during postburn succession while coverage of *Bromus erectus* increased. Orthoptera species richness showed a highly significant quadratic relationship with postburn age and was lowest at intermediate time spans after burning. Thus postburn species richness patterns of both vascular plants and Orthoptera seemed to contradict one of the predictions of the intermediate disturbance hypothesis (IDH). We argue that fire as a disturbance in the dry grassland investigated does not meet some of the requirements of IDH. In the light of the recent discussion on IDH, our results provide further evidence of more complex interactions of disturbance and species richness than previously assumed.

K e y w o r d s : postburn succession, species richness, competition, Orthoptera, vascular plants, dry grasslands, intermediate disturbance hypothesis, *Bromus erectus*.

Introduction

Grasslands are considered ideal ecosystems to study the interaction between competition and disturbance on species richness (HUSTON 1994). Disturbance, such as fire, is regarded as an important factor in maintaining species richness in dry grassland ecosystems (COLLINS & BARBER 1985, BELSKY 1992, KNAPP et al. 1999, HART 2001), because it retards the succession process and prevents the dominance of few highly competitive species (HUSTON 1994). Fire in dry grassland is sometimes discussed in connection with the intermediate disturbance hypothesis (IDH) (e.g. COLLINS et al. 1995, ENGLE et al. 2000). The IDH predicts species richness to be highest at intermediate disturbance intensity (INTEN) and disturbance frequency (FREQ) and at intermediate time spans during post-disturbance succession (TIME) (CONNELL 1978). Some authors do not refer to the TIME prediction as part of the intermediate disturbance hypothesis (GRIME 1973, HUSTON 1979), but it is difficult to disentangle the impact of FREQ and TIME (COLLINS et al. 1995). The TIME prediction postulates that immediately after a disturbance only few pioneer species become established and hence species richness is low (CONNELL 1978). Species richness then increases as more and more species colonize the newly created gap. In later successional stages competitive exclusion again reduces species richness.

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[1] This paper is dedicated to Prof. Dr. Hans Malicky on the occasion of his 75th birthday.

In Central European dry grasslands grazing and mowing are the key management tools for maintaining species richness in practice (BOBBINK & WILLEMS 1991, HANSSON & FOGELFORS 2000, BARBARO et al. 2001, POSCHLOD & WALLISDEVRIES 2001). Currently, the use of fire as a management instrument in Central European dry grasslands remains uncommon but increases in importance (GOLDAMMER et al. 1997). An extensive grassland area (ca. 1.500 ha) near Vienna provides the opportunity to test the influence of fire on a Central European dry grassland ecosystem in terms of species richness of vascular plants and Orthoptera. Here, fires are an annual but accidental occurrence during military training activities. In our system a tussock grass, *Bromus erectus*, is the most competitive species, partly due to stimulating effects of airborne nitrogen pollutants (BIERINGER & SAUBERER 2001a).

The aims of our study were to test (1) whether there is evidence for a competitive exclusion of forbs during post-burn succession and (2) whether species richness patterns for vascular plants and Orthoptera in post-burn succession agree with the time prediction of the intermediate disturbance hypothesis.

Methods

Study area

This research was conducted in the military training area of "Großmittel" in Eastern Austria, some 35 km south of Vienna (47°53' N, 16°19' E; elevation 218-271 m above the Adriatic Sea). The study region is characterized by a subcontinental climate (mean annual temperature 9.4 °C, mean annual precipitation 614 mm) with a considerable water deficit during the growing season and by shallow, dry and nutrient-poor soils upon coarse calcareous gravel (BIERINGER & SAUBERER 2001b). Today, dry grassland covers more than 1500 ha of the military training area Großmittel. Part of it has never been ploughed and can be regarded as natural edaphic steppe (MALICKY 1969, SAUBERER & BIERINGER 2001). Due to the flat relief and the uniformity of soil conditions there are extremely homogenous site conditions and hence there is little variation in vegetation composition in Großmittel. Thus the entire study area is covered by the same plant community, classified as Fumano-Stipetum eriocaulis (SAUBERER & BUCHNER 2001). Species within the Fumano-Stipetum eriocaulis with high constancy values include for example *Festuca stricta*, *Stipa eriocaulis*, *Bromus erectus*, *Carex liparocarpos*, *Galium lucidum*, *Seseli hippomarathrum*, *Helianthemum canum*, *Teucrium montanum*, *Potentilla arenaria* (= *P. incana*) and *Globularia punctata* (for a complete list see SAUBERER & BUCHNER 2001).

