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Effect of fire on vegetation dynamics and plant types in subtropical grassland in southern Brazil

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Contents

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Preface

      The presented thesis is written as a cumulative PhD thesis. Chapters 1 to 5 each are independent papers that have been submitted for publication in different scientific journals. A general introduction and a concluding chapter with an integrating discussion (Chapter 6) create the necessary frame for joint consideration of the different chapters. Each of these chapters (papers) originally had been formatted according to the instructions given by the respective journal. To facilitate reading of the thesis, tables and figures were always inserted into the text and formatted in the same way, and font size, line spacing and captions were adjusted to one format. Other formatted objects, e.g. of references in the text and in the bibliography were left unchanged, i.e. may differ slightly in style between the different chapters, depending on the rules of the journal where the paper was submitted. Enumeration of tables and figures was conducted separately for each chapter.

      In addition to the synthesizing summaries in English and German, the thesis at its end contains an expanded summary in Portuguese, briefly presenting the contents of each of the different chapters.

INTRODUCTION

Grasslands in southern Brazil – the setting

Overview of present vegetation and vegetation history of southern Brazil

Due to its geographic position around the 30° parallel of latitude, a limit for tropical vegetation types (Cabrera & Willink 1973), and at the eastern side of South America, southern Brazil is characterized by a transitional situation between tropical and temperate climate, with hot summers and cool winters and no dry season. Differences in geological substrate and altitudinal variation further contribute to diversity of vegetation types in the region (Waechter 2002). The natural vegetation in Brazil's southernmost state, Rio Grande do Sul (RS), presents itself as mosaics of grassland, shrubland and different forest types (e.g. IBGE 1986, Leite & Klein 1990, Pillar & Quadros 1997; see Fig. 1).
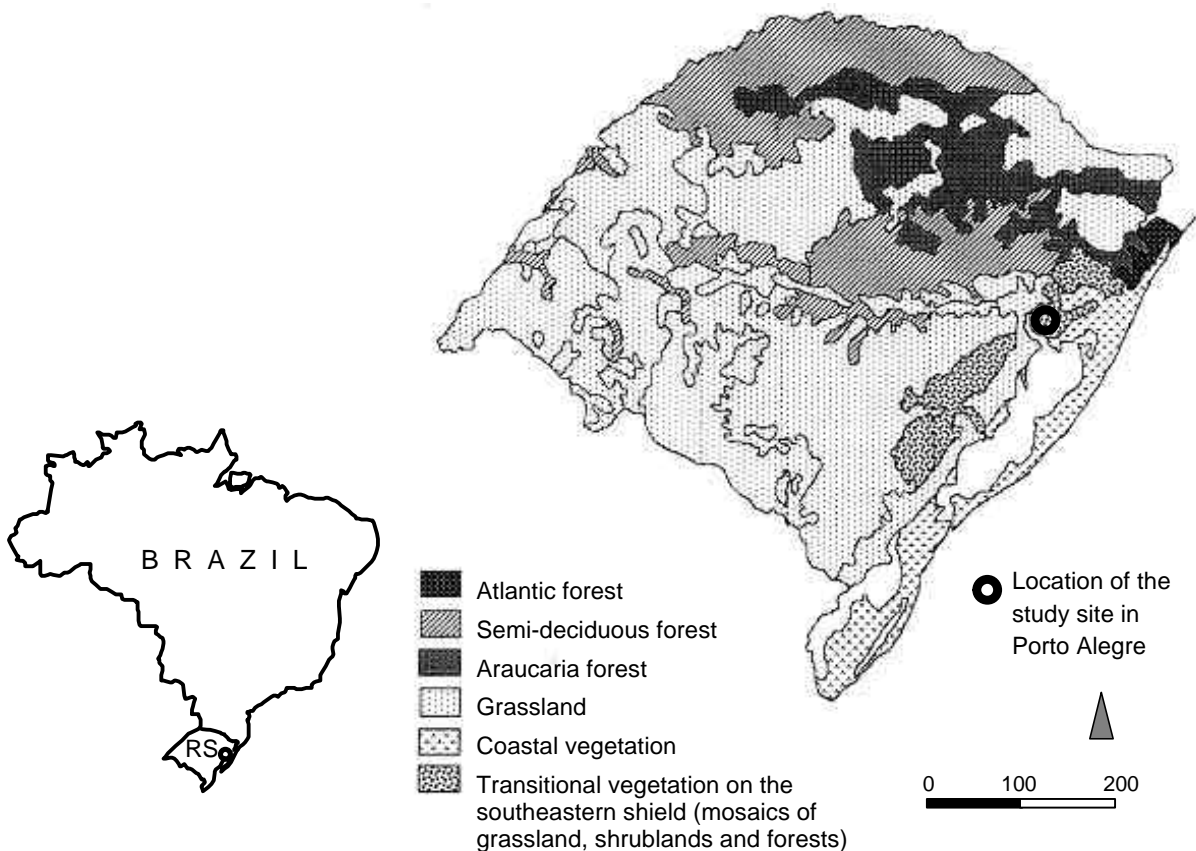
Figure 1: Location of Rio Grande do Sul (RS) state in Brazil and principal vegetation types of Rio Grande do Sul, Brazil (from Pillar & Quadros 1997), with indication of the study site of this work, Porto Alegre (see Fig. 2).

Atlantic forest (Atlantic forest *sensu strito*, Oliveira-Filho & Fontes 2000) occupies the eastern slopes and valleys of the South Brazilian Planalto highland in the North Eastern part of RS. Araucaria forests, physiognomically dominated by *Araucaria angustifolia* in the upper stratum, are found principally on the Planalto, in mosaics with grassland areas. Semi-deciduous forest, like the Araucaria forest included in Atlantic forest *sensu latu* (Oliveira-Filho & Fontes 2000), can be found along the upper Uruguai river, at the northern border of RS, and in the Ibicuí and Jacuí river basins in Central

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RS. The southern and western parts of RS are dominated by grassland, on the Crystalline shield in South Eastern RS (including the granitic hills in the Porto Alegre region) in a complex mosaic of forest, shrublands and grasslands, dissected by riverine forests (Rambo 1954, 1956b). Grasslands comprise tropical elements from Central Brazilian savanna (Cerrado), continental elements from the Gran Chaco and Paraguay in the west, and temperate elements from the extended grasslands of Uruguay and Argentina to the south (Rambo 1954, Schultz 1956, Waechter 2002). In the westernmost part of the state, an Acacia-Prosopis parkland presents a transition to Chaco and Espinal further to the west (Waechter 2002). Grasslands in the southern half of RS often are considered to make part of the Río de la Plata grasslands (Soriano *et al.* 1992, Bilenca & Miñarro 2004), i.e. of the Pampas province (Cabrera & Willink 1973). Along the Atlantic, coastal vegetation (different successional stages on sandy plains and dunes; Pfadenhauer 1980) stretches from the border with the adjacent state of Santa Catarina in the north to the border with Uruguay in the south.

Already Lindman (1906) had noted the contradiction between presence of grassland vegetation in southern Brazil and humid climatic conditions that allow for forest development. Similarly, the presence of grasslands in a climate apparently supporting forest vegetation has led to intense debate of the so-called "Pampas problem" in the Río de la Plata region (e.g. Walter 1967, Eriksen 1978, Box 1986). Discussion, however, focused on relations between climate and vegetation in a rather static view, neglecting vegetation history and the possibility of rather recent climatic changes. Rambo (1956a, 1956b), based on geological and phytogeographical evidence, concluded that grasslands were the oldest vegetation type in southern Brazil (stemming from the Tertiary), with forests expanding over grassland only recently, both southwards along the Atlantic coast (Atlantic forest) and from the northwest (semi-deciduous forest). According to Rambo, Araucaria forests had reached the region before semi-deciduous forest, but remained constricted to refugia in deep valleys or lowlands south of the Planalto until expansion began relatively recently (Rambo 1956a). More recently, palynological research clarified climate and vegetation history of southern Brazil, supporting Rambo's theories (e.g. Behling 1998, Ledru *et al.* 1998, Behling *et al.* 2001, Behling 2002, Behling *et al.* 2004). Summarizing these studies, four distinct climatic periods from late Pleistocene until recent Holocene periods can be recognized for southern and south-eastern Brazil. Between about 42,000 to 27,000 years ago, before the last glacial maximum, grasslands dominated in the region, with forest elements restricted to climatically more favorable sites in deep river valleys, the South Brazilian lowland or along the coast. From about 27,000 to 10,000 years BP, i.e. during glacial times, climate was markedly cooler and probably drier, with possibly pronounced dry seasons. Grasslands dominated during this period. After 10,000 years BP, climate remained dry, but temperatures rose, allowing for migration of the Atlantic forest southwards. From 7,400 years BP onwards, fire, likely related to arrival of indigenous populations in the region, became markedly more frequent, as evidenced by greater presence of charcoal particles in peat profiles. At roughly the same time, large grazing animals became extinct (Kern 1994). Indigenous people most likely used fire for hunting and for land management

(Kern 1994, Schmitz 1996); direct evidence, however, is scarce. At the beginning of the late Holocene, around 4,000 years BP, climate turned moister, allowing for expansion of Araucaria forest principally along rivers, at first increasing little in total cover. Velocity of expansion greatly increased after 1,100 years BP, now leading to a more pronounced substitution of grassland by forest vegetation. In the 17th century, Jesuite missionaries introduced horses and cattle in the region (Pillar & Quadros 1997), and beef cattle production became, and is until today, an important land use in southern Brazil: in RS, 40% of the land surface today are covered by natural grassland (i.e. grassland composed of native species), almost entirely grazed by cattle (Nabinger *et al.* 2000). Just as known from other continents (e.g. Bond *et al.* 2003 for South Africa; Sauer 1950, Vogl 1974, Anderson 1982 for North America), fire and/or grazing thus can be considered the principal factors impeding development of woody vegetation types after climatic conditions turned to be favorable for forest development.

Impact of fire on forest-grassland distribution and dynamics

Forest expansion and forest-grassland distribution are mediated through numerous factors, such as local edaphic conditions and microclimatic variation over the border gradient (e.g. Furley 1999, Hopkins 1992), dispersal and recruitment abilities of tree species (e.g. Hoffmann 1998, Holl 1999, Cabral *et al.* 2003, Hoffmann *et al.* 2004), competition between trees and grasses (e.g. Scholes & Archer 1997, Jeltsch *et al.* 2000), and disturbance agents, such as grazing (e.g. van Langenvelde *et al.* 2003) and fire (e.g. Braithwaite 1996, Higgins *et al.* 2000, Hoffmann & Moreira 2002, Miranda *et al.* 2002). At this place, only the effect of fire shall be considered briefly. In southern Brazil, woody species in grasslands in their majority are shrubs, but, in contrast to the Brazilian Cerrado or other savanna systems (e.g. Sarmiento & Monasterio 1983, Sarmiento 1990, Higgins *et al.* 2000, Hoffmann & Moreira 2002), no distinct tree layer exists, with the exception of the Acacia-Prosopis parklands in the more continental western part of RS. Published information on forest-grassland dynamics in the region still is scarce, but based on recent hypotheses (Pillar & Quadros 1997, Pillar 2003) and ongoing research (Müller *et al.*, unpublished) a few general conjectures can be made. Forest species seem to invade grassland areas, but in general do not survive fires, at least when young. Therefore, even low fire frequencies should be able to kill seedlings or samplings of forest trees that invaded into the grassland. Adult trees will only be able to survive on sites protected from fire or only subject to low-intensity fires, i.e. at sites with very shallow soil and thus low productivity of grasses or between rock outcrops. It has been hypothesized that these sites may thus serve as nuclei for forest expansion. Forests in southern Brazil do not burn (Pillar & Quadros 1997), and, even under dry conditions, grassland fires will not enter into the forest, due to changes in fuel distribution and microclimate at the forest edge (see Biddulph & Kellman 1998 for discussion of a similar situation in south-eastern Venezuela). Fires thus lead to abrupt transitions between forest and grassland, and to spatial stability of the forest borders, as observed, for example, in the comparison of aerial photographs spanning a time of several decades (W. Adelmann, pers. comm.). In the absence of fire, a slow advancement of

the forest border over grassland and an increase of shrubs within the grassland can be observed (Waechter *et al.* 1984, Oliveira & Pillar 2004).

Ecology of grasslands in southern Brazil

Various classification systems have been proposed for the South Brazilian grassland biome, however, the term "Campos" remains the only applicable term, as denominations like "savanna" or "steppe" – used for example in the RADAMBRASIL classification (IBGE 1986) – are in clear violation with the climatic situation of southern Brazil (see Machiori 2002 for a discussion of terminology of South Brazilian grassland vegetation). Distinction into "Campo limpo" and "Campo sujo", i.e. grasslands without or with a distinct shrub component, respectively, has become common usage. Number of species in the South Brazilian Campos biome has been estimated to be around 3,000 (Boldrini 2002), i.e. substantially more than present, for example, in the Pampas grasslands in the province of Buenos Aires (Rapoport 1996). This high species richness, together with a lack of taxonomic studies for many families, complicates work in South Brazilian grasslands. Species distribution patterns and species-area relationships (see e.g. Girardi-Deiro & Gonçalves 1987) are poorly studied, and the majority of publications on grasslands in southern Brazil presents little more than a species list with, if at all, indication of abundance and importance values. Only few ecological studies on South Brazilian grasslands exist (see e.g. Eggers & Porto 1994, Boldrini & Eggers 1997, Garcia *et al.* 2002, Sosinski & Pillar 2004 for effect of different forms of land management; Pillar *et al.* 1992, Tcaceno & Pillar 1996, Boldrini *et al.* 1998, Focht & Pillar 2003 for influence of site conditions, principally soil factors and exposition, on species composition). Species composition varies between the different phytogeographical regions of RS as a consequence of climatic differences (Köppen's cfb on the highlands in North Eastern RS, Köppen's cfa in the southern half of RS; Moreno 1961) and geological substrates (Boldrini 1997). Topographic position can exert high influence on species composition, principally related to differences in moisture regime between wet lowlands and drier sites on slopes and top of hills (Focht & Pillar 2003). Species variation also exists in relation to exposition (Boldrini *et al.* 1998). Within any grassland area, grazing regime and related management practices, e.g. fire, seem to be the principal factors determining compositional changes and physiognomy. Grazing exclusion leads to dominance of tall tussock grasses, whereas grazed grasslands are dominated by low or prostrate rhizomateous or stoloniferous species (Boldrini & Eggers 1997). Longer absence of grazing from a few years to decades can lead to development of shrublands, with subsequent development into forest vegetation (see above).

In southern Brazil, fire is used as a tool in grassland management, with burns traditionally conducted approximately every two years (Vincent 1935). As grassland productivity varies greatly between the cool winter season and the hot, but usually sufficiently moist, summers, ranchers adjust the stocking rate of their pastures in relation to carrying capacity in winter, i.e. large part of the biomass produced by highly productive C_4 grasses in summer will not be consumed, and thus needs to

be removed by burns, usually at the end of winter. Further, grassland fires are used for reduction of shrub cover, especially in south-eastern RS (Gonçalves *et al.* 1997). Use of fire for land management often has been and is being discussed rather polemically, and reliable scientific studies on its impact on species or functional type composition and soil properties are scarce. Fires in winter or early spring are known to diminish contribution of cool season C_3 grasses, at the expense of warm season C_4 grasses (Llorens & Frank 2004). Common burning practice – fires are set at the end of winter – thus favors C_4 grasses and decreases forage availability in winter, the most critical period (Nabinger *et al.* 2000). It has been suggested that grassland burns, leading to short-term increases of total N, K, Ca, Mg and pH values in the uppermost soil layer (Rheinheimer *et al.* 2003), can have negative effects on soil fertility and thus forage production on the long run (Heringer *et al.* 2002, Jacques 2003), but studies are too few to allow for general conclusions. Grassland research in general has mostly focused on improvement of pasture productivity for agronomic purposes, e.g. by introduction of exotic forage species (see Nabinger *et al.* 2000), and not on a better understanding of vegetation processes in natural grasslands. Only few studies treat the effect of fire on grassland composition and dynamics. Quadros & Pillar (2001) hypothesized that grasslands were not greatly affected by burns in species composition, but results of their study were not clear enough as to support or reject this hypothesis. Eggers & Porto (1994) found that species composition returned to the pre-burn state in a period of nine months, after an experimental burn in August. A few studies have treated effect of fire on individual species (Trindade & da Rocha 2001, for *Andropogon lateralis*, Fidelis *et al.* submitted, for *Eryngium horridum*), but it is too early to allow for general conclusions. In many other grassland regions of the world, the effect of fire is well understood (e.g. Vogl 1974, Kucera 1981, Collins & Wallace 1990). However, effects of fire on grassland vegetation may vary greatly, depending on species and functional type composition, season of burn, frequency and intensity of burns, interactions with other disturbances, site conditions, climatic factors and weather, impeding generalizations on the effect of fire in grassland (Uys *et al.* 2004).

Objectives of this study and integration into larger research efforts

If South Brazilian grasslands have been stabilized by the action of fire, and if fire has been part of the grassland's evolutionary history (see Anderson 1982), it seems reasonable to assume that the species present in South Brazilian grassland are adapted to fire, i.e. the grassland should not suffer substantial changes in community composition or structure if under a level of disturbance similar to what they experienced during their evolutionary history (Denslow 1980), even though it may be difficult to define this historic fire frequency. Vegetation development after a burn and impact of fire on species richness and diversity has hardly been studied in southern Brazil. This thesis presents a first step in a better understanding of the effect of fire on South Brazilian humid subtropical grassland vegetation.

The principal objectives of this study thus were to

1) describe floristic composition of a regularly burned grassland, considering the relative importance of site conditions (e.g. soil conditions, exposition) and fire,

2) analyze vegetation dynamics after fire, considering both species composition and grassland structure,

3) discuss functional type composition and adaptive strategies in relation to fire in subtropical grasslands in southern Brazil.

The study was conducted on Morro Santana, Porto Alegre, RS, Brazil (30°03' S, 51°07' W, max. alt. 311m a.s.l.; see Fig. 2), large parts of which belong to the Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, and are to be turned into a conservation area. Grassland areas are predominantly found on the top and on the northern slopes, while forests cover the major part of the southern, eastern and western slopes (Aguiar *et al.* 1986). Of the total area of Morro Santana, ca. 220 ha are grassland, 25 ha shrubland, 339 ha forest and 42 ha forest plantations (*Pinus*/*Eucalyptus*). The rest of the areas underlies strong anthropogenic influence (e.g. expansion of squatter settlements; Adelmann & Zellhuber 2004).
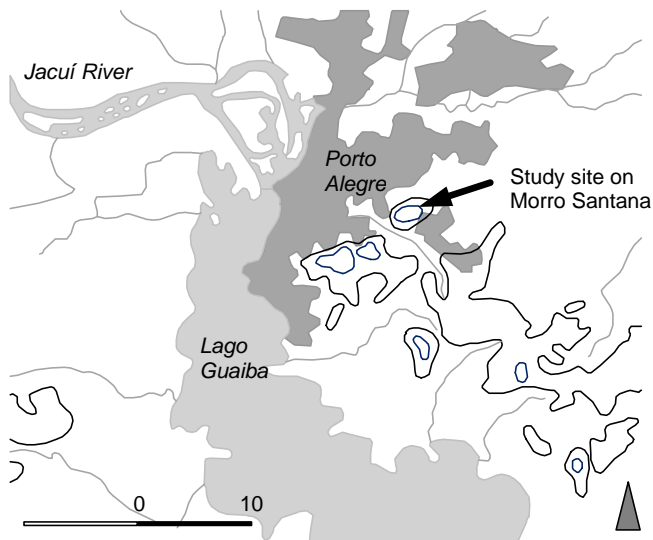
Fig. 2: Location of the study site near Porto Alegre, RS, Brazil. The granitic hills, among them Morro Santana, are indicated by the 100 and 200m isoclines.

Chapter 1 of this thesis presents data on the floristic composition of the grassland areas on Morro Santana and discusses species richness and species distribution patterns, also touching upon the definition of the forest-grassland-boundary concerning differences both in species composition and vegetation structure in the herbaceous layer. In Chapter 2, the effects of a single fire event on vegetation dynamics in the grassland are treated, with an emphasis on vegetation structure and species

diversity. Functional attributes of South Brazilian grassland species are discussed in Chapters 3 and 4 in two differing, but complementary approaches: while Chapter 3 is based on the life-form classification and on direct reaction of plant species to fire events and presents a review-like characterization of the main species groups in South Brazilian grassland, Chapter 4 employs recently developed multivariate methods for the identification of functional types and focuses on effect of vegetation on the fire regime. Finally, Chapter 5 presents an experimental study of the effect of heat on seed germination of dominant species from South Brazilian grassland. In the concluding synthesis of these chapters (Chapter 6), the concept of fire as a disturbance is discussed critically and an outlook on the importance of fire for management in forest-grassland-mosaics in southern Brazil is given.

The work presented in this thesis is part of a larger research effort on forest-grassland dynamics in southern Brazil, in a cooperation between the Chair of Vegetation Ecology of the Technische Universität München (TUM), Freising, Germany, and the Departamento de Ecologia of the Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil. The joint projects abrange different sites in RS state and treat forest-grassland dynamics in several approaches, focusing on spatio-temporal expansion of forest and shrubland patches over grassland (Oliveira 2003, Machado 2004, Oliveira & Pillar 2004), on the role of bird dispersers for establishment of trees (Duarte *et al.* submitted), on distribution patterns and population biology of pioneer shrubs and trees (Müller & Forneck 2004), and on impact of fire on woody species communities. Further, this thesis work is integrated into a project on protection and management of fragments of natural vegetation in the urban area of Porto Alegre, RS, Brazil, whose results are to be implemented in urban planning decisions in the municipality (Porto 2004). As outlined above, this thesis limits itself to discussion of composition and vegetation dynamics of the grassland and, to some extent, of areas at the forest-grassland border. Overall discussion of forest-grassland dynamics under the impact of fire can be expected from a synthesis of the different studies at a later point, both considering the study site on Morro Santana (this thesis and two further PhD theses on population dynamics of woody plants under the impact of fire), and a more general discussion of forest-grassland-dynamics in different regions in RS.

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CHAPTER 1

Floristic composition, environmental variation and species distribution patterns in burned grassland in southern Brazil

with Sandra Cristina Müller, Valério DePatta Pillar and Jörg Pfadenhauer

Abstract

In regularly burned grassland on Morro Santana, Porto Alegre, RS, Brazil, we investigated differences in floristic composition and their relation to soil properties, aspect, and distance from the forest border. In 48 plots of $0.75m^2$, we identified a total of 201 species, from a local species pool of approximately 450 to 500 species. Most species occurred in low frequencies, showing clumpy distribution patterns in the studied area. Multivariate analysis showed that plots close to the forest edge clearly differed from plots in the open grassland concerning composition and structure. Plots exposed to the north differed from plots on the top of the hill both in species composition as in soil variables, principally due to shallower soil in the former. No strong relation between soil properties and variation in vegetation composition could be detected at a finer scale. The studied grassland, like all grassland vegetation in southern Brazil, is very rich in species compared to other grassland formations worldwide. However, this high biodiversity and conservational value of Campos vegetation so far have not been recognized adequately. Disturbance is essential to maintain this open vegetation type and its species richness. Fire should be considered as a management option in the absence of grazing.

Keywords: Campos, diversity, fire, southern Brazil, species distribution patterns

Resumo

Composição floristica, variação ambiental e distribução das especies em um campo queimado no sul do Brasil. Em um campo regulamente queimado no Morro Santana, Porto Alegre, RS, Brasil, foram investigadas diferenças na composição florística e suas relações com as propriedades do solo, a distância da borda florestal e a exposição do relevo. Em 48 parcelas de 0,75 m^2, foram amostradas 201 espécies identificadas, de um total estimado para o local de aproximadamente 450 a 500 espécies. A maioria das espécies apresentou baixas freqüências e uma distribuição aglomerada na área de estudo. A análise multivariada dos dados indicou que as parcelas adjacentes à borda florestal claramente diferem florística e estruturalmente das parcelas do campo. As parcelas com exposição norte diferiram das do topo do morro, tanto pela composição florística quanto pelas variáveis do solo, principalmente em relação à menor profundidade do solo no norte. Nenhuma relação forte foi detectada entre as propriedades do solo e a variação na composição da comunidade em escala mais fina. A área estudada, assim como a vegetação campestre no sul do Brasil em geral, apresenta-se muito rica em espécies, se comparada a outras formações de campo ou savana no mundo. Apesar disso, a alta biodiversidade e o valor de conservação da vegetação campestre não têm sido reconhecidos. Na ausência do pastejo, o fogo é um imporante fator de manejo para a conservação da vegetação campestre, uma vez que o distúrbio parece ser necessário para manter um tipo de vegetação aberta, com alta riqueza em espécies.

Palavras-chave: Brasil meridional, Campos, distribuição de espécies, diversidade, fogo

Introduction

Grassland vegetation is typical for southern Brazil, despite climatic and edaphic conditions favorable for forest development (Rambo 1956, Pillar 2003). In the region, grasslands were predominant under cooler and drier glacial and warmer and drier postglacial climates, and have been subjected to forest expansion only since about 4000 years BP, when climate became moister and cooler (e.g. Klein 1975, Behling *et al.* 2004). Fire is present since early in the Holocene (Behling *et al.* 2004) and likely occurred even before human occupation (see e.g. Furley 1999 for Cerrado), thus, together with grazing by native or domestic animals, fire is stabilizing grasslands until present times. Since the introduction of cattle by European settlers, grazing has been the predominant land use, with fire used for pasture management (Pillar & Quadros 1997). Brazilian humid subtropical grasslands have received relatively little attention both by science and conservation policies (MMA 2000). Quantitative data on species composition and distribution patterns in relation to environmental variables is scarce. Various studies have characterized the floristic composition (e.g. Buselato & Bueno 1981, Aguiar *et al.* 1986, Boldrini & Miotto 1987), while only few consider relations between vegetation and abiotic or management factors (Girardi-Deiro *et al.* 1992, Pillar *et al.* 1992, Boldrini & Eggers 1996, Boldrini *et al.* 1998). This is alarming, as grasslands composed of native species are rapidly disappearing due to "improvement" with exotic forage species and expansion of crops or tree plantations (Nabinger *et al.* 2000, MMA 2000, Pillar 2003, Bilenca & Miñarro 2004).