The investigated 850 ha of the military training area are almost free of trees and shrubs. Military training (artillery shooting) is the only form of land use. In the study area there are no other forms of disturbance such as soil disturbance by tank movements or similar activities typical for most other military training areas. Most fires are triggered by military shooting, but lightning-caused fires occur as well. Prescribed burning, however, is not performed, hence all fires are predominantly accidental. The fires show a bimodal frequency distribution with peaks in early spring and late summer.

Sampling design

For each of four postburn age classes (1-5, 6-10, 11-15 and >15 years after burning), at least five sampling points (total 25 sampling points) were randomly selected. Each random point was assigned a certain post-fire age and fire history by the detailed fire reports of the military garrison command. Since fire intensity was not assessed, the INTEN prediction of the IDH could not be investigated. Only fires extending over at least 1 ha were considered. Points which were less than 100 m apart from the nearest forest edge were not included in the sample to avoid possible edge effects on the Orthopteran species composition (BIERINGER & ZULKA 2003). All field work was done in 1998.

Fire history

The timespan since the last burn ranged from one to at least 20 years, and the number of fires during the two decades prior to the sampling year ranged from zero to three. Burning frequency and years since the last burn proved to be highly intercorrelated (Kendall´s $\tau = -0.77$, $p < 0.001$) and thus could not be statistically separated. For further analyses we only used the timespan since the last burning.

Habitat variables

The percentage of bare ground was assessed on 26/27 June 1998 by horizontally placing a 1 m long ruler on the vegetation and counting the centimeter-units which were not covered by living plants or litter. This was done at three random points within a circle of 0.1 ha around the center of each site. Standing crop was yielded on 26 June (when it is at its peak) at one randomly placed square of 20 x 20 cm per site. It was sorted for forbs and grasses, dried at 40 °C to weight constancy and weighed by a laboratory scale (Mettler PM 4600) as a measure of productivity.

Vascular plants

Vascular plants were sampled on 21/22 May 1998 within a quadrat of 5 x 5m, which is a commonly-used sample size for dry and semidry grasslands (DIERßEN 1990). All species were recorded, and their respective quantity was estimated using an ordinal 7-level Braun-Blanquet scale (BRAUN-BLANQUET 1964).

Orthoptera

A circle of 0.1 ha (about 35 m diameter) around the marked center of each site was observed for a period of 10 minutes. All Orthoptera species were identified in the field according to morphologic or acoustic characters. This was done three times at each site (18 July, 15/16 August and 30 August), and the results were pooled.

Statistical analysis

From the TIME prediction of IDH, a hump-shaped relationship between the timespan since the last disturbance and species richness should be expected. We therefore fitted a quadratic model to our data and by a t-test tested for the statictical significance of the quadratic term. When the quadratic term was not significant, a linear model was fitted. All other relationships were tested for by Kendall´s τ since there were no theoretical considerations suggesting certain mathematical (e.g. linear) models. All analyses were done using the statistical package SPSS.