The granitic hills in the surroundings of Porto Alegre contain remnants of natural vegetation within the urban area. Unlike the largest part of grasslands in southern Brazil, the grasslands in this region, whose floristic richness has been pointed out by Rambo (1954), in their majority are not being grazed and are under no formal land use. Often, grassland can be found in a heterogeneous mosaic with small forest patches and shrubland. Due to accumulation of senescent biomass, the grasslands are subjected to frequent burns caused by local population, and suffer strong anthropogenic influences, principally expansion of irregular settlements (Adelmann & Zellhuber 2004). Without detailed studies of the present state of the vegetation, it will be impossible to assess value and endangerment of the vegetation. In this paper, we report findings on the floristic composition of a grassland area on Morro Santana, Porto Alegre, RS, exploring relationships between species distribution and abiotic site conditions, and use this to discuss biodiversity and conservational value of South Brazilian Campos vegetation in general. The role of fire in grassland dynamics will be touched upon, but, as it is not the main focus of this study, will be addressed in detail elsewhere (Overbeck *et al.* submitted).

Material and methods

Study area

The study took place on Morro Santana (30°03' S, 51°07' W, max. alt. 311m a.s.l.). The hill is covered by forests (Atlantic forest) predominantly on the southern slopes and by a mosaic of forest

and grassland on the top and with grasslands dominating on the northern slopes (Aguiar *et al.* 1986). Due to ongoing forest expansion processes, isolated patches of woody species can be found throughout the grassland (Müller & Forneck 2004). Climate in the region is Köppen's Cfa, with mean annual temperature from 18° to 20° C and mean precipitation of aprox. 1,400 mm yr^{-1}, without dry season (Nimer 1990). The predominant soil type can be classified as a typical dystrophic red-yellow argisol (Streck *et al.* 2002). The grassland areas are ungrazed and are subject to frequent (average fire interval: 3 years), today mostly anthropogenic, burns, affecting differently sized patches of the grassland every year. Fire history at the study site is poorly known: palaeoecological data (Behling *et al.*, unpubl.) indicate the occurrence of fire during the past 1200 years, but no data from longer back exists.

Methods

Vegetation sampling

In the forest-grassland ecotone, six pairs of transects from the forest edge into the grassland were installed at sites with different aspect (top and northern slope). Four of the transects had been subjected to an experimental burn at the end of October 2002. Transects consisted of seven 4.5m by 4.5m plots used in a study on woody components in the grassland. The grassland composition presented in this work was sampled in three contiguous plots of 0.5m by 0.5m marked permanently in the center of plots 1, 3, 5 and 7 of these transects, 1 being closest, 7 farthest from the forest border. Species composition and cover of soil, litter, mosses and rocks were recorded in January and February of 2003, i.e. two to three months after the burn in some of the transects, using the Londo (1976) decimal scale, i.e. 10% cover steps. Cover data of the three adjacent 0.25m^2 plots were pooled into plots of 1.5 by 0.5m (0.75m^2) for all analyses by taking the average value for each species or structural attribute.

Soil sampling

For each of the 4.5 by 4.5m plots, a mixed soil sample of the first ten centimeters of the soil profile was taken at five points randomly distributed in the plot and analyzed by the Laboratório de Análises de Solo, UFRGS, Porto Alegre, determining the following parameters (following the methodology described in Tedesco *et al.* 1995; units see Tab. II): pH value, share of the clay fraction (clay), content of organic matter (org. mat), available phosphorus (P), available potassium (K), exchangeable aluminium (Al), calcium (Ca) and magnesium (Mg), potential cation exchange capacity (CECpot), potential Al (AlSpot) and base (BsSpot) saturation and potential acidity (Al+H). Depth of soil available for penetration by roots was measured using a Pürkhauer drill, calculating the mean value from two drillings conducted per plot. It was not possible to conduct drillings deeper than one meter.

Data analysis

Following Boldrini & Miotto (1987), we calculated mean cover over all plots (MC$_s$), relative frequency (RF$_s$), relative cover (RC$_s$ = MC$_s$/ Σ MC$_n$) and importance value (IV$_s$ = RC$_s$ + RF$_s$) for all species. To investigate species distribution patterns, we calculated the Jaccard-coefficient S for all plots taken pairwise (Krebs 1998), thus obtaining percentage values for the relative similarity of composition between two plots. Coefficient values were categorized according to distance between plots, i.e., 1) within the same transect, 2) between transects in the same transect pair, 3) between adjacent transect pairs and 4) between distant transect pairs, and compared by analysis of variance with randomization testing (Pillar 2004a).

Compositional patterns were analyzed using species cover and species grouped according to biological forms. For the latter, individual species cover values were summed for each plot according to the following groups: Succulents, grasses, Cyperaceae, bulbous geophytic species (e.g. from Iridaceae, Liliaceae, Amarylidaceae), herbs (excluding Fabaceae), herbs from the Fabaceae, shrubs, lianas, and trees, and joined by cover of structural variables (litter, open soil, rocks, mosses). Species present in less than 10% of the plots involved in the analysis were not considered in analyses of species data. Ordination by Principal Coordinates Analysis (PCoA) was applied to species and biological forms data sets, using chord distance as resemblance measure (Podani 2000). This distance implies normalization of data within sampling units and thus disregards differences in total cover between plots, which may result from fire history. Ordination axes were tested by bootstrap resampling (Pillar 1999).

We tested for the influence of the situation of the plots along the gradient border-grassland, of the location of transects on Morro Santana (aspect), and of the interaction of these factors on species composition by multivariate analysis of variance with randomization testing (Pillar & Orlóci 1996, Pillar 2004a). Further, plots grouped according to their position along transects were compared for each biological form by the same technique in its univariate form. Correspondingly, the soil data set was analyzed separately for each variable, testing for the factors position of plot along the transect and aspect. As soil sampling had been conducted almost one year after the fire experiments, differences in fire history were not considered (Rheinheimer *et al.* 2003). Further, plots were ordinated by PCoA using all variables (based on Euclidean distance after centering and normalization within variables, Podani 2000).

Congruency between environmental and vegetation data was calculated to find out which environmental variables were the most relevant for explaining vegetation composition patterns, following the stepwise procedure presented by Pillar & Orlóci (1993). The algorithm involves the computation of a matrix correlation between plot data dissimilarities based on species composition and dissimilarities of the same plots based on the environmental variables in a stepwise process, giving both the correlation coefficient for those variables that maximize correlation, and total congruence for the set of all variables, similar to a Mantel test.

We used software SYNCSA (Pillar 2004b) for ordination analyses and for ranking environmental variables by congruence, and software MULTIV (Pillar 2004a) for performing bootstrap resampling in ordination and for randomization testing. Randomization tests involved 1000 random permutations and bootstrap resampling 1000 bootstrap samples. A threshold of $\alpha=0.05$ was adopted for rejecting the null hypothesis in randomization tests.

Results

Overall species composition and vegetation structure

In our survey, a total of 232 (morpho-)species was recorded. Of these, eight could not be identified at all, seventeen only to the family and six only to the genus level, resulting in a total of 201 identified species belonging to 136 genera and 49 families (see Appendix for list). Considering only totally identified species, Poaceae (21 genera; 40 species) and Asteraceae (21; 42) had the highest number of genera and families, followed by Leguminosae (14; 16), Rubiaceae (5; 12) and Cyperaceae (5; 9). 28 families were represented with one species only.

Table 1: Mean cover values of species groups and structural attributes for plots with different distance from the forest border on Morro Santana, Porto Alegre, RS, Brazil. Significant differences of the contrast between plot 1 (border plot) and plots 3, 5 and 7 (grassland plots) taken as a group are indicated above each variable (n.s.: not significant, **: p<0.01, ***: p<0.001). Stem succulents are not included, as present in one plot only. Plots 3,, and 7 did not differ significantly for any of the parameters.

Species groups	plot 1 (border)	grassland plot 3	grassland plot 5	grassland plot 7
tree **	4.84	0.11	0.86	0.00
shrubs [ns]	6.28	16.53	11.69	10.97
Lianas ***	15.44	0.39	0.36	0.47
grasses ***	23.39	55.28	48.61	46.42
herbs ***	12.64	28.72	26.86	27.33
Fabaceae [ns]	0.94	2.78	2.61	2.64
Cyperaceae **	0.81	3.19	2.36	2.56
geophytes [ns]	0.47	0.97	0.31	0.58
litter ***	56.61	17.72	15.92	14.28
open soil **	3.50	22.44	23.67	24.19
rocks [ns]	0.00	1.67	6.22	6.06
mosses [ns]	0.11	0.25	0.00	0.08

Even though explanatory power of PCoA axes using species data of all plots was low (13.8%, 11.0% and 9.0% for axes 1, 2 and 3, respectively; diagram not shown), the plots close to the forest-grassland border were clearly separated from the grassland plots which did not show any grouping according to distance from the border (see Tab. 1). Using species groups and structural data for the ordination, this separation became a lot more obvious: explanation of the axes now amounted to 46.7%, 20.7% and 14.0%, for axis 1, 2 and 3, respectively, with border plots clearly separated along the first ordination axis (Fig. 1A). Due to these differences in composition and structure between

border and grassland plots, we separated grassland plots (i.e. plots 3, 5, 7) and border plots (plot 1) for further analysis and description, focusing on the grassland plots in this presentation.

Grassland plots: species composition and distribution

In the grassland itself, 198 (morpho-)species were found. Of these, 170 species, belonging to 114 genera and 38 families, were identified (see Appendix 1). In average, 18.6 species (range: 4 to 33) were found for each grassland plot of $0.25m^2$, and 33.9 (range: 19 to 48) for each pooled plot of $0.75m^2$. The species area curve (Fig. 2A) indicates that stability was not reached for evaluating species richness, as it is rising constantly over its second half.
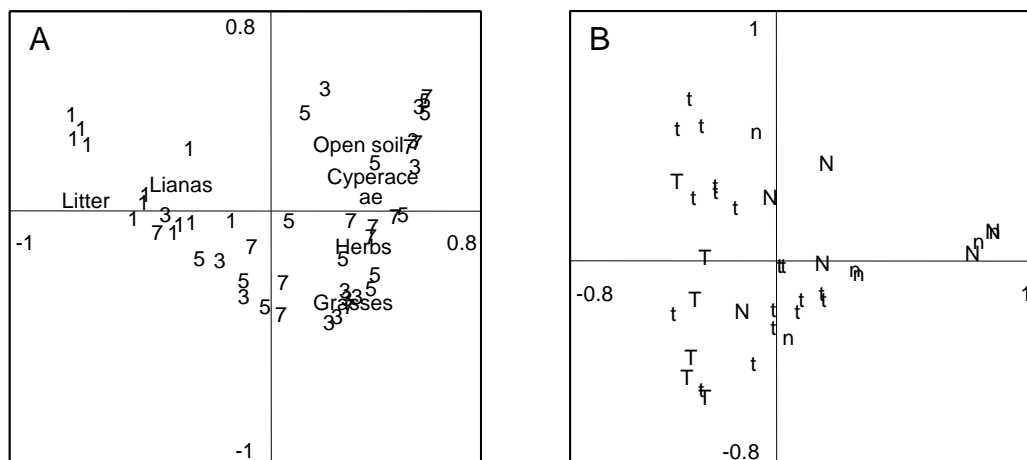
Figure 1: Ordination diagrams (PCoA; chord distance as resemblance measure) of grassland vegetation on Morro Santana, RS, Brazil. A) All plots (n=48), based on cover of species groups and structural variables. Plots are labelled according to the distance from the forest border (1: border plots, 3, 5, 7: grassland plots with increasing distance from the forest border). Position of original descriptors (see text for details) is shown when correlation to at least one of the ordination axes was greater than 0.4. For clarity of the diagram, symbols are omitted and labels centered on the coordinate values. Explanatory power of ordination axes: 46.7%, 20.7% and 14.0% for axes 1, 2 and 3 (not shown), respectively. Axes were not stable to bootstrap sampling. B) Plots of the open grassland (n=36), using species data. Plots are labelled according to aspect (t=top, n=northern slope). Capital letters indicate plots burned three months before the survey. Explanatory power of ordination axes was 15.8%, 11.9% and 10.2% for axes 1, 2 and 3 (not shown), respectively. Axes were not stable to bootstrap sampling

Even in burned areas, caespitose grasses clearly dominated the studied grassland. Among the ten most dominant species, accounting for 41.4% of total species cover, seven were grasses, and among the 30 most dominant species, already accounting for 71.2% of total species cover, 16 were grasses (note that total species cover is the cumulative value of single species' relative cover values, i.e. total cover of all species will exceed vegetation cover). The most dominant grass species were *Elionurus muticus*, *Aristida flaccida*, *Aristida laevis*, *Andropogon lateralis* and *Leptochoryphium lanatum*. All shrub species together accounted for 14.4% of total species cover, the most dominant being *Baccharis patens*, *B. cognata*, *Vernonia nudiflora*, *Heterothalamus psiadioides* and *Croton* cf. *nitrariaefolius*. Among forb species, the rosette species *Eryngium pristis* and *E. horridum* showed the highest cover and importance values, followed by *Vernonia flexuosa*, *Aspilia montevidensis*, *Pfaffia tuberosa*, *Pterocaulon rugosum* and *Eryngium sanguisorba*. The largest part of the species had very

low RC_s and IV_s values, with 128 species showing RC_s values of only 0.25% or less, and 107 species a IV_s value below 0.50 (Appendix 1). While total cover of plants was lower in recently burned plots, dominance relations did not differ substantially when compared to unburned plots (see also below; compare Fig. 1B).

Species composition over the total area was very heterogeneous. Only one species – *Rhynchospora globularis* – occurred in more than 75% of the plots and only five more (*V. nudiflora*, *V. flexuosa*, *Evolvulus sericeus*, *P. tuberosa* and *E. muticus*) in more than 60% of all plots. More than 50% of the species occurred in less than 10% of the plots (Fig. 2B), 59 species only in one plot. When looking at species frequency independent of cover values, grass species were of less relevance: of the 30 most frequent species, only six were grasses (see Appendix 1). Some herbaceous species, especially small perennial herbs such as *E. sericeus*, *Chaptalia runcinata*, *Lucilia acutifolia*, *Hydrocotyle exigua*, *Euphorbia selloi* or *Relbunium hirtum*, showed high frequency values, just like a number of shrub species (*V. nudiflora*, *C.* cf. *nitrariaefolius*, *Porophyllum lanceolatum*, *B. cognata*, *Eupatorium ligulaefolium*).
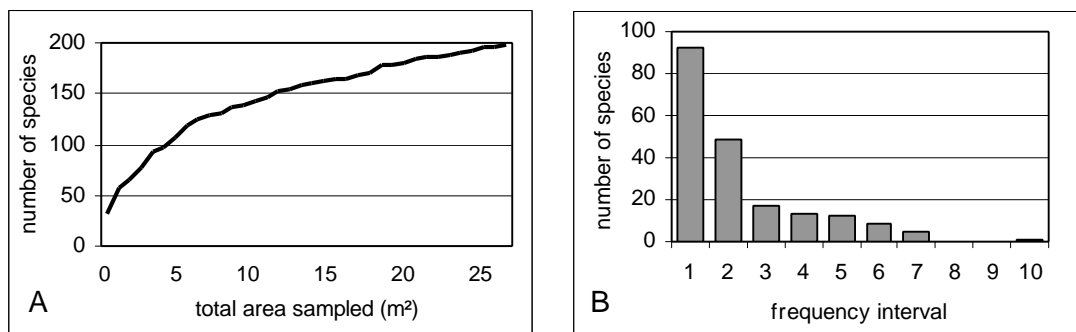
Figure 2: Heterogeneity of grassland vegetation, based on data from 36 grassland plots (0.75m^2) on Morro Santana, Porto Alegre, RS, Brazil. A) Species area curve. B) Frequency histogram of grassland species. Species grouped into 10% frequency intervals (1: >0 ≤10, 2: >10 ≤20, 3: >20 ≤30, 4: >30 ≤40, 5: >40 ≤50, 6: >50 ≤60, 7: >60 ≤70, 8: >70 ≤80, 9: >80 ≤90, 10: >90 <100).

Species distribution generally was patchy, and most species were not widely distributed in the study area. The comparison of joint species in any pair of plots by help of the Jaccard-coefficient showed that plots within the same transect shared more species (31.5%) than plots in paired transects of the same transect pair (26.4%), plots in adjacent transect pairs (21.6%), and plots in distant transect pairs (18.0%; differences always significant).

When ordinating grassland plots using species data, explanatory power of the axes was low (15.8%, 11.9%, 10.2% for axes 1,2 and 3, resp.; Fig. 1B), however, clearly separating plots on the top and on the northern side of Morro Santana. Apart from this, plots were mostly kept together according to geographical vicinity: plots from one transect pair usually were packed quite closely in the ordination space, albeit overlapping with other transect pairs. No relation could be detected considering situation of grassland plots on the gradient from the forest border. Distribution of plots did

not reflect the burns conducted in part of the plots three months before: burned and unburned plots were mixed throughout the ordination space.

Border plots: species composition and structural attributes

Concerning species composition in the border plots, we did not reach sampling sufficiency, especially when considering that 67 of the 125 species found occurred only in one plot each, even though – as in the grassland plots – a large proportion of herbaceous species most likely would show a very sparse distribution in the border plots as well. We therefore will only give a brief description of species groups, structural variables and the most dominant species sampled in the border plots (see also Appendix 2). 34 species were found exclusively in the border plots, some of them, however, species known from the literature as grassland species, supposedly not found there due to patchy distribution patterns. With a mean value of 57%, border plots – where generally no burns occur due to lack of continuous flammable biomass – showed significantly and substantially higher values for litter than grassland plots. Lianas and trees had significantly higher cover values, whereas cover of herbs, grasses, Fabaceae and Cyperaceae generally was a lot and partially significantly lower, just like values for open soil (Tab. 1, Fig. 1). *Calea serrata*, *Dioscorea multiflora* (lianas), *Calamagrostis viridiflavescens*, *Oplismenus hirtellus*, *Panicum ovuliferum* (grasses), *Diodia cymosa*, *Peperomia pereskiaefolia* (herbs), *Dodonaea viscosa*, *Psychotria carthagenensis* (shrubs), *Myrsine coriacea* (tree) and *Rumohra adiantiformis* (herbaceous fern) were frequent species found exclusively at the border. In total, seven tree, six shrub and six liana species were found only in border plots (see Appendix 2). In average, border plots were less rich in species than grassland plots: 10.4 species could be found for plots of $0.25m^2$, and 21.8 species (range: 9 to 32) for pooled plots of $0.75m^2$.

Explanatory variables

Multivariate analysis of variance of the species data revealed that plots situated at the forest-grassland border (plot 1) differed significantly from plots 3, 5 and 7, thus confirming the trends shown in Fig. 1A. Plots from the northern side of the hill differed from those on the top; the interaction between the factors distance from border and aspect was not significant.

Along the gradient from grassland into forest, the soil tended to get deeper closer to the forest edge, even though differences were not significant. pH values were lowest in plots closer to the forest border, albeit differing significantly between 1 and 3 and 1 and 5 only, just like Al and Al+H, which showed higher values in the border plots. CECpot at the border was significantly higher than in plots 3 and 5, but not plots 7. None of the other factors analyzed differed significantly in respect to distance to the forest border (Tab. 2A). Differences in soil properties between plots on the top and the northern slope of the hill were much more pronounced, differing significantly for almost all parameters (Tab. 2B). Soils on the northern slope were shallower, had higher pH values, higher contents of Mg, K, Ca and higher CECpot and BsSpot. Clay and Al content and AlSpot were higher in soils on the top.

Concordingly, PCoA of plots using soil data revealed a clear separation of northern slope and top along the first axis (explanation: 64.3%, 12.5%, 8.5%, for axis 1, 2, and 3, resp.; graph not shown).

Table 2: Mean values of soil properties in grassland plots on Morro Santana, Porto Alegre, RS, Brazil. A) Plots with different distance from the forest border (1: border; 3, 5, 7: grassland). B) Plots with different location in the study area (top and northern slope). Analyses A and B were conducted separately, with random permutations restricted within transect pairs in A. Values followed by identical letters did not significantly differ within A or B (p<0.05).

soil properties	A plot 1		plot 3		plot 5		plot 7		B top		north	
depth (cm)	81.1	a	75.3	a	72.1	a	66.4	a	90.7	a	39.8	b
org. mat. (%)	4.6	a	4.6	a	4.5	a	4.9	a	4.7	a	4.7	a
clay (%)	35.6	a	36.3	a	35.9	a	38.8	a	40.3	a	29.3	b
pH	4.8	a	5.1	b	5.0	b	5.0	ab	4.9	a	5.2	b
Al (cmol$_C$ L^{-1})	2.4	a	1.5	b	1.8	b	1.9	ab	2.3	a	1.1	b
Ca (cmol$_C$ L^{-1})	2.4	a	2.7	a	2.3	a	2.7	a	2.2	a	3.2	b
K (cmol$_C$ L^{-1})	145.8	a	162.8	a	174.3	a	178.2	a	155.1	a	185.5	b
Mg (cmol$_C$ L^{-1})	1.2	a	1.3	a	1.2	a	1.3	a	1.2	a	1.4	b
P (cmol$_C$ L^{-1})	2.2	a	2.0	a	1.9	a	2.0	a	2.1	a	1.9	a
Al+H (cmol$_C$ cm^{-3})	8.8	a	7.0	b	7.1	b	7.9	ab	8.8	a	5.6	b
CECpot (cmol$_C$ L^{-1})	12.8	a	11.5	bc	11.1	b	12.4	ac	12.6	a	10.7	b
AlSpot (% of CECpot)	17.3	a	12.9	a	14.9	a	15.2	a	17.9	a	9.4	b
BsSpot (% of CECpot)	32.7	a	40.3	a	36.6	a	37.2	a	30.8	a	48.3	b

Congruence of vegetation and environmental data

Total congruence with environmental data (soil parameters and aspect) was 0.19 for the full data set. Maximum congruency was reached with the variables aspect, pH, content of clay, depth, and content of P (congruence coefficient: 0.30). Concerning only the grassland plots, congruence between vegetation data and the full environmental data set (soil variables and aspect) reached a value of 0.29. Here, maximum congruence was reached with aspect, content of clay, aluminium content, depth, and content of organic material, giving a correlation coefficient of 0.43. Aspect alone led to a congruence coefficient of 0.36 for grassland plots, and 0.21 when using all plots.

Discussion and conclusions

The vegetation matrix of the studied grassland is formed by caespitose grasses, only three of which (*E. muticus*, *A. flaccida*, *A. laevis*) occur in more than 50% of the plots. Interstitial gaps between the grass tussocks are being populated by grassland shrubs and by a large number of herbaceous species, in their majority only sparsely distributed in the area and thus primarily contributing to the high diversity. The grassland vegetation on Morro Santana includes some relatively rare species: the Asteraceae *Schlechtendalia luzulaefolia*, possibly endemic for the granitic hills near Porto Alegre, *Moritzia ciliata* (Boraginaceae), endemic for Rio Grande do Sul, *Butia capitata* (Arecaceae), *Waltheria douradinha* (Sterculiaceae) and *Parodia ottonis* (Cactaceae), all listed in the red data book for Rio Grande do Sul (IBAMA 2004). No exotic species were sampled in our study.

A study by Aguiar *et al.* (1986), mentioning 867 forest and grassland species for the granitic hills of the Porto Alegre region, gives an additional 140 grassland species and 20 species of the forest border for Morro Santana that had not been found in our study. The species list given by Mohr (unpubl.) for his study on Morro Santana contains another 24 species. Outside the plots, we collected an additional 15 species and found 30 more species in an evaluation of the soil seed bank of the grasslands on Morro Santana (unpubl.). Together with the data presented, this adds up to 430 completely identified species in a grassland area of approx. 220 ha. Considering that all surveys present a large number of not completely identified species, we estimate total species number to be between 450 and 500. Thus, grassland vegetation on Morro Santana can be considered very species-rich compared to other vegetation types in the region, or to other grassland ecosystems worldwide. Total species number in grasslands in the Porto Alegre region in general is more than twice as high than that of forests (Aguiar *et al.* 1996). Walker (2001) mentions the presence of 80 to 100 vascular species per ha in South African savannas, and of 300 to 330 species for Brazilian Cerrado. Filgueiras *et al.* (1998) evaluated species composition of six different Cerrado areas in Central Brazil and found species numbers between 52 and 121 for the herbaceous layer (area sampled $50m^2$ for each area). Numbers from Morro Santana seem to lie at least in the same range as in these studies. Small-scale richness on Morro Santana was higher that that cited for Cerrado in Filgueiras (2002), where eight to 28 species were found per $1m^2$, and similar to that of species-rich limestone meadows in Sweden, where van der Maarel & Sykes (1993) found maxima of around 33 species per $0.25m^2$. Clearly, comparison of species numbers between surveys is problematic due to different sampling methods, different homogeneity of the vegetation and size of studied area. Nonetheless, the data presented here indicates high species richness in comparison with other grasslands. Total number of grassland species in southern Brazil has been estimated to be around 3,000 (Boldrini 2002), thus lower than the one proposed for the Cerrado region (6,000 vascular species) by Furley (1999). However, it has to be remembered that Cerrado *sensu latu* comprises other physiognomic vegetation types besides campo sujo and campo limpo, the equivalent to grassland vegetation in southern Brazil, and shows a very diverse woody component that is lacking in Campos grassland. Furthermore, Cerrado (total area 2 million km^2) covers a much larger area than South Brazilian Campos, therefore also including higher variability in climatic and edaphic conditions (Furley 1999) than the comparatively uniform Campos region (MMA 2000). This emphasizes species richness of the Campos vegetation as a whole and indicates that the South Brazilian humid subtropical grassland biome should be considered as biodiversity hotspot, as, for example, the Cerrado or the Mata Atlântica region (Myers *et al.* 2000). The necessity exists to conduct vegetation sampling with comparable methods in the whole region to obtain interpretable information on species distribution patterns and diversity on a larger scale and to be able to compare Campos vegetation of southern Brazil to the Pampas in Argentina and Uruguay and to Cerrado vegetation in central Brasil.

When comparing species composition of the (ungrazed) grassland studied in our study to that of other grasslands in Rio Grande do Sul, it becomes obvious that rhizomateous or stoloniferous grasses favored by cattle grazing, e.g. *Axonopus affinis*, *Paspalum notatum* or *P. paucifolium*, often forming a dense carpet in the lower strata of grazed grasslands (e.g., Boldrini & Miotto 1987), were of low importance on Morro Santana, both concerning total cover and species number. Concordingly, Boldrini & Eggers (1996) stated a shift from rhizomateous and stoloniferous species to high tussock grasses in the absence of grazing. The strong presence of the woody component in our study when compared to grazed grassland (e.g., Boldrini 1993) indicates that these species may be less tolerant to grazing than to fire, and that diversity of growth forms may be higher in grasslands in close contact with forest, as is the case on Morro Santana, where grasslands are subject to invasion of woody species (Müller & Forneck 2004). In our study, plots situated close to the forest border showed a marked structural and compositional difference, caused by lower light availability and the pronounced litter layer. The number of herbaceous species adapted to these conditions, e.g. *Oplismenus hirtellus* or *Peperomia pereskiaefolia*, seems to be much lower, just as the herbaceous strata in subtropical forests only comprise relatively few species (Müller & Waechter 2001). Plots situated 10m from the forest border, on the other hand, could clearly be considered as grassland plots, not differing from plots farther in the grassland. This indicates that the transitional zone between forest and grassland is very abrupt, most likely due to the frequent burns that burn all the grassland but stop at the border due to lack of flammable biomass. The forests themselves are too moist to burn (Pillar & Quadros 1997). Despite the abrupt border between forest and grassland, the proximity of forest does increase species number and structural heterogeneity in the grassland due to establishment of forest pioneer species and the presence of small shrubland patches, considered to be *nuclei* of forest expansion (Müller & Forneck 2004). Ecotones like the forest-grassland mosaic on Morro Santana show complex interactions between vegetation types and abiotic factors, such as soil properties or aspect, and fire regime. Even though young individuals of forest species may not survive all fires and shrubland patches may not be stable under the present disturbance regime as well, they contribute to spatial and temporal heterogeneity, affecting species diversity and vegetation structure (Hopkins 1992). This emphasizes that one vegetation type cannot be considered isolated from its surroundings and underlines the high biodiversity of vegetation mosaics, such as in the Porto Alegre region.

In our study, correlations of compositional data and environmental data seemed to indicate a rather strong influence principally of aspect on species composition. Boldrini *et al.* (1998) linked differences between vegetation composition on southern and northern slopes on Morro de Polícia, Porto Alegre, to higher solar radiation causing drier conditions on the northern slope. Focht & Pillar (2003) found that soil moisture related to topographic position was the most important factor explaining species composition in grazed grassland. While we did not have such a pronounced topographic gradient, nonetheless nearly all soil factors analyzed differed significantly between the top and the northern slope of the hill, which will be drier due to lower depth, slope and aspect. Thus,

grassland in these areas may burn more frequently and intensively and therefore suffer stronger erosion processes, with principally the latter changing soil properties. This may of course influence species composition on the long run. However, the pronounced presence of some species at only one side of the hill or in only some of the transects, as indicated by the separation of plots on the top and on the northern slope in the ordination diagram (Fig. 1B), may simply be a consequence of the heterogeneous species distribution revealed by our study; the low explanation of the ordination axes supports this hypothesis. According to Grubb (1986), most species in very species-rich communities are likely to have sparsely distribution and, "consistently low populations" (Rabinowitz 1981, cited in Grubb 1986). In our case, few species were distributed throughout the entire study area. We suppose that the lack of stabilization of the species-area-curve does not stem from sampling insufficiency, but from the high proportion of rare species – the curve will never stabilize in such a species-rich system. Vegetation structure, at least when only considering the grassland matrix, was relatively homogeneous throughout the grasslands, but compositional differences increased with distance between plots compared. This clumped distribution of species makes causal explanations concerning the role of environmental factors much more difficult. Differences in composition might be related to abiotic factors, but also to dispersal limitation over space (Tilman 1997, Turnbull *et al.* 2000) or stochastic fluctuation processes, which are thought to be of special importance in grasslands, where patch structure is not necessarily correlated with species composition (Glenn & Collins 1993).

The studied grassland is subjected to frequent anthropogenic burns. Fire is an important factor in many grassland systems (e.g. Vogl 1974, Bond & Wilgen 1996), and its central role in maintaining open, i.e. non-forest, vegetation under climatic conditions favorable for forest development is generally accepted (e.g. Sauer 1950, Vogl 1974, Hobbs & Huenneke 1992). The few studies conducted so far on the influence of fire on vegetation of grasslands in southern Brazil have shown that grassland vegetation most likely will recover quickly to its pre-burn state concerning species composition and cover, as the majority of species resprouts shortly after the fire (Eggers & Porto 1994, Quadros & Pillar 2001). While this remains to be studied in detail for our study area, we do suppose that the high fire frequency at least partially explains the high species richness found, as disturbance generally is considered to enhance species diversity in grassland communities (e.g. Denslow 1985). This is principally due to decreased competitive interactions of dominant species, which would become more important in the absence of disturbance, leading to loss of weaker competitors (e.g. Crawley 1997), and to increased possibilities for seedling recruitment in the post-fire environment. At any rate, regular disturbances such as fire and grazing seem to be the key-factors necessary for the maintenance of grassland vegetation under the present climatic conditions (Pillar & Quadros 1997), and thus for preservation of biodiversity in the region. Considering the fast conversion of South Brazilian natural grassland into *Pinus* plantations, principally in the north-eastern Planalto region of Rio Grande do Sul, and into agricultural production area in large parts of the Campos region, research on biodiversity and conservation value of grasslands in southern Brazil and subsequent

implementation of conservation measures are clearly necessary in order to impede irreversible losses in an extremely species-rich biome.

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Appendix 1: Family, species name, biological form (see text), absolute frequency (F_s), relative frequency (RF_s), relative cover (RC_s) and importance value (IV_s) of the species in plots of the open grassland (n=36) of 0.75m^2 on Morro Santana, Porto Alegre, RS, Brazil. For grasses, basal architecture is indicated (c: caespitose, s: stoloniferous, r: rhizomateous, cr: caespitose or rhizomateous). Nomenclature follows IPNI (2004).

Family	Species	Biol. form	F_s	RF_s	RC_s	IV_s
Amaranthaceae	*Pfaffia tuberosa* (Moq. ex DC.) Hicken	herb	61%	1.80%	0.84%	2.65%
Amaryllidaceae	*Habranthus gracilifolius* Herb.	geophyte	11%	0.33%	0.05%	0.38%
Anacardiaceae	*Schinus weinmanniaefolius* Engl.	shrub	11%	0.33%	0.65%	0.98%
Apiaceae	*Eryngium ciliatum* Cham. & Schlecht.	herb	8%	0.25%	0.07%	0.31%
	Eryngium elegans Cham. & Schlecht.	herb	3%	0.08%	0.09%	0.18%
	Eryngium horridum Malme	herb	50%	1.48%	3.10%	4.58%
	Eryngium pristis Cham. & Schlecht.	herb	17%	0.49%	4.72%	5.21%
	Eryngium sanguisorba Cham. & Schlecht.	herb	44%	1.31%	0.87%	2.18%
	Hydrocotyle exigua (Urb.) Malme	herb	50%	1.48%	0.52%	2.00%
Asteraceae	*Acmella bellidioides* (Sm.) R.K.Jansen	herb	17%	0.49%	0.37%	0.86%
	Achyrocline satureioides Gard.	herb	25%	0.74%	0.26%	0.99%
	Aspilia montevidensis (Spreng.) Kuntze	herb	53%	1.56%	1.32%	2.88%
	Baccharis articulata Pers.	shrub	3%	0.08%	0.04%	0.12%
	Baccharis cognata DC.	shrub	53%	1.56%	2.65%	4.20%
	Baccharis dracunculifolia DC.	shrub	8%	0.25%	0.21%	0.45%
	Baccharis leucopappa DC.	shrub	28%	0.82%	0.24%	1.06%
	Baccharis ochracea Spreng.	shrub	6%	0.16%	0.30%	0.47%
	Baccharis patens Baker	shrub	14%	0.41%	2.68%	3.09%
	Baccharis sessiliflora Vahl	shrub	25%	0.74%	0.52%	1.26%
	Baccharis trimera (Less.) DC.	shrub	22%	0.66%	0.26%	0.91%
	Calea uniflora Krasch.	herb	3%	0.08%	0.01%	0.09%
	Chaptalia integerrima (Vell.) Burkart	herb	19%	0.57%	0.17%	0.74%
	Chaptalia runcinata Kunth	herb	56%	1.64%	0.83%	2.48%
	Chaptalia sinuata Baker	herb	25%	0.74%	0.31%	1.05%
	Conyza bonariensis (L.) Cronquist	herb	3%	0.08%	0.01%	0.09%
	Conyza chilensis Spreng.	herb	6%	0.16%	0.04%	0.20%
	Eupatorium ascendens Sch.Bip. ex Baker	herb	6%	0.16%	0.04%	0.20%
	Eupatorium ivaefolium L.	herb	33%	0.98%	0.47%	1.46%
	Eupatorium lanigerum Hook. & Arn.	herb	3%	0.08%	0.02%	0.10%
	Eupatorium ligulaefolium Hook. & Arn.	shrub	50%	1.48%	0.93%	2.41%
	Eupatorium tweedianum Hook. & Arn.	herb	6%	0.16%	0.11%	0.28%
	Heterothalamus psiadioides Less.	shrub	33%	0.98%	1.23%	2.22%
	Hieracium commersonii Monnier	herb	11%	0.33%	0.13%	0.46%
	Hypochoeris sp.	herb	3%	0.08%	0.04%	0.12%
	Lucilia acutifolia Cass.	herb	56%	1.64%	0.50%	2.14%
	Lucilia nitens Less.	herb	14%	0.41%	0.17%	0.58%
	Noticastrum gnaphalioides (Baker) Cuatrec.	herb	8%	0.25%	0.12%	0.37%
	Orthopappus angustifolius Gleason	herb	31%	0.90%	0.46%	1.37%
	Porophyllum lanceolatum DC.	shrub	56%	1.64%	0.37%	2.01%
	Pterocaulon alopecuroideum DC.	herb	3%	0.08%	0.08%	0.16%
	Pterocaulon rugosum Malme	herb	44%	1.31%	0.89%	2.20%
	Senecio heterotrichius DC.	herb	14%	0.41%	0.10%	0.51%
	Stenachaenium riedelii Baker	herb	6%	0.16%	0.09%	0.26%
	Stevia aristata D.Don ex Hook. & Arn.	herb	8%	0.25%	0.07%	0.31%
	Stevia cinerascens Sch.Bip. ex Baker	herb	31%	0.90%	0.68%	1.59%
	Verbesina subcordata DC.	shrub	8%	0.25%	0.12%	0.37%
	Vernonia flexuosa Sims	herb	67%	1.97%	1.47%	3.44%
	Vernonia nudiflora Less.	shrub	69%	2.05%	1.30%	3.35%
	Viguiera anchusaefolia (DC.) Bak.	herb	6%	0.16%	0.08%	0.24%

(continued)

Family	Species	Biol. form	F_s	RF_s	RC_s	IV_s
Asteraceae	Asteraceae 1	herb	3%	0.08%	0.02%	0.10%
	Asteraceae 2	herb	3%	0.08%	0.01%	0.09%
Bromeliaceae	*Dyckia leptostachya* Baker	herb	3%	0.08%	0.57%	0.65%
Cactaceae	*Parodia ottonis* (Lehm.) N.P.Taylor	cactus	3%	0.08%	0.11%	0.20%
Campanulaceae	*Wahlenbergia linarioides* DC.	herb	3%	0.08%	0.01%	0.09%
Cistaceae	*Halimium brasiliense* Gross.	herb	17%	0.49%	0.10%	0.60%
Commelinaceae	*Commelina erecta* L.	geophyte	14%	0.41%	0.09%	0.50%
Convolvulaceae	*Convolvulus crenatus* Vahl	liana	3%	0.08%	0.09%	0.18%
	Dichondra sericea Sw.	liana	22%	0.66%	0.16%	0.82%
	Evolvulus sericeus Sw.	herb	64%	1.89%	0.56%	2.45%
Cyperaceae	*Bulbostylis closii* Barros	Cyp.	11%	0.33%	0.08%	0.40%
	Bulbostylis juncoides (Vahl) Kük. ex Osten	Cyp.	42%	1.23%	0.29%	1.52%
	Bulbostylis sphaerocephalus C.B.Clarke	Cyp.	11%	0.33%	0.18%	0.51%
	Bulbostylis sp.	Cyp.	11%	0.33%	0.09%	0.41%
	Carex phalaroides Kunth	Cyp.	6%	0.16%	0.03%	0.19%
	Cyperus aggregatus Endl.	Cyp.	14%	0.41%	0.08%	0.49%
	Cyperus lanceolatus Poir.	Cyp.	6%	0.16%	0.03%	0.19%
	Rhynchospora globularis Small	Cyp.	92%	2.71%	1.58%	4.29%
	Rhynchospora setigera Boeck	Cyp.	19%	0.57%	0.09%	0.67%
	Scleria sellowiana Kunth	Cyp.	36%	1.07%	0.28%	1.35%
	Scleria sp.	Cyp.	3%	0.08%	0.02%	0.10%
	Cyperaceae 1	Cyp.	3%	0.08%	0.02%	0.10%
Ebenaceae	*Diospyros inconstans* Jacq.	tree	3%	0.08%	0.01%	0.09%
Erythroxylaceae	*Erythroxylum argentinum* O.E. Schulz	tree	3%	0.08%	0.02%	0.10%
Euphorbiaceae	*Croton* cf. *nitrariaefolium* Baill.	shrub	56%	1.64%	1.07%	2.71%
	Croton thermarum Müll.Arg.	shrub	11%	0.33%	0.17%	0.50%
	Euphorbia selloi (Klotzsch & Garcke) Boiss. in DC.	herb	44%	1.31%	0.30%	1.62%
	Tragia emrichii Herter	herb	3%	0.08%	0.02%	0.10%
	Euphorbiaceae 1	herb	3%	0.08%	0.02%	0.10%
	Euphrobiaceae 2	herb	3%	0.08%	0.01%	0.09%
Fabaceae	*Aeschynomene elegans* Cham. & Schlecht.	herb	22%	0.66%	0.17%	0.83%
	Centrosema virginianum Benth.	herb	17%	0.49%	0.29%	0.79%
	Chamaecrista nictitans Moench	shrub	8%	0.25%	0.19%	0.44%
	Clitoria nana Benth.	herb	33%	0.98%	0.31%	1.30%
	Collaea stenophylla Benth.	shrub	3%	0.08%	0.32%	0.40%
	Crotalaria tweediana Benth.	herb	11%	0.33%	0.08%	0.40%
	Desmanthus tatuhyensis Hoehne	shrub	50%	1.48%	0.46%	1.94%
	Desmodium affine Schltdl.	herb	3%	0.08%	0.06%	0.14%
	Desmodium incanum DC.	herb	8%	0.25%	0.20%	0.45%
	Galactia gracillima Benth.	liana	6%	0.16%	0.02%	0.18%
	Galactia marginalis Benth.	herb	25%	0.74%	0.23%	0.97%
	Macroptilium prostratum Urb.	herb	25%	0.74%	0.25%	0.98%
	Mimosa parvipinna Benth. in Hook	shrub	3%	0.08%	0.03%	0.11%
	Rhynchosia diversifolia Micheli	herb	11%	0.33%	0.09%	0.42%
	Stylosanthes montevidensis Vogel	herb	14%	0.41%	0.11%	0.52%
	Zornia sericea Moric.	herb	6%	0.16%	0.04%	0.20%
Iridaceae	*Cypella coelestis* (Lehm.) Diels	geophyte	11%	0.33%	0.05%	0.38%
	Herbertia pulchella Sweet	geophyte	6%	0.16%	0.05%	0.21%
	Sisyrinchium macrocephalum Graham	herb	17%	0.49%	0.17%	0.66%
Iridaceae	*Sisyrinchium scariosum* I.M.Johnst.	herb	11%	0.33%	0.05%	0.38%
	Sisyrinchium vaginatum Spreng.	herb	14%	0.41%	0.19%	0.60%
Lamiaceae	*Glechon squarrosa* Benth.	herb	17%	0.49%	0.30%	0.80%
	Hyptis stricta Benth.	herb	3%	0.08%	0.04%	0.12%

(continued)

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Family	Species	Biol. form	F_s	RF_s	RC_s	IV_s
Lamiaceae	*Salvia procurrens* Benth.	herb	11%	0.33%	2.58%	2.91%
Linaceae	*Cliococca selaginoides* (Lam.) C.M.Rogers & Mild.	herb	3%	0.08%	0.02%	0.10%
Lythraceae	*Cuphea glutinosa* Cham. & Schlecht.	herb	6%	0.16%	0.03%	0.19%
Malpighiaceae	*Janusia* cf. *guaranitica* A.Juss.	liana	3%	0.08%	0.02%	0.10%
Malvaceae	*Krapovickasia urticifolia* (A. St.-Hil.) Fryxell	herb	3%	0.08%	0.04%	0.12%
	Pavonia hastata Cav.	herb	11%	0.33%	0.10%	0.43%
	Sida rhombifolia L.	herb	6%	0.16%	0.06%	0.22%
	Wissadula glechomatifolia R.E.Fr.	herb	17%	0.49%	0.31%	0.81%
Melastomatacea	*Tibouchina gracilis* (Bonpl.) Cogn.	herb	42%	1.23%	0.83%	2.06%
Myrsinaceae	*Myrsine umbellata* Mart.	tree	6%	0.16%	0.04%	0.20%
Myrtaceae	*Campomanesia aurea* O.Berg	shrub	3%	0.08%	0.04%	0.12%
	Myrcia palustris DC.	tree	3%	0.08%	0.23%	0.31%
Orchidaceae	*Stenorrhynchus arechavaletsmii* Barb.Rodr.	herb	3%	0.08%	0.02%	0.10%
Oxalidaceae	*Oxalis brasiliensis* Lodd.	herb	11%	0.33%	0.07%	0.39%
	Oxalis conorrhiza Jacq.	herb	19%	0.57%	0.11%	0.69%
Poaceae	*Andropogon lateralis* Nees	grass (c)	33%	0.98%	3.65%	4.64%
	Andropogon leucostachyus H. B. & K.	grass (c)	25%	0.74%	1.52%	2.26%
	Andropogon selloanus (Hack.) Hack.	grass (c)	31%	0.90%	1.06%	1.96%
	Andropogon ternatus Nees	grass (c)	6%	0.16%	0.22%	0.38%
	Aristida circinalis Lindm.	grass (c)	17%	0.49%	1.95%	2.45%
	Aristida condylifolia Caro	grass (c)	6%	0.16%	0.06%	0.22%
	Aristida filifolia (Arechav.) Herter	grass (c)	25%	0.74%	1.50%	2.24%
	Aristida flaccida Trin. & Rupr.	grass (c)	58%	1.72%	5.75%	7.47%
	Aristida laevis Kunth	grass (c)	58%	1.72%	4.35%	6.08%
	Aristida venustula Arechav.	grass (c)	6%	0.16%	0.02%	0.18%
	Axonopus argentinus Parodi	grass (s)	17%	0.49%	0.52%	1.01%
	Axonopus suffultus (Mikan ex Trin.) Parodi	grass (c)	17%	0.49%	1.92%	2.41%
	Axponopus sp.	grass (s)	33%	0.98%	2.11%	3.10%
	Briza calotheca (Trin.) Hack	grass (c)	3%	0.08%	0.02%	0.10%
	Briza subaristata Lam.	grass (c)	17%	0.49%	0.13%	0.62%
	Briza uniolae Nees ex Steud.	grass (c)	17%	0.49%	0.18%	0.67%
	Briza sp.	grass (c)	11%	0.33%	0.06%	0.39%
	Danthonia montevidensis Hackel & Arech.	grass (c)	28%	0.82%	0.86%	1.68%
	Danthonia secundiflora J.Presl & C.Presl	grass (c)	3%	0.08%	0.04%	0.12%
	Dichanthelium sabulorum (Lam.) Gould & C.A.Clark	grass (r)	56%	1.64%	1.00%	2.64%
	Elionurus muticus (Spreng.) Kuntze	grass (c)	61%	1.80%	7.60%	9.41%
	Eragrostis polytricha Nees	grass (c)	17%	0.49%	0.21%	0.70%
	Leptocoryphium lanatum Nees	grass (c)	33%	0.98%	3.56%	4.54%
	Melica brasiliana Ard.	grass (r)	3%	0.08%	0.02%	0.10%
	Panicum peladoense Henrard	grass (c)	6%	0.16%	0.02%	0.18%
	Paspalum plicatulum Michx.	grass (c)	25%	0.74%	0.35%	1.09%
	Piptochaetium montevidense (Spreng.) Parodi	grass (c)	42%	1.23%	1.17%	2.40%
	Saccharum alopecuroides (L.) Nutt.	grass (c)	8%	0.25%	0.57%	0.82%
	Schizachyrium microstachyum (Ham.) Roseng., B.R.Arill. & Izag.	grass (c)	28%	0.82%	1.14%	1.96%
	Schizachyrium spicatum (Spreng.) Herter	grass (c)	6%	0.16%	0.04%	0.20%
	Schizachyrium tenerum Nees	grass (c)	36%	1.07%	3.22%	4.29%
	Setaria parviflora (Poiret) M.Kerguélen	grass (cr)	33%	0.98%	0.52%	1.51%
	Setaria vaginata Spreng.	grass (cr)	25%	0.74%	1.42%	2.16%
	Sporobolus multinodis Hackel	grass (c)	3%	0.08%	0.04%	0.12%
	Stipa filiculmis Delile	grass (c)	19%	0.57%	0.81%	1.38%
	Stipa filifolia Nees	grass (c)	14%	0.41%	0.69%	1.10%
	Stipa tenuiculmis Hackel	grass (c)	11%	0.33%	0.08%	0.40%

(continued)

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Family	Species	Biol. form	F_s	RF_s	RC_s	IV_s
Poaceae	*Trachypogon montufari* Nees	grass (c)	25%	0.74%	2.74%	3.48%
	Poaceae 1	grass (c)	3%	0.08%	0.01%	0.09%
	Poaceae 2	grass (c)	3%	0.08%	0.01%	0.09%
	Poaceae 3	grass (c)	3%	0.08%	0.02%	0.10%
	Poaceae 4	grass (c)	3%	0.08%	0.04%	0.12%
	Poaceae 5	grass (c)	3%	0.08%	0.05%	0.13%
	Poaceae 6	grass (c)	3%	0.08%	0.02%	0.10%
	Poaceae/trib. Andropogoneae 1	grass (c)	3%	0.08%	0.02%	0.10%
	Poaceae/trib. Andropogoneae 2	grass (c)	3%	0.08%	0.01%	0.09%
	Poaceae/trib. Andropogoneae 3	grass (c)	3%	0.08%	0.02%	0.10%
	Poaceae/trib. Andropogoneae 4	grass (c)	3%	0.08%	0.02%	0.10%
Polygalaceea	*Monnina oblongifolia* Arechav.	shrub	17%	0.49%	0.23%	0.72%
Rubiaceae	*Borreria capitata* DC.	herb	11%	0.33%	0.16%	0.49%
	Borreria fastigiata K.Schum.	herb	42%	1.23%	0.68%	1.91%
	Borreria verticillata G.Mey.	herb	6%	0.16%	0.06%	0.22%
	Chiococca alba Hitchc.	liana	8%	0.25%	0.07%	0.31%
	Diodia apiculata K.Schum.	herb	14%	0.41%	0.13%	0.54%
	Galium uruguayense Bacigalupo	herb	22%	0.66%	0.11%	0.77%
	Relbunium hirtum K.Schum.	herb	39%	1.15%	0.35%	1.50%
	Richardia grandiflora Steud.	herb	50%	1.48%	0.83%	2.31%
	Richardia humistrata Steud.	herb	3%	0.08%	0.02%	0.10%
	Rubiaceae sp.	herb	3%	0.08%	0.01%	0.09%
Scrophulariaceae	*Angelonia integerrima* Spreng.	herb	3%	0.08%	0.08%	0.16%
	Gerardia communis Cham. & Schlecht.	herb	11%	0.33%	0.06%	0.39%
	Mecardonia herniarioides (Cham.) Pennell	herb	3%	0.08%	0.02%	0.10%
Smilacaceae	*Smilax campestris* Griseb.	liana	6%	0.16%	0.05%	0.21%
Solanaceae	*Petunia integrifolia* (Hook.) Schinz & Thell.	herb	8%	0.25%	0.07%	0.31%
	Petunia ovalifolia Miers	herb	3%	0.08%	0.01%	0.09%
Sterculariaceae	*Waltheria douradinha* A. St.Hil.	herb	11%	0.33%	0.09%	0.41%
Symplocaceae	*Symplocos uniflora* Benth.	tree	3%	0.08%	0.04%	0.12%
Turneraceae	*Turnera selloi* Arechav.	herb	14%	0.41%	0.09%	0.50%
	Turnera sidoides L.	herb	3%	0.08%	0.04%	0.12%
Verbenaceae	*Glandularia megapotamica* (Spreng.) Cabrera & Dawson	herb	3%	0.08%	0.02%	0.10%
	Lantana montevidensis (Spreng.) Briq.	shrub	17%	0.49%	0.37%	0.86%
	Verbena ephedroides Cham.	herb	11%	0.33%	0.04%	0.37%
	Verbena pseudojuncea Gay	herb	8%	0.25%	0.06%	0.30%
Vitaceae	*Cissus striata* Ruíz & Pav.	liana	3%	0.08%	0.01%	0.09%
Unidentified	Sp. 1	herb	3%	0.08%	0.03%	0.11%
	Sp. 2	herb	3%	0.08%	0.01%	0.09%
	Sp. 3	herb	3%	0.08%	0.01%	0.09%
	Sp. 4	herb	3%	0.08%	0.01%	0.09%
	Sp. 5	herb	3%	0.08%	0.01%	0.09%
	Sp. 6	herb	3%	0.08%	0.01%	0.09%
	Sp. 7	herb	3%	0.08%	0.01%	0.09%

Appendix 2: Species found in grassland plots at the forest-grassland border on Morro Santana, Porto Alegre, RS, Brazil. Given are family, species name, biological form (see text), with indication of basal architecture for grasses (see Appendix 1), and frequency (F_s) in border plots (n=12). Only species found exclusively in the border plots, i.e. species not listed in Appendix 1, are given. Nomenclature follows IPNI (2004).