Results

Competition

During post-burn succession the coverage of *Bromus erectus* significantly increased (Kendall´s $\tau = 0.44$, $p = 0.005$). Bare ground markedly decreased ($\tau = -0.60$, $p < 0.001$), and after five to 10 years in post-burn succession the vegetation closure became almost complete. The biomass of forbs was negatively correlated with years since the last burn ($\tau = -0.36$, $p = 0.020$). The correlation between plant species richness and the estimated cover of *Bromus erectus* revealed a strong negative trend but was not significant at the 5 % error level ($\tau = -0.29$, $p = 0.061$). There was also a trend for a negative correlation between cover of *Bromus erectus* and forb species richness ($\tau = -0.26$, $p = 0.093$).

Species richness of vascular plants

Species richness ranged from 14 species on a plot unburned for at least 20 years to 34 species on a plot in its second year of post-fire succession. The quadratic model revealed a significant relation between the number of years since the last burn and plant species richness ($r^2 = 0.33$, $p = 0.011$) but was the opposite of what would be predicted by the IDH. The quadratic term of the equation, however, was not significant ($t = 1.15$, $p = 0.264$), hence a linear model was calculated ($r^2 = 0.29$, $p = 0.005$). The hypothesis of a quadratic relationship was rejected and a linear relationship adopted (Fig. 1).

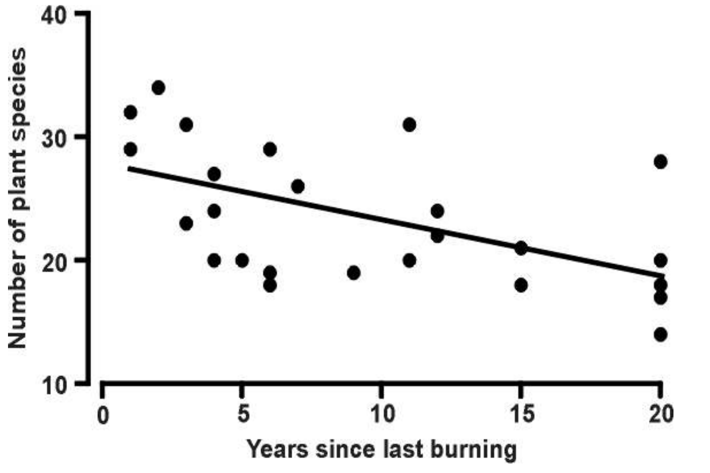

Fig. 1: Relationship between vascular plant species richness and time since last burning ($r^2 = 0.29$, $p = 0.005$, $y = 27.6-0.4\ x$).

Species richness of Orthoptera

A minimum of six species was found at two sites nine and 12 years after the last burn, respectively. Two sites in the first and third year of post-fire succession reached a maximum of 13 species each. There was a higly significant quadratic relationship between the number of years since the last burn and Orthoptera species richness (r^2 = 0.54, p < 0.001) but again its shape was the opposite of that predicted by the IDH (richness (y) = 12.71 - 0.74 x + 0.03 x^2). The quadratic term of the equation was significant (t = 3.03, p = 0.006) and thus the quadratic relationship was adopted (Fig 2).

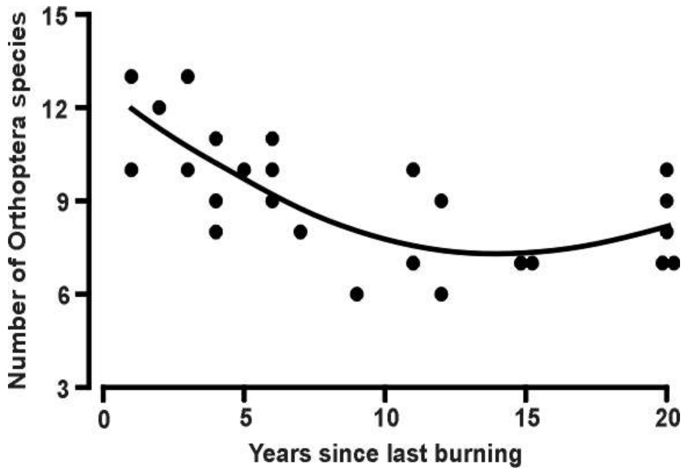

Fig. 2: Relationship between Orthoptera species richness and time since last burning (r^2 = 0.54, p < 0.001, y = 12.71-0.74 x + 0.03 x^2).