Family	Species	Biol. Form	F_s
Acanthaceae	*Justicia brasiliana* Roth	shrub	8.3%
	Stenandrium Nees sp.	herb	8.3%
Apocynaceae	*Forsteronia glabrescens* Müll.Arg.	liana	8.3%
Aspidiaceae	*Rumohra adiantiformis* (G.Forst.) Ching	herb. fern	16.7%
Asteraceae	*Baccharis rufescens* Spreng	shrub	8.3%
	Calea serrata Less.	liana	66.7%
	Eupatorium intermedium DC.	shrub	8.3%
	Asteraceae 3	herb	8.3%
Bignoniaceae	*Dolichandra cynanchoides* Cham	woody liana	8.3%
	Macfadyena unguis-cati (L.) A.H.Gentry	woody liana	8.3%
Boragniaceae	*Moritzia ciliata* DC.	herb	8.3%
Caryophylaceae	*Spergularia grandis* Cambess.	herb	8.3%
Convolvulaceae	*Ipomoea nitida* Griseb.	herb. liana	8.3%
Cyperaceae	*Cyperus incomtus* Kunth	Cyperaceae	8.3%
Dioscoreaceae	*Dioscorea multiflora* Mart. ex Griseb.	liana	33.3%
Ericaceae	*Leucothoe eucalyptoides* DC.	tree	8.3%
Euphorbiaceae	*Sebastiania brasiliensis* Spreng.	tree	8.3%
Liliaceae	*Nothoscordum bonariense* Beauverd	geophyte	8.3%
Myrsinaceae	*Myrsine coriacea* R.Br	tree	16.7%
Myrtaceae	*Blepharocalyx salicifolius* O.Berg	tree	8.3%
Piperaceae	*Peperomia pereskiaefolia* H.B.& K.	herb	25.0%
Poaceae	*Calamagrostis viridiflavescens* Steud.	grass (r)	41.7%
	Oplismenus hirtellus (L.) P.Beauv.	grass (s)	33.3%
	Panicum ovuliferum Trin.	grass (s)	25.0%
	Paspalum mandiocanum Trin.	grass (c)	8.3%
	Paspalum sp. 1	grass (c)	16.7%
Rubiaceae	*Diodia cymosa* Cham.	herb	16.7%
	Guettarda uruguensis Cham. & Schlecht.	tree	8.3%
	Psychotria carthagenensis Jacq.	tree	16.7%
Sapindaceae	*Cupania vernalis* Cambess.	tree	8.3%
	Dodonaea viscosa Jacq.	tree	25.0%
Solanaceae	*Cestrum strigillatum* Ruiz & Pav.	shrub	8.3%
Styracacae	*Styrax leprosum* Hook. et Arn.	tree	8.3%
Symplocaceae	*Symplocos tetandra* Mart.	tree	8.3%

CHAPTER 2

Small-scale dynamics after fire in South Brazilian humid subtropical grassland

with Sandra Cristina Müller, Valério DePatta Pillar and Jörg Pfadenhauer

Abstract

Question: How does fire influence species richness and diversity in subtropical grassland in Southern Brazil?

Location: Regularly burned grassland in Porto Alegre, RS, Brazil (30°03' S, 51°07' W; max. elevation 311m a.s.l.) and abandoned grassland near São Francisco de Paula, RS, Brazil (29°47' S, 50°22' W; approx. 900m a.s.l.).

Methods: In the burned grassland, between-year changes in community composition and single-plot diversity, species number and vegetation structure were analyzed in two consecutive years for plots with different time since last fire. Individual species' reactions to burns were analyzed. At the abandoned site, diversity, species number and vegetation structure were examined.

Results: Species number and small-scale dynamics were highest about one year after the burn, and decreased as caespitose grasses increased in cover with time since fire until reaching a stable, but less diverse state three to four years after a burn. The abandoned grassland showed higher dominance of caespitose grasses and lower richness and diversity.

Conclusions: Fire clearly leads to short-term increase in species richness and diversity on the plot scale, as competitive interactions are being reduced and recruitment possibilities are high in early post-fire vegetation development. Overall community composition does not change after a fire. While small herbs seem to be slightly favored in early post-fire environment, no group of fire-following species was observed, indicating that the community is adapted to the current fire regime and may have evolved under the influence of fire.

Keywords: disturbance, diversity, burning, grassland, southern Brazil, species richness, vegetation dynamics

Abbreviations: PCoA: Principal Coordinates Analysis

Introduction

Disturbance is an important component of natural systems (e.g. Grime 1979, Souza 1984, Pickett & White 1985, Pickett *et al.* 1989, Hobbs & Huenneke 1992), in general enhancing species diversity by lowering dominance of one or more species and by increasing spatial heterogeneity (Denslow 1985). Denslow (1980) hypothesized that species diversity would be highest at the historic, i.e. natural, rate of disturbance, as regeneration conditions for the majority of species present would be met, thus giving an evolutionary prediction of the disturbance level where diversity was to be maximized under the intermediate disturbance hypothesis (Grime 1973, Connell 1978, Huston 1979). Human activity has led to changes in disturbance regimes in many ecosystems. Fire frequency in grasslands, for example, may have been greatly altered by burns set for management purposes or by protection from fire, by removal of fuel through pasture use, or by changes in landscape structure, limiting spread of fires. In many grasslands ecosystems, fire is necessary for suppression of shrubs and trees and thus maintenance of an open community under climate favorable to forest development (Sauer 1950, Vogl 1974, Howe 1994, Bond *et al.* 2003). Grassland fires generally lead to almost total loss of aboveground biomass, with plants recovering their cover values either by resprouting from belowground or protected buds or by germination from the seed bank or newly arrived propagules. Pronounced changes in resource availability for plants may further change community processes. Effects of fire on grassland diversity vary according to general climatic conditions and corresponding functional plant composition (e.g. arid vs. humid, temperate vs. tropical grasslands), differences in topography and year-to-year climatic conditions, and interactions with other disturbances (Collins 1987). In many grassland systems, fire has been shown to increase species richness, with peaks sometimes after one (e.g. Collins 1987, Harrison *et al.* 2003), sometimes a few years after the burns (Gibson & Hulbert 1987), with richness attributed to the presence of mixtures of invaders, opportunistic pioneer species, annuals and perennials with different life spans (Vogl 1974). Thus, diversity of functional groups may be related to the burning cycle (Gibson 1988), with, for example, small-statured and small-seeded species (Leach & Givnish 1996) or annual/biennial species (e.g. Ramsay & Oxley 1986, Lunt & Morgan 2001, Ghermandi *et al.* 2004) appearing only in early post-fire stages. In other cases, dominant species may be favored by fire (Collins & Glenn 1991, Collins *et al.* 1995): generalizations are difficult, requiring local studies to understand the effect of fire on plant diversity in a particular system (Uys *et al.* 2004).

In subtropical southern Brazil, fire and grazing are thought to be responsible for the persistence of mosaics of grassland and forest under a climate suitable for forest development (Pillar & Quadros 1997). Phytogeographical and palynological evidence suggest that the grasslands in the region are relicts from a cooler and drier climate about 10,000 years ago (e.g. Rambo 1953, 1956, Klein 1975, Behling 2002, Behling *et al.* 2004), stabilized by large-scale disturbance. As concluded from distribution of charcoal particles in peat profiles, fire frequency in southern Brazil rose markedly

after 7,400 B.P., i.e. man may have used fire as a tool for hunting (Behling *et al.* 2004). Today, fire is a common part of pasture management. Studies on the impact of fire, however, are scarce. Eggers & Porto (1994), working in a grazed grassland, have suggested that after a burn, vegetation will quickly recover to its pre-burn state concerning species composition, as the majority of species resprouts shortly after the fire. However, they did not discuss effects of fire on species dynamics and on diversity patterns of species groups under regimes of recurrent fires. This study analyzes the effect of a single fire event on species diversity, vegetation structure and species group dynamics over a period of two years, comparing plots with different fire histories in an ungrazed grassland subject to frequent anthropogenic burns. Data was collected in a frequently burned grassland in Porto Alegre, RS, Brazil, with comparative data from an abandoned grassland area near São Francisco de Paula, RS, Brazil.

Material and Methods

Study sites and experimental design

The study was conducted in grassland areas on Morro Santana (Santana hill), Porto Alegre, RS, Brazil (30°03' S, 51°07' W; max. elevation 311m a.s.l.) and at the Pró-Mata Research Center (29°47' S, 50°22' W; approx. 900m a.s.l.). The granitic hill is covered by forests (Atlantic rainforest) on the southern slopes and by grasslands on the top and on large parts of the northern slopes (Aguiar *et al.* 1986). Climate in the region is Köppen's Cfa, with mean annual temperature ranging from 18° to 20° and mean precipitation of 1,300 to 1,500 mm yr^{-1}, without dry season (Nimer 1990). The predominant soil types are Acrisols and Umbrisols (FAO classification; Martinez 2005). The grasslands on Morro Santana are very species rich, with a total of 430 identified plant species cited for the area of approx. 220 ha, and characterized by a matrix of caespitose grasses with a large number of sparsely distributed herbs and grassland shrubs in intertussock spaces (Overbeck *et al.*, submitted). Presently, no formal land use such as grazing exists, but differently sized parts of the grassland burn each year, caused mostly by accidental anthropogenic fires or fires laid by population of nearby squatter settlements. Fire intervals are around 3 to 5 years, allowing for a mosaic of sites with different development time since fire and, as a result of ongoing forest expansion processes, a heterogeneous distribution of shrubland patches or woody species islands within the grassland, principally on the shallower and drier northern slope (Müller & Forneck 2004).

At six sites along the grassland-forest border, differing in exposition and inclination, pairs of transects from the forest border into the open grassland were installed. Sites also differed in fire history: four transect pairs had not been burned in the past three years, whereas the other two had burned 10 months before the beginning of our study. Each transect consisted of 7 plots of 4.5 by 4.5m, used to study forest expansion processes under the impact of fire (Müller *et al.*, in prep.). Within plots 3 (the third plot from the border), 5 and 7 (furthest in the grassland) of each transect, contiguous plots of 0.5 by 0.5m² were installed for analysis of floristic composition of the grassland (Overbeck *et al.*, submitted) and impact of fire on vegetation dynamics. In October 2002, one of the two transects in

each pair was subjected to an experimental burn. In the two transect pairs that had burned recently before, total vegetation cover was too sparse to allow for the fires set to carry on; thus, transects did not burn. After the burns, we were able to study the following treatment groups: 1) four transects burned in our experiments (group 1), 2) four transects that had burned 10 months before (group 2) and 3) four transects that had burned three years ago for the last time (group 3). Of the last four transects, one suffered an accidental anthropogenic burn right after we had conducted our first survey. This transect therefore could be used for a comparison of pre- and post-fire vegetation (group 0). Vegetation was sampled in January/February 2003, i.e. approximately three months after the experimental burns (first survey), and then in November/December 2003, i.e. almost one year after the experiment (second survey), recording cover of all vascular plant species and cover of litter, open soil, rocks, mosses and total cover of standing dead biomass, using the Londo (1976) decimal scale. Data from the three contiguous plots was pooled to one plot of 0.75m² for some of the analyses by taking the average value for each species or structural variable.

Additionally, we investigated plots at the CPCN Pró-Mata research area, São Francisco de Paula, RS, Brazil, to compare the Morro Santana data with data from an unburned grassland. The 130 ha of grassland at the site, in a mosaic with *Araucaria* forest, are excluded from fire and grazing since 1992 (Bertoletti & Teixeira 1995). Located at the southern rim of the South Brazilian Planalto, climatic conditions at the site differ from those on Morro Santana (mean annual temperature 16°C, mean precipitation 2,250mm yr^{-1}; São Francisco de Paula meteorological station). A description of the area and vegetation development since abandonment is given in Oliveira & Pillar (2004). A small portion of the grassland burned in October of 2003, set to fire by lighting which struck a telephone post, in a not very intense burn, leaving large patches of unburned litter. On Pró-Mata, we placed six transects randomly in the grassland, each with plots positioned like in transects on Morro Santana, with 36 plots situated in the area not burned since 1992 and 18 in the recently burned area. Vegetation sampling was conducted in January 2004, following the methods used on Morro Santana. Due to the great climatic differences, we did not conduct any statistical analyses using both data sets, but used the data from Pró-Mata for discussion of the results obtained on Morro Santana.

Data analysis

Effect of time since fire on overall species composition

To compare the four treatment groups on Morro Santana in respect to magnitude of compositional change between the two surveys, we calculated the Jaccard-coefficient (Krebs 1998) for data from the two sampling periods, using both plots of 0.25m² and 0.75m². The obtained values, indicating percentage similarity of species composition between any two plots, were categorized according to treatment groups and compared by analysis of variance with randomization testing (Pillar & Orlóci 1996, Pillar 2004a). Compositional data from both years on Morro Santana were analyzed

separately for overall differences in composition between the treatment groups by Principal Coordinates Analysis (PCoA). First, we analyzed species data only, using chord distance as resemblance unit (Podani 2000), to detect effects of different fire history on species composition. Then, we included cover of litter and bare soil, now using Euclidean distance as resemblance unit, to clarify the influence of time since fire on structural attributes of vegetation. Further, we tested the treatment groups for significant differences concerning species composition by analysis of variance with randomization testing (chord distance as resemblance measure). Our experiment was not fully randomized, but partially presented a pseudoreplication (Hurlbert 1984), as all plots of group 2 were situated in one area; thus, we conducted an additional analysis by subjecting only plots from groups 1 and 3, i.e. the most contrasting treatments, to PCoA, using transect pair as block factor. A complete randomization clearly would have been advantageous and would have allowed for a more straight-forward analysis, but was not possible due to the given fire history in the area and legal restrictions on number of experimental burns by local environmental authorities. Only species present in more than 10% of plots of each group were included in analyses using species data. For ordination analyses, concerned with species composition, we used pooled plots of 0.75m² as the three contiguous plots were not independent. For all analyses described in the following, plots of 0.25m² were used, as this should give a finer resolution.

Overall changes in species richness and diversity in relation to time since fire

The data from the two sampling times on Morro Santana were tested separately for each treatment group by univariate analysis of variance with randomization testing (Euclidean distance as resemblance measure), comparing species number (S), Shannon's index (H', to the natural logarithm) as diversity measure, evenness (J= lnS/H'; Pielou 1969), cover of litter, percentage of open soil and total cover of dead biomass in order to evaluate direct effect of time since the last burn on structure and diversity of plots with different fire treatments. The same procedure was followed for the Pró-Mata data. With the Morro Santana data, we analyzed the change of each of these factor from the first to the second survey, separately for each treatment group.

For each plot on Morro Santana, we calculated the number of species found in the first survey and not present any more in the second survey (lost species), or had not been present in the first period but were encountered the second time (new species). Additionally, total change in species number per plot was calculated (i.e., not considering species identity, as by the Jaccard index; see above). These three values were standardized to the species number obtained in the first survey in order to obtain comparable data. Plots were classified according to time since the fire (groups 0, 1, 2, 3, see above), and values were tested for significant differences by analysis of variance with randomization testing (Euclidean distance).

We used MULTIV (Pillar 2004a) and SYNCSA (Pillar 2004b) application programs for all analyses. Randomization tests involved 1000 random permutations, and a threshold of $\alpha= 0.05$ was

adopted for rejecting the null hypothesis.

Reaction of single species and species groups to fire

To evaluate changes in frequency and cover between the different treatment groups for individual species, we separated the unpooled plots into treatment groups, and ordered all species according to changes in frequency, only considering species present in more than 10% of plots of each group for either one of the two sampling periods. Species were classified into 1) species keeping the same or almost same frequency between the two samplings (-10% to 10% change), 2) increasers (change of more than +10%) and 3) decreasers (change of less than –10%), and then grouped into woody species (trees and shrubs), graminoids (grasses, Cyperaceae) and herbs for presentation. Then, we calculated the absolute change in cover value for each species per plot, took the mean value for plots where present, and ordered species according to cover change between the two surveys, grouping them into species 1) increasing in abundance (increase more than 1% cover), 2) staying the same (between –1% and 1%), and 3) decreasing in cover (decrease more than –1%), again classifying species into woody species, graminoids, and herbs. The criterion of 1% change may seem to be very small, but it has to be remembered that in total, 198 (morpho-)species were found in the study plots, most of them in low frequencies and thus with low mean cover values (Overbeck *et al.*, submitted).

Results

Effect of time since fire on overall species composition

As ordination diagrams were essentially the same for the two sampling periods, we only present the results for the first survey, i.e. use the data with relatively larger differences between treatment groups considering time since fire. Ordination of the plots using species data did not reveal any clear separation of the plots according to treatment groups (Fig. 1A). When including cover of open soil and litter in the analyses, plots were clearly separated according to their fire history along the first axis (Fig. 1B). Open soil and litter were highly correlated to the first axis (open soil: R=0.96, litter: R=-0.76); these correlations were almost the same (differences of only 0.1) when using data from the second survey (graph not shown).

Randomization testing of species data revealed significant differences between plots from group 1 or 3 and group 2. When applying randomization testing only to data from plots of groups 1 and 3, differences were not significant; we thus conclude that the different composition on plots of group 2 was caused by the distinct location of the respective transects in the study area (see methods).

Jaccard´s S_j, using data from the 0.25m² plots, indicated less compositional change between the two surveys in plots unburned for longer period, and strongest changes (coefficient value <50%) for plots that burned between the two treatments (Tab. 1). For data from the pooled 0.75m² plots, no significant differences between treatment groups existed.
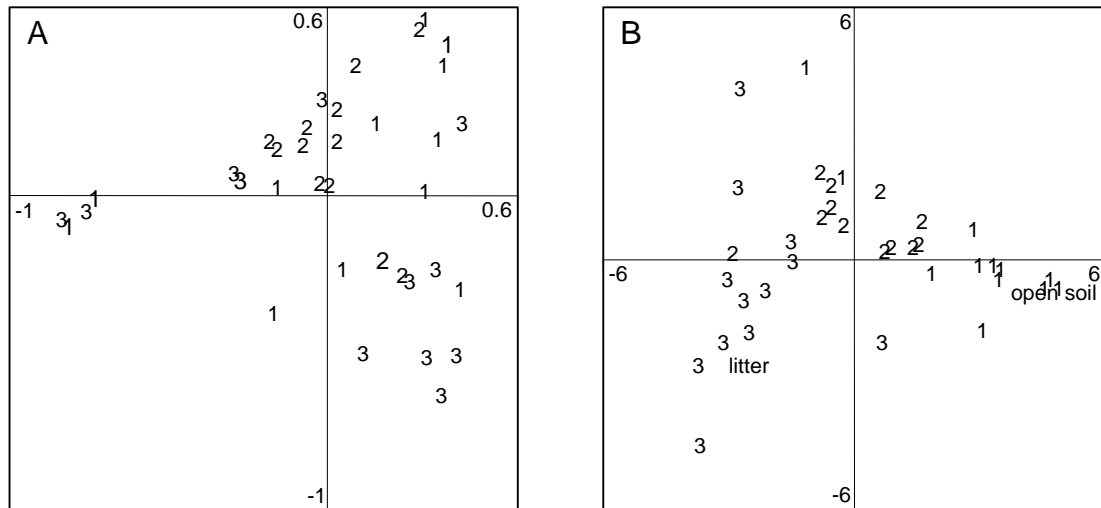
Figure 1: PCoA of species composition data in 0.75m² plots with different time since the last fire on Morro Santana, Porto Alegre, RS, Brazil, using data from the first survey. A) species data, chord distance as resemblance measure, explanation of axis 1: 15.8%, of axis 2: 12.0%; B) species data plus cover of open soil and litter, Euclidean distance as resemblance measure, explanation of axis 1: 31.7%, of axis 2: 13.8%. Plot symbols are omitted for clarity of the diagram; 1: recently burned plots, 2: plots burned one year before, 3: plots burned 3 years ago. Situation of litter and open soil in the diagrams is shown in B, with codes for treatment groups centered over coordinates.

Table 1: Jaccard's coefficient indicating compositional change of 0.25m² and 0.75m² grassland plots on Morro Santana, Porto Alegre, RS, Brazil, from the first to the second survey. Values categorized according to treatment group. 0: plots burned between survey period (n=9), 1: plots burned experimentally (n=36); 2: plots burned one year before the experimental burns (n=36), 3: plots not burned for three years (n=27). Differences tested by analysis of variance with randomization testing p<0.05). Different letters behind values, to be read separately for each plot size, indicate significant differences between groups (p<0.05).

Plot size	Group 0	Group 1	Group 2	Group 3
0.25m²	46.1% a	57.3% b	60.3% b	66.4% c
0.75m²	57.6% a	61.7% a	66.7% a	65.9% a

Overall changes in species richness and diversity in the transects

When comparing plots from the different treatment groups, significant differences could be found for most of the structural and diversity-related parameters, indicating a clear temporal sequence (Tab. 2, Fig. 2) for each of the two study periods and for both combined. Plots in transects that had burned one year before and were not inflammable in our experiments (group 2) showed a strong and significant reduction in open soil and an increase in standing dead biomass from the first to the second study period; only those two parameters differed significantly between the two survey dates in plots of group 2. In plots of group 3 that had not burned for more than 3 years, species number decreased by more than 1 species, from 16.7 to 15.1. Here, litter increased very slightly on a high level, while open soil was reduced to almost zero. Percentage of standing dead biomass increased on a high level. In plots that had been sampled three months and one year after the experimental burn (group 1), significant changes could be observed between the two surveys for all factors, except for evenness and

diversity. In average, more than five species more per plot could be found in the second survey. Litter cover and cover of standing dead biomass rose significantly, while open soil decreased.

Table 2: Diversity and structural variables of 0.25 m² grassland plots on Morro Santana, Porto Alegre, and at CPCN Pró-Mata, São Francisco de Paula, RS, Brazil, separated for the two study sites (numbers: Morro Santana, letters: Pró-Mata) and periods (Morro Santana only). 0: plots burned between survey period (only for second survey; n=9), 1: plots burned experimentally (n=36); 2: plots burned one year before the experimental burns (n=36), 3: plots not burned for three years (n= 36 for first survey; n=27 for second survey); A: area burned in October of 2003 (three months before the survey; n = 18), B: area not burned since 1992 (n=36). Different letters between values should be read for each row and survey and indicate significant differences between treatment groups, separately for each survey period/site (p<0.05).

	First survey				Second survey								Pró-Mata survey		
Treatment group	1		2		3		0		1		2		3		A	B
Diversity (nats)	2.19	a	2.38	a	1.93	b	2.72	a	2.38	b	2.43	b	1.84	c	0.93 a	1.2 b
Evenness	0.78	a	0.78	a	0.70	b	0.82	a	0.77	a	0.79	a	0.70	b	0.48 a	0.56 b
Species number	17.1	a	21.9	b	16.7	a	28.0	a	22.5	b	21.8	b	15.1	c	6.9 a	8.3 a
Litter (% cover)	4.1	a	8.9	b	34.9	c	3.2	a	7.9	a	13.1	b	37.2	c	38.9 a	5.8 b
Open soil (% cover)	46.6	a	17.6	b	4.0	c	46.7	a	31.2	b	5.2	c	1.0	d	8.3 a	1.5 b
Stand. dead (% cov.)	2.5	a	9.8	b	23.2	c	6.7	a	8.3	a	18.1	b	28.0	c	44.3 a	4.6 b

In the only transect allowing a comparison of pre- and post-fire conditions, diversity and evenness were significantly higher in the second survey. Mean species number rose from 19 to 28. Cover of litter and open soil changed significantly as well, just like total cover of standing dead biomass. In plots in the Pró-Mata area, species number, Shannon's diversity and evenness were markedly lower, with species number ranging between 3 and 13, as opposed to maxima of 33 attained on Morro Santana. Diversity and evenness were significantly higher in the area not burned for 10 years. Standing dead biomass reached values of over 44% in the unburned area (Tab. 2).

Species dynamics in relation to time since fire

Principally in plots from Group 0, i.e. those plots that had burned after the first study period, the colonization rate, measured by percentage of species found in the plots in the second survey only, was very high (75%; Tab. 3).
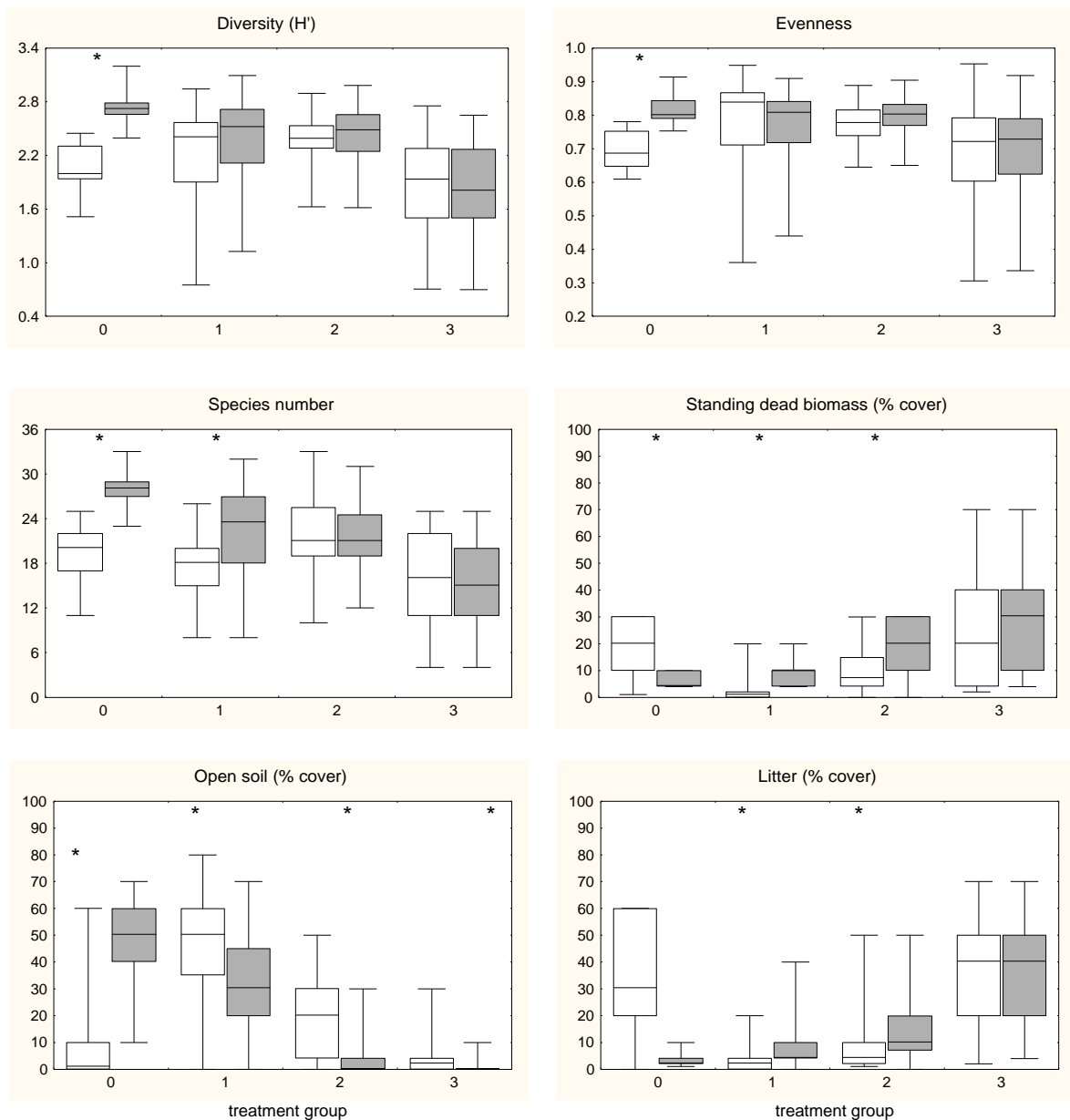
Figure 2. Diversity and structural variables of 0.25 m² grassland plots on Morro Santana, Porto Alegre, RS, Brazil, for two consecutive surveys. Box and whisper plots show median value (bar), upper and lower 25% percentiles (boxes) and minimum and maximum values (whiskers). Scale of figures varies, with units indicated in title (where needed). 0: plots unburned for more than 3 years at the first survey, burned between first and second survey (n=9), 1: plots burned 3 months before the first and 1 year before the second survey (n=36), 2: plots burned 1 year before the first and two years before the second survey (n=36), 3: plots unburned for more than 3 years at the first and second survey (n=27). White boxes: data from the first survey, gray boxes: data from the second survey. Asterixes above a pair of boxes indicate significant differences between the two surveys for the respective treatment group, tested by randomization testing with analysis of variance (p<0.05).

In plots from group 1, new colonization in the first post-burn year reached 50% in relation to the number of species present at the first sampling period. In plots that had been burned one year before the first study period, colonization rate was only slightly higher than in plots of group 3. Mortality rates, measured as percentage of species that had disappeared from the first to the second sampling period, only differed significantly between plots from group 1 to plots from group 2 and 3:

only 15% of the species (at the base of the species present the first sampling period) could not be found the second time in plots from group 1, in contrast to about 25% in the other plots. In plots of group 0, mortality rate was 21%.

Table 3: A) Percentage of new species and lost species and resultant total turnover rate in 0.25m² plots in grassland on Santana hill, Porto Alegre, RS, Brazil. All values given in percentage of number of species present at the first sampling period. The cross-table shows the probability level obtained by randomization testing; probabilities <0.05 are printed in bold. Group 0: the one transect that burned after the first sampling; group 1: plots burned in our experiments; group 2: plots burned one year before; group 3: plots burned more than 3 years ago. B) Percentage of new species and lost species and resultant total turnover rate in pooled plots of 0.75m², whole transect, and complete treatment. Number of plots per group indicated after group specification (n). Please note that data in the last column of B (data pooled to complete treatment) should be considered with caution, as number of plots/transects was not the same between groups.

A - New species – differences between treatment groups							B - New species – different spatial scales				
	n	Plot 0.25m²	0	1	2	3		0.25m²	0.75m²	Transect	Treatm.
Group 0	9	74.8%	0	.	**0.000**	**0.003**	**0.017**	Group 0	74.8%	46.6%	31.4%	31.4%
Group 1	36	49.5%	1		.	**0.000**	**0.000**	Group 1	49.5%	45.7%	38.3%	25.4%
Group 2	36	26.6%	2			.	0.193	Group 2	26.6%	28.3%	20.6%	15.6%
Group 3	27	19.8%	3				.	Group 3	19.8%	19.6%	16.1%	13.6%

A - Lost species – differences between treatment groups							B - Lost species – different spatial scales				
	n	Plot 0.25m²	0	1	2	3		0.25m²	0.75m²	Transect	Treatm.
Group 0	9	21.0%	0	.	0.341	0.133	0.374	Group 0	21.0%	19.8%	15.7%	15.7%
Group 1	36	15.4%	1		.	**0.000**	**0.005**	Group 1	15.4%	12.5%	11.8%	9.3%
Group 2	36	24.8%	2			.	0.961	Group 2	24.8%	23.8%	14.1%	9.8%
Group 3	27	24.9%	3				.	Group 3	24.9%	24.3%	19.5%	17.8%

A - Total – differences between treatment groups							B - Total – different spatial scales				
	n	Plot 0.25m²	0	1	2	3		0.25m²	0.75m²	Transect	Treatm.
Group 0	9	53.8%	0	.	**0.000**	0.093	**0.000**	Group 0	53.8%	28.6%	15.7%	15.7%
Group 1	36	34.1%	1		.	**0.000**	**0.000**	Group 1	34.1%	33.2%	26.1%	16.1%
Group 2	36	1.8%	2			.	0.254	Group 2	1.8%	4.5%	6.5%	5.7%
Group 3	27	-5.0%	3				.	Group 3	-5.0%	-4.7%	-3.40%	-4.2%

Overall, these colonization and mortality rates led to an increase in species number (without considering species identity) of over 54% in plots burned between the two study periods and to an increase of 34% in the year right after the burn. In the second year after the burn, the net turnover rate was close to 0%, while in plots unburned for at least 3 years, there was a slight decline in species number (Tab. 3A). When pooling the 0.25m² plot data to plots of 0.75m², whole transects, and all plots of the treatment group, a general decline in magnitude of change can be observed, without, however changing general trends (Tab. 3B).

Changes in frequency and cover values of individual species

In the burned plots, the great majority of species increased in frequency (Tab. 4; Appendix 1). Six herbs appeared in these plots for the first time in the second survey: *Sisyrinchium vaginatum* (Iridaceae), *Prescottia oliganta*, a small orchid, *Hypoxis decumbens* (a bulbous Amaryllidaceae), *Galium uruguayense*, *Petunia integrifolia* and *Polygala pulchella* (small herbs). However, except for *Prescottia* and *Polygala*, all of these were present in plots from the other treatment groups as well. A number of rather frequent small herbs (such as the rosettes *Chaptalia sinuata* and *C. runcinata*, the bulbous *Oxalis conorrhiza* and *O. brasiliensis*, or the reptant species *Hydrocotyle exigua*, *Dichondra sericea* and *Evolvulus sericeus*), increased in frequency after fire, along with larger herbs such as *Eryngium ssp.*, *Tibouchina gracilis*, *Pfaffia tuberosa*, *Aspilia montevidensis*. The majority of graminoid species also increased in frequency, especially large caespitose grasses and the Cyperaceae *Bulbostylis closii*, *Rhynchospora setigera* and *Scleria selloi*. Considering woody species, likewise an increase in frequency could be observed for the majority of the species.

Table 4: Overview of change in cover and frequency of woody, herbaceous and graminoid species for treatment groups 1, 2 and 3, for 0.25m² grassland plots on Morro Santana, Porto Alegre, RS, Brazil. Calculations are based on species present in 10% or more of plots in each treatment group of either one of the surveys A) Change in cover. Increase: species with difference in mean cover values over all plots of each treatment between the two surveys greater than 1%; Same: species with difference in cover between both surveys between –1% and 1%; Decrease: difference in cover lower than –1%. B) Change in frequency. Increase: increase in frequency by 10% of more from survey 1 to survey 2, Same: change in frequency between –10% and 10%; Decrease: change in frequency lower than –10%. See Appendix for individual species' changes in frequency and cover.

A) Change in cover				B) Change in frequency			
Burned plots (treatment group 1)				Burned plots (treatment group 1)			
	Woody	Herbs	Graminoids		Woody	Herbs	Graminoids
Increase	45.5%	56.4%	66.7%	Increase	63.6%	74.4%	70.8%
Same	54.5%	33.3%	29.2%	Same	18.2%	5.1%	4.2%
Decrease	0.0%	10.3%	4.2%	Decrease	18.2%	20.5%	25.0%
Burned 1 year before (treatment group 2)				Burned 1 year before (treatment group 2)			
	Woody	Herbs	Graminoids		Woody	Herbs	Graminoids
Increase	53.8%	8.8%	37.5%	Increase	46.2%	35.3%	37.5%
Same	30.8%	73.5%	54.2%	Same	15.4%	17.6%	41.7%
Decrease	15.4%	17.6%	8.3%	Decrease	38.5%	47.1%	20.8%
Burned 3 years ago (treatment group 3)				Burned 3 years ago (treatment group 3)			
	Woody	Herbs	Graminoids		Woody	Herbs	Graminoids
Increase	23.1%	19.2%	33.3%	Increase	46.2%	34.6%	14.3%
Same	53.8%	73.1%	38.1%	Same	15.4%	26.9%	52.4%
Decrease	23.1%	7.7%	28.6%	Decrease	38.5%	38.5%	33.3%

When considering not changes in frequency, but increase or decrease in cover of individual species, ranking of species changed. For none of the woody species, a decrease in cover could be observed, for herbaceous and graminoid species, number of species decreasing in cover also was lower when compared to frequency. Due to the large number of species, changes in cover for individual

species generally were small.

In plots that had burned a year before our experimental burns, percentage of species decreasing in frequency already was higher, even though not yet reaching the number of species increasing in frequency in woody species and graminoids. Woody species did increase slightly more in cover value than in burned plots, while herbs and graminoids showed less increase in cover. More than two thirds of the herbaceous species were stable concerning their cover values. In plots not burned for three years, more graminoid species decreased in frequency than increased, while for woody species and for herbs, the numbers stayed almost the same. While some of the herbaceous decreasing in frequency were small prostrated herbs, e.g. *Evolvulus sericeus*, *Dichondra sericea*, other small species increased, e.g. *Oxalis ssp.* and *Relbunium hirtum*. Among the woody species, especially *Heterothalamus psiadoides* showed a strong decline in frequency and cover: in some of the plots, it had been present with high cover values at the time of the first survey, but died before the second survey. Especially species from the genus *Baccharis* increased markedly in cover in plots unburned for a longer period. Most of the tall caespitose grasses also increased substantially in cover.

Discussion

Fires clearly led to increased species richness, with species net turnover on the plot level highest in plots most recently burned, and decreasing with time since fire until reaching a negative level. In plots unburned for a longer period, in our study three to four years, species number and diversity were strongly reduced in comparison to recently burned plots: the effect of the matrix species dominates system structure due to accumulation of a dense litter layer and standing dead biomass (Collins 1987, Facelli & Pickett 1991). Herbs are being outcompeted by the dominant tussock grasses and get lost in aboveground vegetation. Species that disappeared will not be replaced by others under these conditions, as chances for recruitment in intertussock-areas are low (Grubb 1977, Lauenroth & Aguilera 2000) and continue decreasing with time since fire, until a species-poor state as seen on the Pró-Mata plots unburned for 10 years is reached.

In unburned plots, dynamics from the first to the second survey period were relatively slow, compared to recently burned plots: species number, diversity and evenness rose markedly in the first post-fire year, indicating rapid recolonization processes. In plots representing the second year of post-fire succession, diversity still was high, dynamics between the two sampling periods, however, already slowed down. We conclude from our data that one year after the fire, species richness will be highest.

Removal of dominant species is considered to be one of the main causes for species richness after disturbance, impeding a state of compositional equilibrium that would lead to the extinction of less competitive species (Connell 1978, Huston 1979, Pickett 1980). Olff & Ritchie (1998) have proposed that local species richness in grasslands is maintained by an interaction between local colonization from the total species pool and local extinction: where extinction rates are lower than colonization rates, plant diversity will be especially high. Tilman (1982) considers space as a resource,

the resource supply rate thus being the rate of disturbance through which open space is formed. Concordingly, a grassland burn equivalates an extremely high resource supply rate, radically changing resource availability of space and other resources (e.g., light, nitrogen, temperature; Whelan 1986, Hulbert 1988, Neary *et al.* 1999), allowing for rapid recolonization processes. A high disturbance frequency, as present on Morro Santana, may further increase species richness on the long run, as the chance of "congruence" between unpredictable recruitment events and suitable microsite conditions will be higher (Morgan 1998). While early post-fire stages of the community thus are characterized by strong colonization, the number of species getting "extinct" at the site is much lower, as competitive exclusion does not come into effect in the early successional stages. In case of recurrent disturbances, i.e. fires returning every few years, impact of competitive dominance and thus extinction processes always be kept low. In the studied grassland, an compositional equilibrium state would not exist on the long run in the absence of disturbance, as the grasslands are subject to invasion of shrubland and forest species (Oliveira & Pillar 2004) and would not persist under the present climatic conditions. Disturbance in our case therefore works in two ways: 1) fire permits the existence of grassland vegetation under climatic conditions favorable to forest establishment, just as would any other large scale disturbance, e.g. grazing (Pillar & Quadros 1997), and 2), by acting in high frequency, it is the cause for high diversity in the system.

Analysis of effect of fire on overall species composition was difficulted by the high species number and heterogeneous distribution of populations in the study area. In the studied plots, only 15 out of 198 species found presented frequencies above 50%, and only 40 above 30% (Overbeck *et al.*, submitted). The fact that plots from treatment group 2 differed from those from 1 and 3 in their species composition can be attributed to the fact that all plots of group 2 were situated apart from the other plots, i.e. to a problem with the experimental design. As plots from the most contrasting treatments, groups 1 and 3, did not show any significant differences, we conclude that difference in species composition of these two groups to group 2 was not a treatment effect, but caused by patchy and heterogeneous species distribution in the study area, not only concerning the infrequent species, but dominants as well (Overbeck *et al*, submitted). Consideration of open soil and litter, on the other hand, led to high explanation of ordination axes and a clear separation of the treatment groups, demonstrating the strong structural changes brought about by the burn and thus reinforcing the importance of high recruitment-possibilities on the one and the low competitive pressures on the other hand in recently burned plots. Glenn & Collins (1993) have suggested that patch structure in grasslands may not depend on species identity: spatial distribution of core species, e.g. caespitose grasses forming the vegetation matrix, may be stable, but interdispersed satellite species may show unpredictable spatial dynamics as a result of stochastic and unidirectional fluctuations. Small-scale instability leads to large-scale stability in time and space, and can explain high species richness despite the apparent lack of niche differentiation of grassland species (v.d. Maarel & Sykes 1993, Herben *et al.* 1993a, Herben *et al.* 1993b). This general explanation of grassland diversity can now be linked to

temporal processes after the disturbance event. Time since fire defines the magnitude of population fluctuations, as shown by differences for the Jaccard-coefficient between the treatment groups: the longer the interval since the last fire, the less expressed the dynamics. Dynamics in species number (considering species identity or not) were highest on the smallest spatial scale, and continuously declined when increasing the scale, indicating that species composition of the whole system does not change in relation to the fires. Relative differences in dynamics between treatment groups were independent of scale, indicating that high post-burn dynamics were mostly dependent on the presence of bare ground (Chytrý *et al.* 2001).

Ghermandi *et al.* (2004), working in Patagonia grassland, have shown the existence of what they called a „phantom community" of fugitive species, i.e. annuals that manage to establish from the seed bank in the post-fire community with decreased competition, but will disappear quickly in the course of vegetation development, after having re-charged the seed-bank. Post-fire colonization by opportunistic species has been observed in many other grassland or shrubland communities, such as Ecuadorian grass páramo (Ramsay & Oxley 1986), Australian temperate grassland (Lunt & Morgan 2001), and California chaparall (Christensen & Muller 1975, Keeley *et al.* 1981), with systems characterized by high dominance by one or few species often subject to invasion of exotic species (Laterra 2004). A group of strict fire-followers, i.e. species depending on fire for appearance in above-ground biomass (annuals or perennials), could not be found in our study. Very few therophytes exist at all in the studied grassland (only two species found in our plots are considered annuals in the literature; Overbeck, unpublished), or in general in grasslands in the region (Boldrini 1993, Garcia *et al*. 2002). Some species could be identified to appear in higher frequencies right after fire, principally geophytes and small herbs, mostly, however, occurring in later successional stages as well, albeit in lower frequencies. Small species, such as bulbous geophytes, small rosettes or prostrated species, usually weaker competitors, will be outcompeted easier in vegetation undisturbed for longer periods and thus profit relatively from early post-burn conditions (Leach & Givnish 1996), while the dominating caespitose grasses and grassland shrubs are those that will suffer the least from the process of „thinning out" of species on the small scale. However, at least for the period abranging our study, small species still managed to survive in unburned plots. In the Pró-Mata area, in contrast, herbaceous species were largely absent in above-ground vegetation, indicating that after longer periods of abandonment, competitive dominance of the caespitose grasses becomes too high for a large proportion of the forb component of the grassland.

The lack of a difference in species composition between recently burned plots and plots unburned for a longer period indicates a fast regeneration of a community well adapted to fire, or – more precisely – adapted to the current fire regime (Pickett *et al.* 1989), thus supporting the hypothesis of development of grasslands in the region under the impact of fire (Denslow 1980, Whelan 1986). Pronounced presence of a group of fire-followers, e.g. annual species appearing only after disturbance had created bare soil and thus recruitment possibilities, would of course not contradict this hypothesis.

The absence of annuals most probably is the result of the climatic conditions: in subtropical climate without cold season and with well-distributed precipitation throughout the year, an annual life-cycle simply may not be advantageous; likewise, fire-controlled grasslands in southern Africa do not have a strong therophyte component, in contrast to climate-controlled grasslands (Bond *et al.* 2003). The high diversity in South Brazilian grassland clearly can be attributed to recurrent disturbances impeding competitive dominance of caespitose grasses, and not to the presence of species specialized on different phases in post-fire vegetation development.

In this study, we have not treated in detail the mechanisms of post-fire colonization, i.e. resprouting from belowground organs or seedling emergence. For grasslands in southern Brazil, no studies exist on the importance of belowground organs and resprouting capacity of grassland species. From population biology studies (the perennial rosette species *Eryngium horridum* (Fidelis *et al.*, submitted) and *Moritzia ciliata*; unpublished data) and our field observations we conclude that the majority of species present possesses some kind of belowground storage organs and will resprout readily after a burn. Data from the one transect burned between surveys shows that mortality was not much higher than in recently burned plots, and even lower than in plots burned one or more years before the first survey: the species present seem to be adapted to regular fires. Seedlings, on the other hand, were never encountered in great quantities (field observations). Benson *et al.* (2004) state that resprouting from belowground organs accounts for more than 99% of above-ground stems in tallgrass prairie; resprouting has also found to be the prevalent recolonization strategy in burned Australian temperate grasslands (Morgan 1999, Morgan 2001). We presume that resprouting has a substantially higher importance than seed germination for post-fire regeneration in South Brazilian grasslands as well, even though data is missing so far.

Our results indicate that maximum species number in the area studied was attained approximately one year after the fire, which – as we did not manage to set fire to an area burned 10 months earlier – should correspond approximately with maximum fire frequency in the system. However, we only studied the effects of a single fire event. Annual burns over a longer period might be detrimental for some of the perennial species, whereas tussock grasses have been shown to profit from higher fire frequencies (Uys *et al.* 2004). If on the other hand fire intervals became very long, the "bud bank" (Harper 1977) of the system might become depleted, and only species present in above-ground biomass would be able to resprout after fire. The complimentary data from the Pró-Mata plots burned after 10 years of abandonment seems to indicate this situation. Bud bank density in relation to time since fire and long-term effects of different fire frequencies on vegetation dynamics and structure remain to be studied in South Brazilian grasslands, both for a better understanding of grassland dynamics and diversity, and as basis for grassland management.

Acknowledgements

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Appendix 1: Changes of frequency and cover of grassland species from 0.25m² plots on Santana hill, Porto Alegre, Brazil. For each treatment group, species are grouped into woody species (trees, shrubs and shubshrubs), forbs and graminoids (Poaceae and Cyperaceae). Shown: frequency values for the first (F1) and second (F2) survey, the relative frequency change in relation to the first survey value (FC) and the mean change in cover value (CC; positive: increase, negative: decrease) between the two surveys, for plots where species was present. Only species found in more than 10% of plots of each treatment in at least one of the two surveys were considered.

Group 1: recently burned					Group 2: burned one year before					Group 3: burned three years before				
WOODY SPECIES:	F1	F2	FC	CC		F1	F2	FC	CC		F1	F2	FC	CC
Eupatorium ligulaefolium	3	13	333%	1.1	*Baccaris sessiliflora*	3	4	44%	2.8	*Croton* cf. *nitrariaefolius*	7	11	57%	0.5
Baccharis leucopappa	3	10	233%	-0.5	*Pavonia hastata*	4	5	31%	2.0	*Baccharis leucopappa*	2	3	50%	1.3
Baccharis cognata	7	23	229%	5.8	*Schinus weimanniaefolius*	4	4	25%	-4.0	*Erythroxylum argentinum*	2	3	50%	0.7
Baccharis trimera	2	4	100%	0.0	*Chamaecrista nictitans*	4	2	13%	0.8	*Baccharis trimera*	6	8	33%	1.9
Porophyllum lanceolatum	11	19	73%	1.0	*Monninia oblongifolia*	6	4	11%	1.0	*Baccharis cognata*	3	4	33%	0.5
Croton cf. *nitrariaefolium*	9	15	67%	1.5	*Baccharis leucopappa*	14	17	9%	1.8	*Porophyllum lanceolatum*	7	8	14%	0.1
Croton thermarum	4	5	25%	1.4	*Porophyllum lanceolatum*	7	4	8%	0.4	*Lantana montevidensis*	4	4	0%	-3.5
Vernonia nudifolia	12	12	0%	0.6	*Vernonia nudiflora*	16	18	7%	2.3	*Vernonia nudiflora*	14	13	-7%	0.9
Desmanthus tatuhyensis	12	11	-8%	0.4	*Baccharis cognata*	18	20	6%	-0.7	*Desmanthus tatuhyensis*	7	6	-14%	0.6
Lantana montevidensis	7	5	-29%	-0.8	*Eupatorium ligulaefolium*	19	21	6%	-1.5	*Baccharis sessiliflora*	6	5	-17%	1.5
Baccharis sessiliflora	6	3	-50%	0.0	*Croton* cf. *nitrariaefolium*	15	12	5%	5.4	*Croton thermarum*	3	2	-33%	-2.3
					Desmanthus tatuhyensis	17	14	5%	0.2	*Myrsine umbellata*	3	1	-67%	-0.7
					Heterothalamus psiadioides	24	22	4%	3.0	*Heterothalamus psiadioides*	3	1	-67%	-20.0
HERBS:	F1	F2	FC	CC		F1	F2	FC	CC		F1	F2	FC	CC
Sisyrinchium vaginatum	0	5	new	0.7	*Zornia sericea*	3	4	44%	0.5	*Eryngium horridum*	2	5	150%	0.4
Prescottia oligantha	0	5	new	1.0	*Sisyrinchium macrocephalum*	5	8	32%	0.4	*Chaptalia runcinata*	2	4	100%	0.6
Polygala pulchella	0	4	new	1.0	*Senecio heterotrichius*	4	5	31%	0.6	*Dichondra sericea*	3	6	100%	0.5
Petunia integrifolia	0	5	new	1.2	*Eupatorium ivaefolium*	6	10	28%	0.3	*Borreria fastigiata*	7	11	57%	2.5
Hypoxis decumbens	0	4	new	1.0	*Viguiera angchusaefolia*	4	4	25%	5.2	*Achyrocline satureioides*	2	3	50%	3.3
Galium uruguayense	0	9	new	1.0	*Halimium brasiliense*	4	4	25%	-0.4	*Oxalis brasiliensis*	6	8	33%	1.8
Cuphea glutinosa	1	6	500%	-0.3	*Macroptilium prostratum*	5	6	24%	0.9	*Relbunium hirtum*	3	4	33%	0.4
Stevia aristata	1	5	400%	1.3	*Achyrocline satureioides*	9	16	20%	8.6	*Pfaffia tuberosa*	5	6	20%	0.2
Oxalis brasiliensis	1	5	400%	0.2	*Galium uruguayense*	8	12	19%	0.9	*Oxalix conorrhiza*	6	7	17%	0.1

(continued)

Group 1: recently burned					Group 2: burned one year before					Group 3: burned three years before				
HERBS:	F1	F2	FC		CC	F1	F2	FC		CC	F1	F2	FC	
Eryngium horridum	3	15	400%	1.5	*Richardia grandiflora*	7	8	16%	0.9	*Chaptalia sinuata*	9	9	0%	0.8
Halimium brasiliense	1	4	300%	1.3	*Pfaffia tuberosa*	11	18	15%	0.9	*Rynchosia diversifolia*	9	9	0%	0.3
Chaptalia sinuata	4	12	200%	0.8	*Pterocaulon rugosum*	7	7	14%	-1.6	*Hydrocotyle exigua*	3	3	0%	0.2
Hydrocotyle exigua	6	17	183%	1.2	*Hydrocotyle exigua*	8	9	14%	-0.2	*Euphorbia selloi*	6	6	0%	0.0
Lucilia acutifolia	5	14	180%	0.9	*Borreria capitata*	8	8	13%	-0.1	*Aspilia montevidensis*	8	8	0%	-0.3
Tibouchina gracilis	4	10	150%	3.0	*Aeschynomene elegans*	7	6	12%	0.2	*Centrosema virginianum*	12	12	0%	-0.4
Dichondra sericea	3	7	133%	1.4	*Galactea marginalis*	9	9	11%	0.1	*Evoluvuls sericeus*	4	4	0%	-1.3
Chaptalia runcinata	9	20	122%	1.1	*Hieracium commersonii*	6	4	11%	-1.0	*Eryngium pristis*	10	9	-10%	-0.2
Stylosanthes montevidensis	5	8	60%	0.5	*Glechon squarrosa*	8	7	11%	0.3	*Eupatorium ivaefolium*	7	6	-14%	-0.1
Evolvulus sericeus	14	22	57%	0.7	*Aspilia montevidensis*	13	18	11%	3.3	*Wissadula glechomatifolia*	5	4	-20%	2.0
Oxalis conorrhiza	8	12	50%	1.1	*Evolvulus sericeus*	12	15	10%	-0.1	*Clitoria nata*	4	3	-25%	2.3
Pterocaulon rugosum	5	7	40%	2.3	*Diodia apiculata*	8	6	9%	0.0	*Vernonia flexuosa*	3	2	-33%	0.5
Acmella bellidioides	5	7	40%	0.7	*Eryngium sanguisorba*	8	6	9%	-0.6	*Pterocaulon rugosum*	9	6	-33%	0.1
Vernonia flexuosa	17	23	35%	1.7	*Setaria vaginata*	14	14	7%	-6.2	*Aeschynomene elegans*	6	4	-33%	-0.5
Eryngium sanguisorba	9	12	33%	1.1	*Eryngium horridum*	13	11	7%	-5.6	*Stevia cinerascens*	4	2	-50%	-0.5
Richardia grandiflora	10	13	30%	0.7	*Orthopappus angustifolius*	13	10	6%	0.1	*Acmella bellidioides*	6	3	-50%	-1.8
Borreria fastigiata	10	13	30%	1.1	*Sisyrinchium vaginatum*	13	10	6%	-0.4	*Richardia grandiflora*	9	4	-56%	-0.6
Pfaffia tuberosa	15	19	27%	2.5	*Euphorbia selloi*	11	7	6%	-0.6					
Aspilia montevidensis	11	13	18%	2.1	*Vernonia flexuosa*	12	8	6%	0.8					
Euphorbia selloi	6	7	17%	-1.2	*Tibouchina gracilis*	11	6	5%	-4.0					
Eryngium pristis	9	9	0%	1.6	*Chaptalia integerrima*	8	3	5%	-0.2					
Clitoria nana	4	4	0%	1.5	*Chaptalia runcinata*	18	12	4%	-0.7					
Eupatorium ivaefolium	10	8	-20%	-7.4	*Lucilia acutifolia*	24	19	3%	0.0					
Centrosema virginanum	10	8	-20%	3.4	*Relbunium hirtum*	24	18	3%	0.3					
Desmodium incanum	5	4	-20%	-2.0	*Salvia procurrens*	10	0	0%	-27.2					
Herbertia pulchella	4	3	-25%	-0.3										
Aeschynome elegans	4	1	-75%	0.0										
Galactea marginalis	4	3	-25%	-0.3										
Stevia cinerascens	7	2	-71%	-1.9										
Wissadula glechomatifolia	11	3	-73%	0.0										