Discussion

Disturbance and competition

In our study an increase in the coverage of the strong competitor *Bromus erectus* during post-burn succession coincided with a decrease in bare ground and in forb biomass. Vascular plant species richness, although not significantly related to the coverage of *Bromus erectus*, decreased also. We therefore suggest that competitive exclusion plays an important role in the investigated grassland ecosystem and that fire reduces competition for several years. Like in a dry heathland in the Czech Republic (CHYTRÝ et al. 2001) the recruitment of less competitive species was enhanced after burning. The main effect of fire is the removal of above-ground biomass including litter (e.g., HULBERT 1969), which promotes penetration of light to the soil surface (HULBERT 1988, JUTILA & GRACE 2002) and creates patches of low vegetation cover. Different plant species of the surrounding area, especially annuals and herbs, can then establish themselves on the partly bare ground. In our case, after five to 10 years in post-burn succession the vegetation closure becomes almost complete. Without light-gaps, annuals and short-living herbs disappear in the absence of other kinds of disturbance. Therefore, the regeneration niche (GRUBB 1977) after fire is essential in maintaining vascular plant species richness in the investigated dry grassland ecosystem.

IDH and fire in grasslands

In our case study in a Central European steppe grassland the species richness patterns of vascular plants and Orthoptera during post-burn succession do not agree with the TIME prediction of the IDH.

Tests of IDH in grasslands under different fire regimes revealed no general patterns with regard to plant species richness but only few studies are available at the moment. In North American tallgrass prairie, COLLINS (1992) found relationships opposite to that predicted by IDH. COLLINS et al. (1995) were able to statistically separate the FREQ and TIME predictions of IDH. In their study fire frequency was negatively related to species richness of vascular plants. However, there proved to be a significant quadratic relationship between species richness and the number of years since the last burn. The TIME prediction of IDH was therefore supported. In contrast, OVERBECK et al. (2005) detected similar patterns like ours in a subtropical grassland in southern Brazil.

The few studies directly addressing the influence of different fire regimes in grassland ecosystems on species richness of Orthoptera are also inconclusive. EVANS (1984) found highest species richness on sites burned every four years compared to sites burnt anually, biennially and every 10 years. While this result supported IDH, two further studies of EVANS (1987, 1988) revealed different patterns. EVANS (1987) reported a greater number of species on sites left unburnt or burnt every four years than on sites burnt annually or biennially. In a third case species richness did not vary in a regular fashion with the four-year fire circle but was often particularly low in the fourth year following fire (EVANS 1988). CHAMBERS & SAMWAYS (1998) reported significantly lower species numbers in triennially burnt plots than in annually, biennially and unburnt plots.

We conclude that support for IDH in fire shaped grassland ecosystems is low for both vascular plants and Orthoptera. Hence it appears probable that in fire ecology in dry grasslands such as in our case some prerequisites of the IDH, in particular competition (for Orthoptera) and initial site conditions (for vascular plants), are often not fulfilled. While it can be assumed that competitive exclusion does reduce vascular plant species richness, there is no proof for such effects among the Orthoptera. It is likely that free-ranging insect herbivores do not experience competition for food resources in grassland ecosystems (EVANS 1992). CHAMBERS & SAMWAYS (1998) suggested that Orthoptera species composition after fire depends solely on the trajectory of plant succession. This is supported by an analysis of the occurrence patterns of Orthoptera species at the same sites that were investigated in this study (BIERINGER 2002). For vascular plants fire is not as destructive in the investigated grassland as it may seem at first. Some perennial species like *Stipa eriocaulis* or *Globularia punctata* can survive on a large scale and the impact of fire on different plant species partly depends on the seasonal occurrence of the fire (Howe 1994, BIERINGER & SAUBERER 2001c). The influence of scale is particularly important. We collected the vascular plant data on larger sample sites than in some other studies (e.g. CHYTRÝ et al. 2001). However, fire causes plant mortality and patches of bare ground which are finer-scaled than detectable with our 5 x 5 m sample sites. Furthermore, some plant species like *Teucrium chamaedrys* (OBERDORFER 2001) or *Thymus* sp. (DIEMER & PROCK 1993, GRIME 2001) have a persistent soil seed bank and can develop rapidly after fire. The fire intensity in our system seems to be generally low, owing to the comparably small amount of combustible plant material. In summary, it appears that the initial site species richness is only partly dependent on a recolonization process following the burn.