(continued)

Group 1: recently burned					Group 2: burned one year before					Group 3: burned three years before				
GRAMINOIDS:	F1	F2	FC	CC		F1	F2	FC	CC		F1	F2	FC	F1
Bulbostylis closii	2	10	400%	2.1	*Briza subaristata*	3	7	78%	1.4	*Stipa filifolia*	3	4	33%	2.5
Briza subaristata	1	5	400%	1.2	*Rhynchospora setigera*	3	6	67%	0.6	*Scleria selloi*	3	4	33%	0.2
Rhynchospora setigera	2	7	250%	1.1	*Bulbostylis sp.*	3	4	44%	-0.8	*Aristida laevis*	6	7	17%	9.7
Scleria selloi	3	9	200%	-0.3	*Briza uniolae*	4	6	38%	1.1	*Andropogon lateralis*	6	6	0%	4.7
Setaria geniculata	4	9	125%	3.1	*Paspalum plicatulum*	4	5	31%	0.8	*Andropogon ternatus*	3	3	0%	3.7
Bulbostylis junceoides	7	13	86%	1.0	*Axonopus pressus*	4	4	25%	0.0	*Dichanthelium sabulorum*	6	6	0%	2.0
Axonopus argentinus	8	14	75%	3.8	*Schizachyrium microstachyum*	6	8	22%	0.9	*Stipa filiculmis*	7	7	0%	1.5
Schizachyrium tenerum	5	8	60%	8.9	*Andropogon lateralis*	5	5	20%	5.0	*Paspalum plicatulum*	4	4	0%	0.8
Danthonia montevidensis	6	9	50%	3.4	*Andropogon selloanus*	6	7	19%	3.6	*Bulbostylis junceoides*	3	3	0%	0.3
Aristida flaccida	16	24	50%	10.0	*Piptochaetium montevidensis*	6	7	19%	0.3	*Briza subaristata*	3	3	0%	0.3
Andropogon lateralis	7	10	43%	1.8	*Axonopus suffultus*	11	14	12%	-0.3	*Axonopus pressus*	12	12	0%	0.2
Elionurus muticus	8	10	25%	8.6	*Scleria selloi*	8	6	9%	-0.5	*Trachypogon montevidensis*	10	10	0%	-2.0
Aristida laevis	8	10	25%	6.5	*Aristida flaccida*	11	11	9%	7.9	*Andropogon leptostachys*	7	7	0%	-2.4
Andropogon leucostachys	5	6	20%	3.9	*Leptochoryphium lanatum*	13	14	8%	-0.7	*Elionurus muticus*	12	11	-8%	2.3
Dichanthelium sabulorum	11	13	18%	1.2	*Aristida circinalis*	11	10	8%	1.5	*Piptochaetium montevidensis*	9	8	-11%	-1.2
Piptochaetium montevidensis	7	8	14%	0.6	*Aristida filifolia*	11	10	8%	-2.4	*Schizachyrium microstachyum*	8	7	-13%	0.1
Eragrostis polytricha	9	10	11%	1.4	*Cyperus aggregatus*	5	2	8%	-0.8	*Danthonia montevidensis*	5	4	-20%	0.3
Andropogon selloanus	11	12	9%	0.5	*Schizachyrium tenerum*	12	11	8%	1.7	*Schizachyrium tenerum*	3	2	-33%	-0.3
Rhynchospora globularis	30	26	-13%	0.0	*Aristida laevis*	18	19	6%	0.3	*Eragrostis polytricha*	3	2	-33%	-1.0
Stipa filifolia	8	6	-25%	-1.7	*Elionurus muticus*	19	19	5%	4.3	*Rhynchospora globosa*	18	10	-44%	-1.2
Leptochoryphium lanatum	12	9	-25%	0.5	*Dichanthelium sabulorum*	19	19	5%	1.2	*Leptochoryphium lanatum*	3	1	-67%	-1.7
Trachypogon montufari	14	7	-50%	0.1	*Setaria parviflora*	14	10	5%	-0.4					
Axonopus pressus	8	3	-63%	2.3	*Rhynchospora globularis*	19	14	4%	-0.8					
Paspalum plicatulum	6	1	-83%	-0.5										

CHAPTER 3

Adaptive strategies to fire in subtropical grassland in southern Brazil

with Jörg Pfadenhauer

submitted to *Flora*

Abstract

Extensive parts of subtropical South America are covered by grassland vegetation, despite climatic conditions allowing for forest development, and fire may have been an important factor in the evolutionary history of these grasslands. In a regularly burned grassland area, situated in a forest-grassland-mosaic near Porto Alegre, RS, Brazil, life-form spectrum and plant species' reaction to fire were examined, allowing for 1) a physiognomic description of the grassland, and 2) a functional classification of grassland species in relation to fire. Grassland sites with different time since the last fire were compared between each other as well as to sites at the forest-grassland border. South Brazilian grassland is dominated by hemicryptophytic caespitose graminoids that resist fires, but contains a large number of geophytic or hemicryptophytic forbs, in general sprouting after fire. Shrubs, mostly sprouting species of the grassland community, were present with high cover values even in recently burned areas. In contrast to Central Brazilian Cerrado, trees were of little importance: most species found were forest pioneer species without the capacity to survive fires unless on sites protected from fire or at the forest border where burns stop. However, non-sprouting species were of little importance in the community, and only two species found were therophytes. Lack of therophytes in South Brazilian grassland vegetation deserves further attention.

Keywords: Campos, fire, fire-life-form, life-form, plant functional type, Raunkiaer

Introduction

While savanna ecosystems cover large parts of tropical South America (e.g. Sarmiento 1990 for an overview), extensive parts of northern Argentina and Uruguay are characterized by grasslands, extended in the form of an arch around the Río de la Plata and continuing in the southern part of Rio Grande do Sul state (RS), Brazil (Soriano *et al.* 1992, Bilenca and Miñarro 2004). South Brazilian Campos grasslands, presenting a mixture of C_4 and C_3 grasses with C_4 dominance, are under subtropical humid climate (Köppen's Cfa) in southern RS, and under warm-temperate humid climate on the highlands in northern RS (Köppen's Cfb; Moreno 1961), in the latter in mosaics with Araucaria forests. Precipitation in southern Brazil ranges from 1,200 (southern RS) to over 2,200 mm yr-1 (northern RS), with no dry season. Hydric deficits may occasionally occur in the summer months, but current climatic conditions allow for forest development (Lindman 1906, Rambo 1956). Phytogeographical and palaeoecological data suggest that grasslands are relics of drier and cooler conditions during the last glacial and postglacial periods, stabilized by herbivory and fire and subject to forest invasion only relatively recently (Rambo 1953, 1956, Bigarella 1971, Klein 1975, Pillar and Quadros 1997, Behling 2002, Behling *et al.* 2004). In contrast to South African savannas and grasslands, large native herbivores are largely missing: they became extinct as the result of climatic changes between the end of the last glaciations and 8,000 yr BP (Kern 1994), coinciding with the arrival of human populations in the regions. The fire history of southern Brazil is poorly know. Palynological studies indicate that fire was rare during early post-glacial times, but became frequent about 7,400 years ago (Behling *et al.* 2004), possibly as it may have been used as a tool for hunting by indigenous people (Kern 1994). In Cerrado (Central Brazilian savannas), fire is considered to have been present long before human occupation, but frequency most probably has increased with anthropogenic use (Miranda *et al.* 2002, Hoffmann and Moreira 2002); the effect has been a stabilization of open vegetation formations by impeding establishment of forest species, and thus a change in physiognomy (Hoffmann 1996, Mirelles *et al.* 1997, Hoffmann 2000). Recent modelling of the distribution of vegetation types in southern Africa in relation to climatic parameters and fire has shown that in regions above a certain limit of precipitation (approx. 650mm for southern Africa), not climatic conditions, but presence of fire determines vegetation physiognomy, independent of historic human action (Bond *et al.* 2003). While less data is available for southern Brazil, the situation likely is similar.

Few studies have been conducted on the effect of fire on grassland communities in southern Brazil. Single fire events do not invoke major overall compositional changes (Eggers and Porto 1994), and fire has been shown to increase small-scale and short-term diversity (Overbeck *et al.* submitted (b)). Noble and Slatyer (1980) have presented a general model of plant strategies in respect to fire, focussing on regeneration or colonization attributes; application of this model to a community, however, requires detailed information on the life-cycle, persistence and dispersal abilities of the

species present. Bond and van Wilgen (1996) classify plants according to the two criteria survival of fire and reproductive response to fire. Similarly, chaparral species are commonly categorized into "obligate seeders", "obligate resprouters" and "facultative seeders/facultative resprouters" (e.g. Keeley 1986, Keeley 1992, Franklin *et al.* 2004). Survival of plants during fire depends principally on protection of buds: situation of buds is the principal criterion in one of the classical functional type systems: Raunkiaer's life-form spectrum (Raunkiaer 1934), applied for prediction of climate in many ecosystems of the world (see Cain 1950 for a compilation of life form spectra for various climatic regions) and considered to be a good predictor of disturbance (McIntyre *et al.* 1999). The growth-form system, an essentially synonymous (Pillar and Orlóci 2004), but somewhat less strict classification as not based on a clear criterion but on general plant architecture, has been identified to be a useful framework for classification into plant functional types in various systems (e.g. McIntyre *et al.* 1995, Chapin *et al.* 1996, Diaz and Cabido 1997). In this paper, we present the physiognomic composition of a grassland community subject to frequent burns in southern Brazil, and discuss functional attributes in relation to fire, evaluating applicability of the classical life-form system and linking it to the main post-fire regeneration mechanisms in an alternative classification. Further, we characterize the principal plant types present in a brief, review-like way and compare the in general still poorly studied South Brazilian Campos grassland with other burned grassland systems concerning life-form composition.

Methods

Study site

Field work was carried out on Morro Santana, Porto Alegre, RS, Brazil. Morro Santana (30°03' S, 51°07' W, max. alt. 311m a.s.l.), situated at the northern limit of the Crystalline shield in RS, is covered by a mosaic of forests (Atlantic forest) and grasslands. The predominant soil types are Acrisols and Umbrisols (FAO classification; Garcia Martinez 2005). Floristic composition of the grassland area has been presented in Overbeck *et al.* (submitted (a)). The grasslands are species rich, with a total of 430 species identified so far in an area of about 220 ha, from a species pool of about 450 to 500 species. Borders between forest and grasslands have been remarkably stable in the past decades, due to frequent fires which prevent expansion of forest into grassland. Isolated patches of shrubs and trees, considered nuclei of forest establishment, can be found principally in areas with rock outcrops. Presence of fire, today anthropogenic, throughout the past 1200 years has been confirmed by a palynological study (Behling *et al.*, unpubl.); even though no data for previous periods exists, we suppose that fire should have been present long before (see Introduction).

Data collection

6 pairs of transects (distance between transects in each pair approximately 5m) were installed from the forest border into the grassland, in areas differing in slope, aspect, degree of shrub

encroachment and time since the last fire. In October 2002, one transect in each of the pairs was subjected to an experimental burn; however, in two of the transects, situated in areas that had burned almost 1 year before, the fire did not spread due to lack of continuous biomass. This left us with four transects burned in our experiments (group 1), 4 transects burned a year before (group 2), and 4 transects burned three or more years before (group 3). To be able to sample both the herbaceous stratum and characterize woody species distribution, we used a stratified plot design. Each transect consisted of 7 contiguous large plots (LPs) of 4.5m by 4.5m. The first plot, situated directly at the forest-grassland border, did not burn in any of the transects. Within LPs, 3 contiguous mid-sized plots (MPs) of 1.5 by 1.5m were marked, totalling 21 contiguous plots from the border into the grassland for each transect. In LPs, all woody vegetation components (trees and shrubs) with height above 80cm were recorded (number of individuals per species), whereas in MPs, cover of all woody individuals above 10cm was estimated, using the Londo (1976) decimal scale. Floristic composition of the herbaceous layer was sampled in three small contiguous plots (SPs) of 50cm by 50cm, marked in the center of LPs 1, 3, 5 and 7 (1 being closest, 7 farthest to the forest border), using the Londo (1976) decimal scale. Additionally, cover of litter, rocks, mosses, open soil and total cover of standing dead biomass were recorded in SPs, while in MPs and LPs, total cover of herbs, grasses (divided into living and dead), lianas, rocks, mosses, litter and open soil and medium height of the herbaceous stratum recorded. All surveys were conducted 2 to 3 months after the experimental fire. A structural survey in MPs and LPs had also been conducted right before, and, in burned plots, one week after the experimental burns.

Data analysis

Data from the three contiguous SPs was pooled to one plot of 0.75m² by taking the mean value across plots for each species or structural category. Species were grouped into life-forms according to Raunkiaer's (1934) system, with a modified classification into subgroups (Tab. 1).

Table 1: Raunkiaer's life-forms and sub-types used in this study. Modified from Raunkiaer (1934).

Main type	Sub-type	Criteria
Therophytes	-	No perennating buds; plants complete life cycle in one year; only seeds as perennating structures
Geophytes	Bulbous geophytes	Bulbs or corms as perennating organs, situated below the soil surface
	Rhizomateous geophytes	Rhizomes or tubers as perennating organs, situated below the soil surface
Hemicryptophytes	Forbs	Forbs with meristems at the soil surface
	Caespitose graminoids	Caespitose graminoids with meristems more or less at the soil surface, usually in densely packed tussocks
Shrubs	-	In general multi-stemmed growth; local denomination of species
Trees	-	In general single-stemmed growth; local denomination of species
Lianas	-	Herbaceous or woody plants without self-supporting structures

Plants were grouped *a posteriori*, i.e. according to potential life-form of the species. Instead of grouping woody species into phanerophytes and chamaephytes as in Raunkiaer's system, they were categorized into the growth-form categories shrubs and trees, considered to reflect differences in plant carbon allocation strategy (Bond and Midgley 2000; see also Sarmiento and Monasterio 1983), thus avoiding the necessity to fix a height limit between the two groups, which would be arbitrary in subtropical vegetation.

We then modified this system according to survival capacity to fire, obtaining the classification into fire-life-forms presented in Tab. 3. In this new classification, position of the buds (Raunkiaer's criterion) is joined by information on whether the plant dies (non-sprouter), looses all aboveground biomass (sprouter) or manages to keep at least some aboveground biomass (resister) during a fire. No evidence of stimulation of heat germination by fire (as known for many hardseeded shrubs in Mediterranean climate regions, e.g. Keeley and Fotheringham 2000) exists for the studied region (Overbeck *et al.* submitted (c)); thus, it was not necessary (nor possible) to include an attribute for this in the classification. For both Raunkiaer's system and the fire-life-form classification, individual species cover values were summed up to the corresponding life-form category, and then the relative cover of each category in relation to total vegetation cover was calculated, allowing for comparison of areas contrasting greatly in total vegetation cover in relation to time since the last burn. Species that had not been totally identified and could not be safely assigned to any life-form group were considered as part of total vegetation cover in calculation of relative cover values of each life-form group, but otherwise left out from the analyses (0.58% of sum of all frequencies). The three plot groups representing different time since the last fire were compared for differences between performance of each life-form and fire-life-form, using univariate analysis of variance with randomization testing (MULTIV software, Pillar 2004; Euclidean distance as resemblance measure, a=0.05 as probability limit for rejection of null-hypothesis). Cover of standing dead biomass was treated the same way. Further, border plots were compared to grassland plots taken as a group. In addition to the vegetation life-form spectrum based on relative cover values, a floristic life-form spectrum based on species number per life-form group was elaborated.

For MP and LP data, species were grouped into shrubs and trees (growth-forms), into species commonly known as grassland species, forest border species, or as forest species (successional groups) and into species with or without sprouting capacity after fire (regenerative types). Total number of individuals (LPs) and total cover (MPs) per plot for each of these groups was compared between grassland plot treatment groups by univariate analysis of variance with randomization testing, and between border plots and grassland plots taken as a group (Euclidean distance; a=0.05). Spearman rank correlations were calculated between total number (LPs and MPs) or total cover (MPs only) of woody individuals and the variables describing vegetation structure for all grassland plots to test if the woody species component in the grassland was related to structural factors of the community, such as

density of the herbaceous layer. For this, data from the survey right before (unburned plots) and right after the burns (burned plots) and from the survey 2 to 3 months after the burns was used.

Results

Raunkiaer's life-form and fire-life-form spectra for the community: data from SPs

When comparing relative cover of the different life-forms in the treatment groups (grassland plots with different time since fire), few significant differences could be found for any of the life-form categories. Over all treatment groups, hemicryptophytes amounted to 67.3% of relative cover (caespitose grasses alone to 50.1%), geophytes to 16.3%, and shrubs to 15.1% (mean values). Therophytes barely contributed to total cover (Tab. 2A). Trees and lianas showed low cover values. In border plots, relative cover of caespitose grasses was significantly lower compared to grassland plots as a group, in contrast to lianas for which the opposite was true. Cover of trees, but not shrubs, was significantly higher at the border (see Appendix 1 for complete list of species from SPs).

Table 2: Vegetation (A) and floristic (B) spectrum of Raunkiaer's life-forms (n=12 for grassland groups and border plots). For the vegetation composition (based on relative cover), plots from group 1 and 2 differed significantly for geophytes and for hemicryptophytic forbs (p<0.05; indicated by an asterix in the table). Relative cover of all hemicryptophytes, caespitose grasses, trees and lianas differed between border plots and all grassland plots taken as a group (p<0.001; indicated by Italics in the table).

	A: Relative cover values (Vegetation spectrum)				B: Percentage of species (Floristic spectrum)			
	Group 1	Group 2	Group 3	Border	Group 1	Group 2	Group 3	Border
Therophytes	**0.22%**	**0.00%**	**0.08%**	**0.00%**	**0.88%**	**0.00%**	**1.56%**	**0.00%**
Geophytes*	**19.55%**	**12.23%**	**16.98%**	**11.86%**	**19.30%**	**17.80%**	**14.84%**	**13.93%**
- bulbous	0.65%	0.14%	0.26%	0.03%	4.39%	2.54%	3.13%	0.82%
- rhizomateous	18.91%	12.09%	16.72%	11.83%	14.91%	15.25%	11.72%	13.11%
Hemicryptophytes	*62.12%*	*70.24%*	*69.54%*	*44.26%*	58.77%	62.71%	55.47%	50.82%
- caespitose graminoids	*42.00%*	*51.01%*	*57.15%*	*31.16%*	25.44%	27.97%	23.44%	20.49%
- forbs*	20.12%	19.24%	12.43%	13.10%	33.33%	34.75%	32.03%	30.33%
Shrubs	**15.70%**	**17.25%**	**12.28%**	**9.82%**	**17.54%**	**19.49%**	**22.66%**	**16.39%**
Trees	*2.05%*	*0.00%*	*0.19%*	*7.91%*	1.75%	0.00%	2.34%	12.30%
Lianas	*0.22%*	*0.00%*	*0.67%*	*25.75%*	1.75%	0.00%	3.13%	6.56%

Concerning number of species in each life-form group, hemicryptophytic forbs were the most important, followed by caespitose grasses, shrubs and rhizomateous geophytes, with little differences between treatment groups (Tab. 2B). Species numbers for the different life-form groups did not differ much at the forest border, except for liana and tree species. Therophytes were almost completely absent.

In the fire-life-form classification, sprouting species summed up to 55.5% of relative cover in recently burned plots. Their contribution, however, was markedly lower in plots of group 2, and relative cover of hemicryptophytic sprouters differed significantly between groups 1 and 3. While

cover of sprouting forbs and shrubs thus decreased with time since fire, relative cover of caespitose grasses, exclusively making up the group of resisters in grassland plots, showed an increase with time since fire. Non-sprouting species contributed less than 10% of relative cover in all groups of grassland plots. Border plots had significantly higher relative cover of non-sprouting trees, sprouting trees and lianas, and significantly less of caespitose grasses, which contributed to less than 1/3 of relative cover at the forest border (see Appendix 1 for complete list of species from SPs).

Table 3: Fire-life-form distribution in frequently burned grassland on Morro Santana, Porto Alegre, RS, Brazil. Groups printed in Italics differed significantly between grassland plots as a group and border plots concerning relative cover value. Sprouting hemicryptophytic forbs differed between plots of groups 1 and 3, indicated by an asterix in the table.

	Relative cover values				Percentage of species	
	Group 1	Group 2	Group 3	Border plots	All Campos plots	Border plots
Nonsprouters[1]	**2.4%**	**9.0%**	**6.9%**	**6.5%**	**7.7%**	**14.5%**
- Therophytes	0.2%	0.0%	0.8%	0.0%	1.1%	0.0%
- Hemicryptophytes	1.3%	6.1%	1.6%	1.7%	2.2%	4.1%
- Shrubs	0.9%	2.9%	4.3%	0.7%	2.8%	2.5%
- Trees	0.0%	0.0%	0.2%	4.1%	1.7%	8.2%
Sprouters (from belowground organs)	**55.5%**	**39.7%**	**36.5%**	**63.0%**	**67.9%**	**63.9%**
- Geophytes	**19.6%**	**12.2%**	**17.0%**	**11.9%**	**17.7%**	**13.9%**
- bulbous	0.6%	0.1%	0.3%	0.0%	3.3%	0.8%
- rhizomateous	18.9%	12.1%	16.7%	11.8%	14.4%	13.1%
- Hemicryptophytic forbs*	18.8%	13.2%	10.9%	12.6%	30.9%	26.2%
- Shrubs	14.8%	14.3%	8.0%	9.1%	15.5%	13.9%
- *Trees*	*2.0%*	*0.0%*	*0.0%*	*3.7%*	1.1%	3.3%
- *Lianas*	*0.2%*	*0.0%*	*0.7%*	*25.7%*	2.8%	6.6%
Resisters (aboveground survival)[2]	**42.0%**	**51.0%**	**57.1%**	**31.3%**	**24.3%**	**21.3%**
- *Caespitose graminoids (hemicryptophytic)*	*42.0%*	*51.0%*	*57.1%*	*31.2%*	24.3%	20.5%
- Shrubs	0.0%	0.0%	0.0%	0.0%	0.0%	0.0%
- Trees	0.0%	0.0%	0.0%	0.1%	0.0%	0.8%

[1]per definition, no non-sprouting geophytic species exist. No non-sprouting grasses were found in our study.
[2]no resisting geophytes, hemicryptic forbs or lianas could be found in the study.

Standing dead biomass differed significantly between the three treatment groups (p<0.001), with mean values of 2.5% in recently burned SPs (group1), 9.8% in SPs of group 2 and 23.2% in SPs of group 3. Standing dead biomass almost completely could be contributed to species from the Poaceae or Cyperaceae. In the border plots (all unburned since 3 years or more), standing dead biomass had a mean cover of 10.4%.

Characterization of the woody stratum: data from MPs and LPs

Cover values for shrub and tree species was higher in MPs than in SPs, most likely due to the very small total area size sampled by SPs. This underrepresentation of shrubs and trees in the SPs has to be kept in mind when interpreting the data on the community level and underlines the importance of a nested design when working in communities with distinct herbaceous and woody strata, where high richness of the herbaceous layer impedes working with larger plot size. Using the MP data, in average, 5.4 shrubs and 0.1 trees could be found per m² in the grassland. 36 of the species (27 shrubs, 9 trees) were sprouters and 20 non-sprouters (8 shrubs and 12 trees); three were able to resist fires with above-ground biomass. Sprouters showed substantially higher cover values than non-sprouters both in grassland and at the border, however, more pronounced in the grassland and relatively more in recently burned areas. In general, cover of shrubs and trees rose with time since fire (Tab. 4A; see Appendix 2 for complete list of species from MPs).

Table 4: Cover and number of shrubs and trees per m², using data from A) 232 plots of 1.5 by 1.5m (cover values; all woody species >10 cm) and B) 84 plots of 4.5 by 4.5m (number of individuals per m², all woody species > 80 cm) on Morro Santana, Porto Alegre, RS, Brazil. Values presented comparing groups of grassland plots with different time since fire (A1, B1) and grassland plots as a group with border plots (A2, B2). Different letters indicate significant differences between groups (p<0.05), to be read per line, separately for A1, A2, B1, B2.

	A) MPs – Cover (all individuals > 10cm)					B) LPs - Number per m² (all individuals > 80cm)				
	A1) Grassland with different time since fire (Groups 1, 2, 3)			A2) Open grassland (Camp.) and border (Bord.)		B1) Grassland with different time since fire (Groups 1, 2, 3)			B2) Open grassland and border	
	Gr. 1	Gr 2	Gr 3	Camp.	Bord.	Gr 1	Gr 2	Gr 3	Camp.	Bord.
Total	20.3% a	29.3% b	35.8% b	28.4% a	45.2% b	0.05 a	0.14 a	0.48 b	0.23 a	0.65 b
Growth forms										
- Trees	1.8%	0.8%	2.9%	1.8% a	21.9% b	0.02	0.02	0.02	0.02 a	0.32 b
- Shrubs	18.5% a	28.5% b	32.9% b	26.6%	23.3%	0.03 a	0.12 a	0.46 b	0.21	0.34
Successional groups										
- Grassland species	18.3% a	28.0% b	29.6% b	25.3% a	14.3% b	0.03 a	0.12 a	0.43 b	0.19	0.21
- Border/Pioneer species	0.4%	0.5%	3.9%	1.6% a	10.3% b	0.00	0.00	0.03	0.01 a	0.14 b
- Forest species	1.4%	0.8%	2.3%	1.5% a	20.6% b	0.02	0.02	0.02	0.02 a	0.31 b
Regenerative types										
- Non-sprouters	1.1% a	3.7% b	12.2% c	5.6% a	15.1% b	0.02 a	0.00 a	0.20 b	0.07 a	0.33 b
- Sprouters	18.8% a	25.6% b	23.0% ab	22.5%	27.4%	0.03 a	0.14 b	0.28 b	0.15 a	0.30 b
- Resisters	0.4%	0.0%	0.6%			0.00	0.00	0.00	0.00 a	0.0b a

Tree species, border species or forest species were of little overall importance in the grassland's woody species community, but present throughout the area, whereas grassland shrubs clearly were the most important component of the grassland. The only resisters were *Leucothoe*

eucalyptoides (Ericaceae), *Butia capitata* (Araceae), both with thick bark, and *Opuntia macrocantha* (Cactaceae), where at least part of the plant survives due to its high moisture content. In grassland LPs, a mean of 0.23 woody plants above 80cm could be found per m², 0.21 of these being shrubs and 0.02 trees (Tab. 4B). Number of woody species was significantly higher ($p<0.001$) in plots of group 3, where 0.48 individuals above 80cm were present per m², in comparison to 0.05 and 0.14 in treatment groups 1 and 2, respectively. The largest part of woody species in the grassland were grassland species, in contrast to the border, where species from the forest or from the border were of importance as well, with in general higher numbers of trees and shrubs from all successional groups (Tab.4B; see Appendix 2 for complete list of species from LPs).

No strong correlations (with a correlation coefficient above 0.4 or below -0.4) between number or cover of woody species in LPs and MPs and structure of the herbaceous stratum (cover of dead and live grasses, herbs, lianas, litter, open soil, rocks, height of grass layer) was detected, for either sampling data of vegetation structure attributes.

Discussion

Applicability of Raunkiaer's life-form system to fire

Application of Raunkiaer's system to tropical ecosystems has been criticized (Sarmiento and Monasterio 1983, Solbrig 1993) because many species cannot readily be classified into the categories, as, depending on events such as heavy drought and fire, growth patterns may undergo changes from one class to another, e.g. trees may resprout like shrubs, recovering their biomass by „crowns on the ground level" (Bellingham and Sparrow 2000). Further, the height limit of 25 to 50 cm between the two groups (Ellenberg and Mueller-Dombois 1966) is a consequence of the height of central European dwarf shrubs and cannot be applied in tropical or subtropical systems, where chamaephytes may grow higher: here, growth forms (shrubs and trees), i.e. a categorization based on plant architecture, seem to be a more useful criterion (Sarmiento and Monasterio 1983). The relatively large overlap between trees and shrubs in relation to other life-forms is well known (Kelley 1996), even though drought periods may be considered to be an adverse season equivalent to Raunkiaer's cold season in a functional sense as they lead to death of aboveground biomass: a relationship between contribution of phanerophytes in the life-form spectrum and total amount and inter-seasonal variation of rainfall has been recognized (Skarpe 1996). However, the life-form system had originally been elaborated to characterized plant strategies in face of an unfavorable season, and not to disturbances, which shape, for example, tropical savannas or subtropical grasslands. In such systems, position of buds is not solely a consequence of climatic conditions, but influenced by other environmental factors, e.g. the action of herbivory or fire (Cain 1950). The life-form system therefore is useful for description of vegetation physiognomy, but does not necessarily serve for prediction of climatic conditions, as originally indented by Raunkiaer.

Fire-life-forms

In vegetation subject to frequent burns, survival and sprouting ability depend on the degree of bud protection: a chamaephyte or phanerophyte may have to sprout from belowground buds after the fire, or a hemicryptophyte may not be able to sprout at all. Plants in fire-prone habitats have been grouped into plants resisting the fire with part of their aboveground biomass (resisters, Rowe 1983), plants dying back completely aboveground, but surviving due to insulation of buds by the soil (endurers, Rowe 1983; sprouters, Bond and van Wilgen 1996) and into plants having to germinate either from the seed bank (evaders, Rowe 1983) or from newly dispersed seeds (invaders, Rowe 1983). If recruitment occurs only right after a fire event, non-sprouters have been termed fire-recruiters (as opposed to fire-persisters; Keeley 1992). Between growth- or life-forms, traits allowing for survival of fire vary. Resistance in woody plants is principally achieved by protective tissues, e.g. thick bark with low heat conductivity (Gill 1981, Bond and van Wilgen 1996), often joined by elevation of buds above the flammable vegetation layer (e.g. Givnish *et al.* 1986). In tussock grasses, densely packed basal leaf sheaths allow for protection of aboveground meristems from fire (e.g. Gill 1981, Sarmiento 1992). Sprouting ability from belowground organs is usually a consequence of buds protected by the soil, where temperature effects on plant tissue stay below values causing damage (45° to 55° C for most plants; Levitt 1980): higher temperatures are only reached in the uppermost centimeter of soil (e.g. Silva *et al.* 1991, Miranda *et al.* 1993, Bradstock and Auld 1995, Auld and Bradstock 1996).

In the studied grassland, very few species managed to keep large amounts of aboveground live biomass through the action of a fire. However, meristems of tussock grasses, making up more than 50% of plant cover one year after a burn, remained alive slightly above the soil surface; species from this group thus have to be considered as resisters, even though their behaviour does not differ much from hemicryptophytes sprouting from buds at the soil surface. Individuals of *Eryngium horridum* (Apiaceae), a large rhizomateous rosette species with fibrous leaves and high water content, sometimes did not burn completely and managed to keep some live biomass at the center of the leaf rosettes, however, regaining aboveground biomass after the fire through sprouting of new rosettes (Fidelis *et al.* submitted), i.e. essentially behaving like a sprouting species. The cactus species *Opuntia macrocantha* and *Pavonia ottonis*, sparsely present in the studied grassland, will not burn due to their high water content, but, if fire is intense enough, aboveground biomass will die due to the effect of fire temperature on plant tissue. It is difficult to classify them into the fire-life-form categories, as resprouting can occur from below- or above-ground organs, depending on fire severity and amount of lignified structures. In a study in subtropical grasslands in Texas, Bunting *et al.* (1980) showed that 20 to 65% of plants from three *Opuntia* species did not sprout after fire, but that mortality rate rose to 60 to 80% in a period of four years after fire, as a consequence of increased herbivory and fungal or bacterial infections on fire-damaged plants. Resisting capacity thus is clearly lower than that of the "true" resisters, in our study only the tree *Leucothoe eucalyptoides* (Ericaceae) and the palm *Butia*

capitata (Arecaceae).

A small percentage of species in the studied grassland was not able to resprout, but depended on regeneration from seeds after fire(obligate seeders; Bond and van Wilgen 1996). This group of non-sprouters comprised plants from all life-forms, except for geophytes. These should be the most successful of the fire-life-forms considering survival of burns (Taylor 1978), explaining why frequent fires often favor sprouting forbs, often geophytes, over grasses, mostly hemicryptophytes (Daubenmire 1968, Rowe 1983). In hemicryptophytes, the large majority of the species in our grassland plots either were sprouters or resisters. In the group of shrubs, however, the majority of species where sprouters, indicating that position of above-ground buds alone is a poor predictor of fire survival for the studied grassland. Both the application of Raunkiaer's system and of the fire-life-form classification showed little overall changes between different treatment groups, reflecting slight shifts in relative importance in different post-fire stages due to differences in competitive ranking (Suding 2001), but no pronounced changes in plant types.

When classifying plant species into fire-life-form categories, two things have to be kept in mind: fire intensity may differ between fires and according to local site characteristics, and resistance capacity in respect to fire may not be the same for all life-stages of plants (e.g. Gill 1981, Bond and van Wilgen 1996). These two factors, alone or in combination, in some cases may allow for survival of above-ground biomass in individuals even without protected buds on protected sites (in the study area, for example, between rock outcrops, where no continuous grass layer exists to support a fire) and for damage of even belowground plant-parts in others when in an early life-cycle phase or when subjected to extremely severe fire event, e.g. on sites with higher fuel availability (see example of Cactus species above). Sensitivity of sprouting species to fire will further depend on season of fire and thus on specific phenology of plant active phases and carbohydrate storage (Bond 1997), requiring for the study of phenological cycles of the species in question for more detailed prediction of the effect of fire on a grassland community (Sarmiento and Monasterio 1983, Towne and Owensby 1984, Loucks *et al.* 1985).

Brief functional characterization of main species groups in relation to fire

Non-sprouting species

No significant differences could be found for cover values of non-sprouting species, i.e. obligate seeders, between the treatment groups, suggesting that, at least in their majority, they cannot be considered to be fire-followers as found in some shrubland or grassland communities (e.g. Keeley *et al.* 1981, Ghermandi *et al.* 2004), but will need some time to regain their pre-fire cover values through new seedling recruitment from the seed bank or through seed dispersal (see also Overbeck *et al.*, submitted (b)). Fire annuals (Keeley *et al.* 1981) were absent in the studied grassland. Within the group of non-sprouters, a small number of hemicryptophytic species with lack of protected buds was

present in all treatment groups. Especially common were *Dichondrea sericea* and *Evolvulus sericeus*, two small creeping herbs (Convolvulaceae) that also appeared in great quantities in a study of the seed banks in the grasslands on Morro Santana (Müller and Overbeck, unpubl.). Of great importance considering cover values, especially in treatment groups 2 and 3 with more time since fire, were the shrubs *Heterothalamus psiadioides* and *Baccharis dracunculifolia*, which do not resprout, in contrast to a number of other Asteraceae shrub species with very similar habitus. Especially *H. psiadioides* showed very strong recruitment in some plots of group 2, where it had been present with large cover values before the last burn (field observation) As this species also was very abundant in the seed bank in the study area (unpubl. data), most probably the creation of open soil by the fire event will have been responsible for its regeneration. In contrast to chaparral (Christensen 1985, Keeley 1986), frequent fires apparently do not eliminate seeders in subtropical grassland.

Graminoids

Caespitose grasses, in their vast majority tussock grasses with the C_4 photosynthetic passway, together with Cyperaceae species accounted for over 50% of vegetation cover in the studied grassland. We did not found any annual grasses, and only a small percentage of grasses was stoloniferous or rhizomateous, in contrast to grazed grasslands in the region (Boldrini and Eggers 1997, Rodríguez *et al.* 2003). The majority of the caespitose grasses found in the study on Morro Santana also occur in the Brazilian Cerrado, including most of the dominant species (e.g., *Andropogon lateralis*, *Leptochoryphium lanatum, Elionurus muticus*). Tussock grasses present densely packed basal shoots that allow for survival of fire despite aboveground location of meristems (Gill 1981); young plants, however, may be seriously affected by fire in their survival (e.g. Silva and Castro 1989). Some tussock grasses depend on regular burns on the long run: without periodic removal of biomass through fire, shading by dead biomass inhibits survival and tillering and higher humidity under the litter may cause death and decay of underground plant parts within a few years (e.g. Vogl 1974, Silva *et al.* 1990, Silva *et al.* 1991, Morgan and Lunt 1999, Bond *et al.* 2003). Increased photosynthetic activity after fire has been documented for *Andropogon gerardii* in tallgrass prairie (Knapp 1985), and increased growth rates after burning are known for many caespitose grass species (Silva *et al.* 1991), e.g. for *Andropogon lateralis*, one of the most dominant grasses in southern Brazil (Trindade and da Rocha 2001). Sexual reproduction is stimulated by burning in many savanna grass species (Gill 1981, Sarmiento 1992). Especially grasses from the Andropogoneae tribe, of high importance in the studied grassland, are extremely productive under suitable, i.e. sufficiently humid, climate conditions, producing large amounts of badly decomposing biomass (Bond *et al.* 2003), thus allowing for yearly burns where dominant (see also Overbeck *et al.* submitted (d)).

Woody plants

Woody species in South Brazilian Campos differ strikingly from woody species both in African and neotropical savanna. In these systems, trees, commonly resisting fire because of protective bark, characterize vegetation physiognomy (e.g. Sarmiento and Monasterio 1983 for an overview). Tree species found in grassland communities in southern Brazil, in contrast, are pioneer trees that usually do not tolerate fire; frequent fires thus should impede recruitment of forest pioneer trees in grassland and thus forest expansion (Müller *et al.*, unpubl.). The woody stratum in Campos grassland is comprised principally of grassland shrubs, in their majority sprouters, with species from the Asteraceae having the greatest importance both in terms of species number and cover values. Usually, these shrubs do not exceed 2m in height, and part of them remains within the height of the grass layer. In the absence of disturbance, the shrubs may form dense stands, often as belts along the forest-grassland border (Oliveira and Pillar 2004). However, it has not been studied so far if and in which ways they facilitate establishment of forest species and to what extent they suppress flammability, thus possibly accelerating vegetation change to forest when fire intervals become longer. In southern Brazil, fires reduce the shrub component more or less to the ground level, with rapid recovery of biomass after the fire. Flowering and fructification for the majority of grassland shrubs (e.g. sprouting Asteraceae) may take place within 3 months after the fire (field obs.), for some species even less (e.g. the resprouter *Schinus weinmanniaefolius,* Anacardiaceae: fruits two months after fire). Distribution of shrubs in the system is rather patchy; this may be due to differences in recruitment behaviour (populations of sprouting species should be spatially more stable), differences in edaphic conditions or different fire history.

From field-observations and considering the lack of significant correlations between the shrub/tree layer and the herbaceous layer, we conclude that shrub density does not become high enough as to impede growth of caespitose grasses and forbs, at least in fire intervals of less than 5 years. If recruitment of shrub species were facilitated by fire (presence of open soil), an interaction between fire regime (colonization sites) and presence of shrubs in nearby unburned areas (seed sources) could exist. For South Brazilian grasslands, studies addressing functional characteristics, life history strategies and population dynamics of woody species under different disturbance regimes are necessary, especially to be able to compare Campos grassland to Brazilian Cerrado or other savanna systems. Under present climatic conditions and without recurrent disturbances, South Brazilian grasslands will turn into shrublands, or into a mosaic of grassland, shrublands, and forest islands, subsequently leading to forest development (Müller and Forneck 2004, Oliveira and Pillar 2004).

Resprouting forbs

High diversity of South Brazilian Campos is largely a consequence to the high number of forb species (see e.g. Overbeck *et al.*, submitted (a)), in their vast majority sprouters. In other burned grasslands, e.g. North American tallgrass prairie (Benson *et al.* 2004) or Australian temperate

grassland (Morgan 1999), resprouting has been identified to be the prevalent strategy for post-fire biomass recovery in forbs. High productivity of caespitose grasses and accumulation of litter leads to the loss of forbs due to dominance effect of graminoids in an apparently relatively random process of thinning out of herbaceous species irrespective of species identity (Overbeck *et al.*, submitted (b)). Litter, which will accumulate in the absence of fire, grazing or mowing, in general is considered to reduce forb density and richness in grasslands around the world (e.g. Knapp and Seastedt 1986, Facelli and Pickett 1991). In the studied grassland, richness of (sprouting and non-sprouting) forb species thus can be directly linked to the fire cycle (Leach and Givnish 1996), even though these should not be important in terms of flammability. Studies of population biology and life history of herbaceous species in southern Brazil are missing almost entirely (but see Fidelis *et al.* submitted).

Life-form composition of Brazilian subtropical grassland in a global perspective

High importance of shrubs and increased recruitment of forest pioneer species in sites close to the forest-border (seed sources) demonstrates the suitability of the Campos biome's climate for woody vegetation types; in fact, longer unburned grassland in southern Brazil resembles secondary succession in areas formerly covered by forests (Reitz and Klein 1964).

Similarly to Campos grassland (this study, Boldrini 1993, Garcia *et al.* 2002, Rodríguez *et al.* 2003) a lack of annual species has also been noted for Brazilian Cerrado, in contrast to many other grasslands and savannas worldwide (Sarmiento and Monasterio 1983, Batalha and Martins 2002). Bond *et al.* (2003) suggest for subtropical Southern Africa that perennial sprouters are characteristic of fire-dependent grasslands, while annuals prevail in climatically defined grassland, i.e. in regions where development of woody vegetation types is impeded by insufficient moisture supply. Similarly, in Australian temperate lowland grasslands, the forb component is dominated by perennials in all but the driest regions (Lunt and Morgan 2001). Most of the Cerrado biome today is considered to be under climate suitable for forest establishment, but – like in southern Africa – fire, interacting with climatic and edaphic factors, determines actual vegetation physiognomy (Henriques and Hey 2002, Oliveira-Filho and Ratter 2002). The same seems to be true for South Brazilian grassland. In the subtropical Campos region, with a humid climate without any dry season, no climatic restriction favors an annual life cycle. On the other hand, in many environments, annual species are known to profit from disturbance events (Grime 1977, Belsky 1992) and in many fire-prone grasslands, opportunistic post-fire colonizers appear in early post-fire vegetation development (e.g., Ramsay and Oxley 1986, Lunt and Morgan 2001, Laterra *et al.* 2003). For tallgrass prairie, some studies have shown that contribution of annuals increases with disturbance (fire, grazing) intensity (e.g., Collins 1987, Gibson *et al.* 1993, Engle *et al.* 2000), while in other studies, therophytes were almost missing (Towne and Owensby 1984); however, we do not know of any study addressing life-form composition on the gradient from tallgrass to shortgrass prairie. In some Australian temperate grasslands, exotic annuals dominate the seed bank and the post-fire seedling flora, which has been attributed to the paucity of native annuals

(Morgan 1998, 2001) and to long-term grazing that led to a loss of native species in the seed bank (Lunt 1990). Exotic annuals could not be found in the grassland studied by us, despite the low contribution of native annuals. Does the "niche for annuals" exist in southern Brazil? The lack of therophytes in South Brazilian grassland likely needs to be addressed in a comparative study of grasslands systems around the world, under various climatic conditions and under different disturbance regimes. The life-form spectrum is a simple, yet meaningful and readily usable classification; however, at present surprisingly little reliable data on life-form spectra for grassland communities can be found in the literature. If joined by regeneration attributes, like in our study, interpretational value of Raunkiaer's system should be enhanced considerably, allowing for comparative analysis of the influence of climatic factors and disturbance on composition and vegetation dynamics in grasslands in a global perspective.

Acknowledgements

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Appendix 1: Species recorded in 144 plots of 0.25m², pooled to 48 plots of 0.75m², on Morro Santana, Porto Alegre, RS, Brazil. Given are family, species name, life-form (LF; modified after Raunkiaer (1934); th: therophyte, gb: bulbous geophyte, gr: rhizomateous geophyte, h: hemicryptophyte (excluding caespitose graminoids), hc: hemicryptophytic caespitose graminoid; s: shrub, t: tree, l: liana) and regenerative type after fire (RT; r: resister, s: sprouter, n: non-sprouter), mean cover value (C) and frequency (F) of species per group of plots, separated for grassland plots at the forest-grassland border (Border, n=12), and plots in the open grassland, grouped into plots burned three months before (Group 1; n=12), burned a year before (Group 2; n=12) and unburned for three years or more (Group 3, n=12). No information is given for species not totally identified.

Family	Species	LF	RT	Border C	F	Group 1 C	F	Group 2 C	F	Group 3 C	F
Acanthaceae	*Justicia brasiliana* Roth	s	n	0.009	1	0	0	0	0	0	0
	Stenandrium Nees sp.	h	s	0.005	1	0	0	0	0	0	0
Amaranthaceae	*Pfaffia tuberosa* (Moq. ex DC.) Hicken	gr	s	0.021	4	0.100	8	0.058	7	0.049	7
Amaryllidaceae	*Habranthus gracilifolius* Herb.	gb	s	0	0	0	0	0.007	3	0.005	1
Anacardiaceae	*Schinus weinmanniaefolius* Engl.	s	s	0.028	3	0.012	2	0.148	2	0	0
Apiaceae	*Eryngium ciliatum* Cham. & Schlecht.	gr	s	0.005	1	0	0	0	0	0.016	3
	Eryngium elegans Cham. & Schlecht.	gr	s	0	0	0	0	0.023	1	0	0
	Eryngium horridum Malme	gr	s	0.289	6	0.037	4	0.468	8	0.252	6
	Eryngium pristis Cham. & Schlecht.	gr	s	0.005	1	0.519	3	0	0	0.634	3
	Eryngium sanguisorba Cham. & Schlecht.	gr	s	0.009	3	0.069	7	0.104	4	0.039	5
	Hydrocotyle exigua (Urb.) Malme	h	n	0.046	2	0.009	3	0.049	5	0.069	10
Apocynaceae	*Forsteronia glabrescens* Müll.Arg.	l	s	0.009	1	0	0	0	0	0	0
Aspidiaceae	*Rumohra adiantiformis* (G.Forst.) Ching	h	s	0.141	2	0	0	0	0	0	0
Asteraceae	*Achyrocline satureioides* Gard.	h	s	0	0	0	0	0.046	5	0.016	4
	Acmella bellidioides (Sm.) R.K.Jansen	h	s	0	0	0.037	2	0	0	0.053	4
	Aspilia montevidensis (Spreng.) Kuntze	h	s	0.037	3	0.102	7	0.185	7	0.035	5
	Asteraceae 1			0.023	1	0	0	0.005	1	0	0
	Asteraceae 2			0	0	0	0	0	0	0.002	1
	Baccharis articulata Pers.	s	s	0	0	0	0	0	0	0.009	1
	Baccharis cognata DC.	s	s	0.023	1	0.171	5	0.347	9	0.127	5
	Baccharis dracunculifolia DC.	s	n	0.002	1	0.002	1	0.002	1	0.046	1
	Baccharis leucopappa DC.	s	s	0	0	0.007	1	0.046	7	0.005	2
	Baccharis ochracea Spreng.	s	s	0.002	1	0	0	0.069	1	0.005	1
	Baccharis patens Baker	s	s	0	0	0.579	1	0	0	0.076	4
	Baccharis rufescens Spreng	s	s	0.002	1	0	0	0	0	0	0
	Baccharis sessiliflora Vahl	s	s	0	0	0.019	2	0.056	2	0.053	5
	Baccharis trimera (Less.) DC.	s	s	0	0	0.019	2	0.007	2	0.037	4
	Calea serrata Less.	l	s	0.882	8	0	0	0	0	0	0
	Calea uniflora Krasch.	gr	s	0.014	1	0	0	0	0	0.002	1
	Chaptalia integerrima (Vell.) Burkart	h	s	0.014	2	0	0	0.032	5	0.009	2
	Chaptalia runcinata Kunth	h	s	0.009	3	0.072	7	0.109	10	0.023	3
	Chaptalia sinuata Baker	h	s	0	0	0.063	6	0.005	1	0.009	2
	Conyza bonariensis (L.) Cronquist	h	s	0	0	0	0	0.003	1	0	0
	Conyza chilensis Spreng.	h	s	0	0	0.005	1	0	0	0.005	1
	Eupatorium ascendens Sch.Bip. ex Baker	h	s	0	0	0.005	1	0.005	1	0	0
	Eupatorium intermedium DC.	s	s	0.005	1	0	0	0	0	0	0
	Eupatorium ivaefolium L.	h	s	0.014	1	0.056	3	0.028	4	0.032	5
	Eupatorium lanigerum Hook. & Arn.	h	s	0	0	0	0	0.005	1	0	0
	Eupatorium ligulaefolium Hook. & Arn.	s	s	0	0	0.014	4	0.183	11	0.030	3
	Eupatorium tweedianum Hook. & Arn.	h	s	0	0	0.028	2	0	0	0	0
	Heterothalamus psiadioides Less.	s	n	0	0	0	0	0.113	10	0.188	2

(continued)

Family	Species	LF	RT	Border		Group 1		Group 2		Group 3	
				C	F	C	F	C	F	C	F
Asteraceae	*Hieracium commersonii* Monnier	gr	s	0	0	0	0	0.032	4	0	0
	Hypochoeris sp.	h	s	0	0	0	0	0	0	0.009	1
	Lucilia acutifolia Cass.	gr	s	0	0	0.021	5	0.081	11	0.021	4
	Lucilia nitens Less.	gr	s	0	0	0.009	1	0.009	2	0.023	2
	Noticastrum gnaphalioides (Baker) Cuatrec.	h	s	0	0	0	0	0.012	2	0.019	1
	Orthopappus angustifolius Gleason	h	s	0.009	1	0.005	1	0.102	8	0.007	2
	Porophyllum lanceolatum DC.	s	s	0.007	2	0.044	8	0.026	5	0.021	7
	Pterocaulon alopecuroideum DC.	h	s	0.009	1	0.019	1	0	0	0	0
	Pterocaulon rugosum Malme	h	s	0	0	0.067	5	0.081	4	0.069	7
	Senecio heterotrichius DC.	s	n	0	0	0	0	0.014	3	0.012	2
	Stenachaenium riedelii Baker	gr	s	0	0	0.014	1	0.009	1	0	0
	Stevia aristata D.Don ex Hook. & Arn.	h	s	0.016	1	0.009	1	0.002	1	0.005	1
	Stevia cinerascens Sch.Bip. ex Baker	h	s	0.005	1	0.035	4	0.102	2	0.030	5
	Verbesina subcordata DC.	h	s	0.032	2	0.028	2	0	0	0.002	1
	Vernonia flexuosa Sims	h	s	0.014	3	0.162	9	0.065	6	0.132	9
	Vernonia nudiflora Less.	s	s	0.023	6	0.093	6	0.109	9	0.116	10
	Viguiera anchusaefolia (DC.) Bak.	h	s	0	0	0	0	0.019	2	0	0
Bignoniaceae	*Dolichandra cynanchoides* Cham	l	s	0.009	1	0	0	0	0	0	0
	Macfadyena unguis-cati (L.) A.H.Gentry	l	s	0.002	1	0	0	0	0	0	0
Boragniaceae	*Moritzia ciliata* DC.	h	s	0.005	1	0	0	0	0	0	0
Bromeliaceae	*Dyckia leptostachya* Baker	gr	s	0	0	0.139	1	0	0	0	0
Cactaceae	*Parodia ottonis* (Lehm.) N.P.Taylor	s	s	0	0	0.028	1	0	0	0	0
Campanulaceae	*Wahlenbergia linarioides* DC.	th	n	0	0	0	0	0	0	0.002	1
Caryophylaceae	*Spergularia grandis* Cambess.	h	n	0.002	1	0	0	0	0	0	0
Cistaceae	*Halimium brasiliense* Gross.	h	s	0	0	0.005	1	0.012	3	0.009	2
Commelinaceae	*Commelina erecta* L.	h	s	0.035	5	0.002	1	0.012	2	0.007	2
Convolvulaceae	*Convolvulus crenatus* Vahl	l	s	0.005	1	0	0	0	0	0.023	1
	Dichondra sericea Sw.	h	n	0.005	1	0.012	3	0.009	2	0.019	3
	Evolvulus sericeus Sw.	h	n	0.030	7	0.056	8	0.049	7	0.032	8
	Ipomoea nitida Griseb.	gr	s	0.009	1	0	0	0	0	0	0
Cyperaceae	*Bulbostylis* sp.	hc	r	0	0	0.012	2	0.009	2	0	0
	Bulbostylis closii Barros	hc	r	0	0	0.007	2	0.012	2	0	0
	Bulbostylis juncoides (Vahl) Kük. ex Osten	hc	r	0.007	1	0.046	9	0.009	1	0.016	5
	Bulbostylis sphaerocephalus C.B.Clarke	hc	r	0.023	1	0.007	1	0.030	1	0.007	2
	Carex phalaroides Kunth	gr	s	0	0	0	0	0	0	0.007	2
	Cyperaceae 1	gr	s	0	0	0	0	0.005	1	0	0
	Cyperus aggregatus Endl.	gr	s	0	0	0.002	1	0.016	4	0	0
	Cyperus incomtus Kunth	gr	s	0.005	1	0	0	0	0	0	0
	Cyperus lanceolatus Poir.	gr	s	0	0	0	0	0.007	2	0	0
	Rhynchospora globularis Small	hc	r	0.023	4	0.192	12	0.079	11	0.116	10
	Rhynchospora setigera Boeck	hc	r	0	0	0.016	4	0.007	3	0	0
	Scleria sellowiana Kunth	gr	s	0.009	3	0.025	5	0.030	6	0.009	3
	Scleria sp.	gr	s	0	0	0	0	0.009	1	0	0
Dioscoreaceae	*Dioscorea multiflora* Mart. ex Griseb.	l	s	0.120	4	0	0	0	0	0	0
Ebenaceae	*Diospyros inconstans* Jacq.	t	n	0.002	1	0	0	0	0	0.002	1
Ericaceae	*Leucothoe eucalyptoides* DC.	t	r	0.005	1	0	0	0	0	0	0
Erythroxylaceae	*Erythroxylum argentinum* O.E. Schulz	t	n	0.009	1	0	0	0	0	0.005	1
Euphorbiaceae	*Croton cf. nitrariaefolium* Baill.	s	n	0.037	3	0.049	6	0.139	7	0.074	7
	Croton thermarum Müll.Arg.	s	n	0	0	0.005	1	0.005	1	0.032	2