Recent discussion on IDH

At least since 2001 the IDH has got into vigorous critique. MACKEY & CURRIE (2001) stated in their review that "species diversity–disturbance relationships are neither consistently strong nor consistently peaked". Nevertheless, they observed a highly explained variance in studies in which disturbance was measured as a gradient of time passed since the last disturbance. Recently, the interaction of IDH and productivity was theoretically analyzed (HUSTON 1979, KONDOH 2001). This means when productivity is low maximum diversity also occurs at lower intensities of disturbance. However, the quantification of disturbance intensity is still unresolved and other factors such as the history of community assembly (FUKAMI & MORIN 2003, SVENSSON et al. 2009) or autecological traits of single species (HADDAD et al. 2008) increasingly gain importance. In the light of this recent discussion on IDH, our results additionally add indication of a more complex context of IDH than thought so far.

Management implications

In the investigated grassland ecosystem, fire is obviously a useful mechanism for the maintenance of species richness. However, for many other dry grasslands in Central Europe this might not be the case. Most of the Central European dry grasslands are small, isolated remnants, and the results obtained in our study area may not be applicable to them. An undifferentiated use of prescribed burning should therefore be avoided. From our present knowledge burning can only be recommended for large, homogeneous areas like our investigated grassland system. According to the patch dynamic model (PICKETT & WHITE 1985, WHITE & JENTSCH 2000), a mosaic structure of different successional stages, representing the whole continuum of postburn age, seems suitable to maintain overall species richness of vascular plants and Orthoptera in the study area.

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Zusammenfassung

In einem 1.500 ha großen Trockenrasengebiet in Ostösterreich wurden die Auswirkungen von Bränden auf die Artenzahlen von Blütenpflanzen und Heuschrecken untersucht. Anhand einer stratifizierten Zufallsstichprobe wurden 25 Aufnahmepunkte ausgewählt, an denen der letzte Brand jeweils zwischen einem und mehr als 20 Jahren zurücklag. Die Brände reduzierten die Konkurrenz durch die dominante Grasart *Bromus erectus* erheblich und spielten dadurch eine wichtige Rolle in der Erhaltung des Artenreichtums der Vegetation. Sowohl die Artenzahl der Blütenpflanzen als auch die Biomasse der krautigen Pflanzen waren in den ersten fünf Jahren nach einem Brand am höchsten und nahmen im Lauf der Sukzession signifikant ab, während die Deckung von *Bromus erectus* zunahm. Die Artenzahl der Heuschrecken zeigte eine hochsignifikante quadratische Beziehung mit der Dauer seit dem letzten Brand und war bei mittleren Zeiträumen am geringsten. Die Muster der Artenzahlen sowohl von Blütenpflanzen als auch von Heuschrecken nach Bränden scheinen somit den Vorhersagen der

Intermediate-Disturbance-Hypothese (IDH) zu widersprechen. Wir nehmen an, dass Brände im untersuchten Ökosystem einige wichtige Voraussetzungen der IDH nicht erfüllen. Unsere Untersuchung stützt die aktuelle Diskussion über die IDH, die mehr und mehr zeigt, dass die Beziehung zwischen Störung und Artenzahl komplexer ist als ursprünglich angenommen.

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