(continued)

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Family	Species	LF	RT	Border C	F	Group 1 C	F	Group 2 C	F	Group 3 C	F
Euphorbiaceae	*Euphorbia selloi* (Klotzsch & Garcke) Boiss. in DC.	h	s	0.012	2	0.019	4	0.042	7	0.014	5
	Euphorbiaceae 1			0	0	0	0	0	0	0.005	1
	Euphrobiaceae 2			0	0	0.002	1	0	0	0	0
	Sebastiania brasiliensis Spreng.	t	n	0.002	1	0	0	0	0	0	0
	Tragia emrichii Herter	h	s	0	0	0.005	1	0	0	0	0
Fabaceae	*Aeschynomene elegans* Cham. & Schlecht.	h	s	0	0	0.002	1	0.028	4	0.012	3
	Centrosema virginianum Benth.	h	s	0.009	1	0.049	3	0	0	0.023	3
	Chamaecrista nictitans Moench	s	s	0	0	0	0	0.042	2	0.005	1
	Clitoria nana Benth.	gr	s	0.007	1	0.028	4	0.009	1	0.039	7
	Collaea stenophylla Benth.	s	s	0.002	1	0	0	0.079	1	0	0
	Crotalaria tweediana Benth.	h	s	0	0	0.009	1	0.005	1	0.005	2
	Desmanthus tatuhyensis Hoehne	s	s	0.021	4	0.039	5	0.053	8	0.021	5
	Desmodium affine Schltdl.	h	s	0	0	0.014	1	0	0	0	0
	Desmodium incanum DC.	h	s	0.007	1	0.039	2	0	0	0.009	1
	Galactia gracillima Benth.	gr	s	0	0	0.005	2	0	0	0	0
	Galactia marginalis Benth.	gr	s	0.014	3	0.009	4	0.039	4	0.007	1
	Macroptilium prostratum Urb.	h	s	0.009	2	0	0	0.021	4	0.039	5
	Mimosa parvipinna Benth. in Hook	s	s	0	0	0.007	1	0	0	0	0
	Rhynchosia diversifolia Micheli	h	s	0.005	1	0.009	2	0	0	0.014	2
	Stylosanthes montevidensis Vogel	gr	s	0.009	2	0.016	3	0.012	2	0	0
	Zornia sericea Moric.	h	s	0	0	0	0	0.009	2	0	0
Iridaceae	*Cypella coelestis* (Lehm.) Diels	gb	s	0	0	0.005	2	0.005	1	0.002	1
	Herbertia pulchella Sweet	gb	s	0	0	0.012	2	0	0	0	0
	Sisyrinchium macrocephalum Graham	h	s	0.002	1	0.005	2	0.028	3	0.009	1
	Sisyrinchium scariosum I.M.Johnst.	h	s	0	0	0.002	1	0.007	2	0.002	1
	Sisyrinchium vaginatum Spreng.	h	s	0.002	1	0	0	0.046	5	0	0
Lamiaceae	*Glechon squarrosa* Benth.	s	s	0.005	1	0.012	1	0.060	4	0.002	1
	Hyptis stricta Benth.	h	s	0	0	0.009	1	0	0	0	0
	Salvia procurrens Benth.	h	n	0.012	1	0	0	0.630	4	0	0
Liliaceae	*Nothoscordum bonariense* Beauverd	gb	s	0.002	1	0	0	0	0	0	0
Linaceae	*Cliococca selaginoides* (Lam.) C.M.Rogers & Mild.	h	s	0	0	0	0	0	0	0.005	1
Lythraceae	*Cuphea glutinosa* Cham. & Schlecht.	h	s	0	0	0.005	1	0.002	1	0	0
Malpighiaceae	*Janusia cf. guaranitica* A.Juss.	l	s	0	0	0.005	1	0	0	0	0
Malvaceae	*Krapovickasia urticifolia* (A. St.-Hil.) Fryxell	s	s	0.009	1	0	0	0	0	0.009	1
	Pavonia hastata Cav.	s	s	0.014	2	0	0	0.023	3	0.002	1
	Sida rhombifolia L.	s	s	0.009	1	0	0	0.010	1	0.005	1
	Wissadula glechomatifolia R.E.Fr.	s	s	0.021	3	0.019	2	0	0	0.058	4
Melastomatacea	*Tibouchina gracilis* (Bonpl.) Cogn.	s	s	0.032	2	0.037	6	0.155	5	0.012	4
Myrsinaceae	*Myrsine coriacea* R.Br	t	n	0.046	2	0	0	0	0	0	0
	Myrsine umbellata Mart.	t	n	0.009	1	0	0	0	0	0.009	2
Myrtaceae	*Blepharocalyx salicifolius* O.Berg	t	n	0.046	1	0	0	0	0	0	0
	Campomanesia aurea O.Berg	s	s	0	0	0	0	0	0	0.009	1
Myrtaceae	*Myrcia palustris* DC.	t	s	0.093	1	0.056	1	0	0	0	0
Orchidaceae	*Stenorrhynchus arechavaletsmii* Barb.Rodr.	gb	s	0	0	0.005	1	0	0	0	0
Oxalidaceae	*Oxalis brasiliensis* Lodd.	gb	s	0	0	0.009	1	0	0	0.007	3
	Oxalis conorrhiza Jacq.	gb	s	0	0	0.016	3	0.002	1	0.009	3
Piperaceae	*Peperomia pereskiaefolia* H.B.& K.	h	s	0.095	3	0	0	0	0	0	0
Poaceae	*Andropogon lateralis* Nees	hc	r	0.093	6	0.218	4	0.123	3	0.551	5

(continued)

Family	Species	LF	RT	Border C	Border F	Group 1 C	Group 1 F	Group 2 C	Group 2 F	Group 3 C	Group 3 F
Poaceae	*Andropogon leucostachyus* H. B. & K.	hc	r	0	0	0.044	4	0	0	0.326	5
	Andropogon selloanus (Hack.) Hack.	hc	r	0	0	0.146	7	0.113	4	0.000	0
	Andropogon ternatus Nees	hc	r	0	0	0	0	0	0	0.053	2
	Aristida circinalis Lindm.	hc	r	0	0	0	0	0.407	5	0.069	1
	Aristida condylifolia Caro	hc	r	0	0	0	0	0.014	2	0	0
	Aristida filifolia (Arechav.) Herter	hc	r	0.002	1	0	0	0.350	7	0.016	2
	Aristida flaccida Trin. & Rupr.	hc	r	0.039	4	0.590	11	0.257	5	0.556	5
	Aristida laevis Kunth	hc	r	0.046	4	0.199	7	0.676	9	0.188	5
	Aristida venustula Arechav.	hc	r	0	0	0.005	2	0	0	0	0
	Axonopus argentinus Parodi	gr	s	0	0	0.127	6	0	0	0	0
	Axonopus suffultus (Mikan ex Trin.) Parodi	hc	r	0.037	2	0	0	0.468	6	0	0
	Axponopus sp.	gr	s	0	0	0.056	1	0.102	3	0.359	8
	Briza calotheca (Trin.) Hack	hc	r	0	0	0	0	0	0	0.005	1
	Briza sp.	hc	r	0	0	0	0	0.010	3	0.005	1
	Briza subaristata Lam.	hc	r	0	0	0	0	0.019	2	0.014	4
	Briza uniolae Nees ex Steud.	hc	r	0	0	0	0	0.014	3	0.030	3
	Calamagrostis viridiflavescens Steud.	gr	s	0.083	5	0	0	0	0	0.000	0
	Danthonia montevidensis Hackel & Arech.	hc	r	0.019	2	0.014	2	0.026	2	0.171	6
	Danthonia secundiflora J.Presl & C.Presl	hc	r	0.009	1	0	0	0.010	1	0.000	0
	Dichanthelium sabulorum (Lam.) Gould & C.A.Clark	gr	s	0.150	8	0.044	6	0.174	8	0.025	6
	Elionurus muticus (Spreng.) Kuntze	hc	r	0.588	8	0.287	5	0.454	8	1.116	9
	Eragrostis polytricha Nees	hc	r	0	0	0.032	4	0	0	0.019	2
	Leptocoryphium lanatum Nees	hc	r	0.171	3	0.296	4	0.528	5	0.044	3
	Melica brasiliana Ard.	gr	s	0.000	0	0	0	0	0	0.005	1
	Oplismenus hirtellus (L.) P.Beauv.	hc	r	0.051	4	0	0	0	0	0	0
	Panicum ovuliferum Trin.	gr	s	0.049	3	0	0	0	0	0	0
	Panicum peladoense Henrard	hc	r	0.005	1	0.000	0	0	0	0.005	2
	Paspalum mandiocanum Trin.	hc	r	0.014	1	0.000	0	0	0	0	0
	Paspalum plicatulum Michx.	hc	r	0.118	4	0.014	2	0.060	3	0.012	4
	Paspalum sp.	gr	s	0.037	2	0	0	0	0	0	0
	Piptochaetium montevidense (Spreng.) Parodi	hc	r	0.016	3	0.023	4	0.035	3	0.227	8
	Poaceae/trib. Andropogoneae 5	hc	r	0	0	0.005	1	0	0	0	0
	Saccharum alopecuroides (L.) Nutt.	hc	r	0.046	1	0.093	1	0.046	2	0	0
	Schizachyrium microstachyum (Ham.) Roseng., B.R.Arill. & Izag.	hc	r	0.030	2	0	0	0.044	4	0.234	6
	Schizachyrium spicatum (Spreng.) Herter	hc	r	0	0	0.005	1	0	0	0.005	1
	Schizachyrium tenerum Nees	hc	r	0.086	4	0.044	3	0.713	5	0.030	5
	Setaria parviflora (Poiret) M.Kerguélen	hc	r	0.007	1	0.023	4	0.104	8	0	0
	Setaria vaginata Spreng.	hc	r	0.102	1	0.012	2	0.331	6	0.005	1
	Sporobolus multinodis Hackel	hc	r	0	0	0	0	0.009	1	0	0
	Stipa filiculmis Delile	hc	r	0.019	2	0	0	0.012	2	0.093	5
	Stipa filifolia Nees	hc	r	0.093	1	0.039	3	0.116	1	0.106	2
	Stipa tenuiculmis Hackel	hc	r	0.037	2	0.002	1	0.009	1	0.007	2
	Trachypogon montufari Nees	hc	r	0	0	0.067	3	0.009	1	0.593	5
	Poaceae 1			0	0	0	0	0	0	0.002	1
	Poaceae 2			0	0	0	0	0	0	0.002	1
	Poaceae 3			0	0	0.005	1	0	0	0	0
	Poaceae 4			0.002	1	0.009	1	0	0	0	0
	Poaceae 5			0	0	0	0	0.012	1	0	0

(continued)

Family	Species	LF	RT	Border C	F	Group 1 C	F	Group 2 C	F	Group 3 C	F
Poaceae	Poaceae 6			0	0	0.005	1	0	0	0	0
	Poaceae/trib. Andropogoneae 1	hc	r	0	0	0	0	0	0	0	0
	Poaceae/trib. Andropogoneae 2	hc	r	0	0	0	0	0	0	0.002	1
	Poaceae/trib. Andropogoneae 3	hc	r	0	0	0.005	1	0	0	0	0
	Poaceae/trib. Andropogoneae 4	hc	r	0	0	0.005	1	0	0	0	0
Polygalaceea	*Monnina oblongifolia* Arechav.	s	s	0.241	4	0	0	0.030	4	0.025	2
Rubiaceae	*Borreria capitata* DC.	h	s	0.009	1	0	0	0.039	4	0	0
	Borreria fastigiata K.Schum.	h	s	0.044	3	0.093	6	0.012	2	0.063	7
	Borreria verticillata G.Mey.	h	s	0	0	0	0	0	0	0.014	2
	Chiococca alba Hitchc.	l	s	0.009	1	0	0	0	0	0.016	3
	Diodia apiculata K.Schum.	h	s	0	0	0	0	0.032	5	0	0
	Diodia cymosa Cham.	h	s	0.023	2	0	0	0	0	0	0
	Galium uruguayense Bacigalupo	h	s	0.007	2	0	0	0.019	5	0.009	3
	Guettarda uruguensis Cham. & Schlecht.	t	n	0.023	1	0	0	0	0	0	0
	Psychotria carthagenensis Jacq.	s	s	0.007	2	0	0	0	0	0	0
	Relbunium hirtum K.Schum.	h	s	0.009	3	0.002	1	0.076	10	0.007	3
	Richardia grandiflora Steud.	h	s	0.005	2	0.102	6	0.039	5	0.063	7
	Richardia humistrata Steud.	h	s	0	0	0	0	0	0	0.005	1
	Rubiaceae sp.	h	s	0	0	0	0	0	0	0.002	1
Sapindaceae	*Cupania vernalis* Cambess.	t	n	0.002	1	0	0	0	0	0	0
	Dodonaea viscosa Jacq.	t	n	0.028	3	0	0	0	0	0	0
Scrophulariaceae	*Angelonia integerrima* Spreng.	s	s	0	0	0	0	0	0	0.019	1
	Gerardia communis Cham. & Schlecht.	th	n	0	0	0.012	3	0	0	0.002	1
	Mecardonia herniarioides (Cham.) Pennel*l*	h	s	0	0	0	0	0.005	1	0	0
Smilacaceae	*Smilax campestris* Griseb.	l	s	0	0	0.002	1	0	0	0.009	1
Solanaceae	*Cestrum strigillatum* Ruiz & Pav.	s	s	0.069	1	0	0	0	0	0	0
	Petunia integrifolia (Hook.) Schinz & Thel*l*.	h	s	0	0	0	0	0	0	0.016	3
	Petunia ovalifolia Miers	h	s	0	0	0.002	1	0	0	0	0
Sterculariaceae	*Waltheria douradinha* A. St.Hil.	s	s	0	0	0.009	1	0	0	0.012	3
Styracacae	*Styrax leprosum* Hook. et Arn.	t	n	0.009	1	0	0	0	0	0	0
Symplocaceae	*Symplocos tetandra* Mart.	t	s	0.116	1	0	0	0	0	0	0
	Symplocos uniflora Benth.	t	s	0.002	1	0.009	1	0	0	0	0
Turneraceae	*Turnera selloi* Arechav.	s	s	0	0	0.009	2	0.009	2	0.002	1
	Turnera sidoides L.	s	s	0	0	0	0	0	0	0.009	1
Verbenaceae	*Glandularia megapotamica* (Spreng.) Cabrera & Dawson	h	s	0.002	1	0	0	0.005	1	0	0
	Lantana montevidensis (Spreng.) Briq.	h	s	0.007	1	0.030	3	0	0	0.060	3
	Verbena ephedroides Cham.	h	s	0.002	1	0	0	0.007	3	0.002	1
	Verbena pseudojuncea Gay	h	s	0.012	2	0.007	2	0.007	1	0	0
Vitaceae	*Cissus striata* Ruíz & Pav.	l	s	0.236	4	0	0	0	0	0.002	1
Unidentified	Sp. 1			0.002	1	0	0	0	0	0	0
	Sp. 2			0	0	0	0	0.002	1	0	0
	Sp. 3			0	0	0	0	0	0	0.002	1
	Sp. 4			0	0	0	0	0	0	0.002	1
	Sp. 5			0	0	0	0	0	0	0.002	1
	Sp. 6			0	0	0	0	0	0	0.002	1
	Sp. 7			0	0	0	0	0	0	0.002	1

Appendix 2: Woody species >10cm, recorded in 252 MPs (1.5 by 1.5m) on Morro Santana, Porto Alegre, RS, Brazil. Given are family, species, regenerative type (RT; r: resister, s: sprouter, n: non-sprouter), successional group (SG, c: grassland species, b: forest pioneer/border species; f: forest species), growth-form (GF; s: shrub, t: tree) mean cover per plot (C) and frequency (F) per group of plots, separated for grassland plots at the forest-grassland border (Bord., n=36) and plots in the open grassland, grouped into plots burned three months before (Group 1; n=72), burned a year before (Group 2; n=72) and unburned for three years or more (Group 3, n=72).

					Border		Group 1		Group 2		Group 3	
Family	Species	RT	SG	GF	C	F	C	F	C	F	C	F
Anacardiaceae	*Lithraea brasiliensis* Marchand	s	f	t	0	0	0	0	0	0	0	0
	Schinus weinmanniaefolius Engl.	s	c	s	0.67	6	0.33	6	2.53	18	0.07	2
Arecaceae	*Butia capitata* Becc.	r	c	t	0.83	2	0	0	0	0	0.06	1
Asteraceae	*Baccharidastrum triplinervium* (Less.) Cab.	s	b	s	0	0	0	0	0	0	0	0
	Baccharis articulata Pers.	s	c	s	0	0	0.33	3	0.53	4	1.44	12
	Baccharis cognata DC.	s	c	s	1.94	4	5.69	36	8.07	53	3.85	30
	Baccharis dracunculifolia DC.	n	c	s	0	0	0	0	0	0	0.97	7
	Baccharis leucopappa DC.	s	c	s	0	0	0	0	0.19	2	0	0
	Baccharis ochracea Spreng.	s	c	s	0	0	0.24	5	0.69	4	0.88	7
	Baccharis patens Baker	s	c	s	0.28	1	0.69	1	0.06	1	2.72	13
	Baccharis rufescens Spreng	s	c	s	0	0	0	0	0	0	0.06	1
	Baccharis sessiliflora Vahl	s	c	s	0.72	5	1.43	17	0.51	7	1.85	28
	Baccharis trimera (Less.) DC.	s	c	s	0	0	0.25	6	0.29	6	0.64	10
	Eupatorium intermedium DC.	s	c	s	0.94	3	0.25	3	0.06	1	0.97	4
	Eupatorium ligulaefolium Hook. & Arn.	s	c	s	0.78	3	2.21	26	3.19	32	2.6	30
	Eupatorium pedunculosum Hook. & Arn.	n	c	s	0.28	1	0	0	0	0	0	0
	Eupatorium tweedianum Hook. & Arn.	s	c	s	0.28	1	0.47	3	0	0	0.19	2
	Heterothalamus psiadioides Less.	n	c	s	0.56	1	0.19	2	0.63	9	3.97	16
	Porophyllum lanceolatum DC.	s	c	s	0.92	6	0.85	19	2.68	37	0.74	14
	Verbesina subcordata DC.	s	c	s	0.28	1	0.25	3	0	0	0	0
	Vernonia nudiflora Less.	s	c	s	1.44	13	3.71	54	4.56	63	3.26	48
Cactaceae	*Opuntia monacantha* Haw.	r/s	b	s	0	0	0	0	0	0	0	0
Celastraceae	*Maytenus cassineformis* Reiss.	s	f	t	0	0	0	0	0	0	0	0
Ebenaceae	*Diospyros inconstans* Jacq.	n	f	t	0	0	0	0	0	0	0	0
Ericaceae	*Leucothoe eucalyptoides* DC.	r	b	t	0	0	0	0	0	0	0	0
Erythroxlaceae	*Erythroxylum argentinum* O.E. Schulz	n	f	t	0.11	1	0	0	0	0	0	0
Euphorbiaceae	*Croton* cf. *nitrariaefolium* Baill.	n	c	s	2.44	11	0.43	10	2.75	35	3.1	31
	Croton thermarum Müll.Arg.	n	c	s	0.39	2	0.42	9	0	0	0.72	7
Euphorbiaceae	*Sebastiania brasiliensis* Spreng.	n	f	t	0	0	0	0	0	0	0	0
	Sebastiania serrata Müll.Arg.	s	f	t	0	0	0	0	0	0	0	0
Fabaceae	*Calliandra tweedii* Benth.	s	b	s	0	0	0	0	0	0	0	0
	Collaea stenophylla Benth.	s	c	s	0	0	0	0	0	0	0	0
	Mimosa parvipinna Benth. in Hook	s	c	s	0	0	0.47	3	0	0	1.25	7
Lamiaceae	*Hyptis mirabilis* Briq.	s	c	s	0.22	2	0	0	0	0	0	0
Lauraceae	*Ocotea puberula* (Rich.) Nees	n	f	t	0	0	0	0	0	0	0	0
Malvaceae	*Pavonia hastata* Cav.	s	c	s	0.5	3	0	0	1.01	13	0.11	2
	Sida rhombifolia L. --	s	c	s	0.22	2	0	0	0.06	1	0	0
Meliaceae	*Trichilia clausseni* C.DC.	n	f	t	0	0	0	0	0	0	0	0
Monimiaceae	*Mollinedia elegans* Tul.	n	f	t	0	0	0	0	0	0	0	0
Myrsinaceae	*Myrsine coriacea* (Sw.) R.Br.	n	f	t	0	0	0	0	0	0	0	0
	Myrsine umbellata Mart.	n	f	t	0	0	0	0	0	0	0	0
Myrtaceae	*Campomanesia aurea* O.Berg	s	c	s	0.39	2	0.21	3	0.22	4	0.13	3
	Eugenia hyemalis Camb.	s	f	t	0	0	0	0	0	0	0	0

(continued)

Family	Species	RT	SG	GF	Border		Group 1		Group 2		Group 3	
					Cov.	Freq.	Cov.	Freq.	Cov.	Freq.	Cov.	Freq.
Myrtaceae	*Myrcia palustris* DC.	s	f	t	0	0	0	0	0	0	0	0
	Myrciaria cuspidata O.Berg	s	f	t	0	0	0	0	0	0	0	0
	Psidium L.	s	c	s	0.11	1	0	0	0	0	0	0
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	n	f	t	0	0	0	0	0	0	0	0
Rosaceae	*Quillaja brasiliensis* Mart.	n	f	t	0	0	0	0	0	0	0	0
Rubiaceae	*Guettarda uruguensis* Cham. & Schltdl.	n	f	t	0	0	0	0	0	0	0	0
	Psychotria carthagenensis Jacq.	s	f	s	0	0	0	0	0	0	0	0
	Psychotria leiocarpa Cham. & Schltdl.	n	f	s	0	0	0	0	0	0	0	0
Rutaceae	*Zanthoxylum rhoifolium* Lam.	s	f	t	0	0	0	0	0	0	0	0
Sapindaceae	*Cupania vernalis* Cambess.	n	f	t	0	0	0	0	0	0	0	0
	Dodonaea viscosa Jacq.	n	b	s	0	0	0	0	0	0	0	0
	Matayba elaeagnoides Radlk.	s	f	t	0	0	0	0	0	0	0	0
Solanaceae	*Cestrum strigilatum* Ruíz & Pav.	s	b	s	0	0	0	0	0	0	0	0
Styracaceae	*Styrax leprosum* Hook. et Arn.	n	f	t	0	0	0	0	0	0	0	0
	Symplocos tetrandra Mart.	s	f	t	0	0	0	0	0	0	0	0
	Symplocos uniflora Bedd.	s	f	t	0	0	0	0	0	0	0	0

Appendix 3: Woody species > 80cm, recorded in 84 LPs (4.5 by 4.5m) on Morro Santana, Porto Alegre, RS, Brazil. Given are family, species, regenerative type (RT; r: resister, s: sprouter, n: non-sprouter), successional group (SG, c: grassland species, b: forest pioneer/border species; f: forest species), growth-form (GF; s: shrub, t: tree) and mean number of individuals per plot, separated for grassland plots at the forest-grassland border (Bord., n=12) and plots in the open grassland, grouped into plots burned three months before (Group 1; n=24), burned a year before (Group 2; n=24) and unburned for three years or more (Group 3, n=24).

Familiy	Species	RT	SG	GF	Border	Group 1	Group 2	Group 3
Anacardiaceae	*Lithraea brasiliensis* Marchand	s	f	t	0.25	0.08	0.13	0.13
	Schinus weinmanniaefolius Engl.	s	c	s	0.17	0	0.13	0.13
Arecaceae	*Butia capitata* Becc.	r	c	t	0.25	0	0	0
Asteraceae	*Baccharidastrum triplinervium* (Less.) Cab.	s	b	s	0	0	0	0
	Baccharis articulata Pers.	s	c	s	0	0	0	0.46
	Baccharis cognata DC.	s	c	s	0.08	0	0.33	1.13
Asteraceae	*Baccharis dracunculifolia* DC.	n	c	s	0.08	0	0	0.83
	Baccharis leucopappa DC.	s	c	s	0	0	0	0.04
	Baccharis ochracea Spreng.	s	c	s	0	0	0.13	0.17
	Baccharis patens Baker	s	c	s	0.08	0.33	0	1.33
	Eupatorium intermedium DC.	s	c	s	1.00	0	0	0.21
	Eupatorium ligulaefolium Hook. & Arn.	s	c	s	0.50	0	0.54	2.13
	Eupatorium pedunculosum Hook. & Arn.	n	c	s	0.42	0	0	0
	Eupatorium tweedianum Hook. & Arn.	s	c	s	0	0	0	0.04
	Heterothalamus psiadioides Less.	n	c	s	0.17	0.25	0	2.29
	Porophyllum lanceolatum DC.	s	c	s	0.17	0	1.13	1.33
	Vernonia nudiflora Less.	s	c	s	0	0	0.04	0.08
Cactaceae	*Opuntia monacantha* Haw.	r/s	b	s	0.17	0	0	0
Celastraceae	*Maytenus cassineformis* Reiss.	s	f	t	0	0.04	0	0
Ebenaceae	*Diospyros inconstans* Jacq.	n	f	t	0.08	0	0	0
Ericaceae	*Leucothoe eucalyptoides* DC.	r	b	t	0.25	0	0	0
Erythroxlaceae	*Erythroxylum argentinum* O.E. Schulz	n	f	t	0.17	0	0	0
Euphorbiaceae	*Croton* cf. *nitrariaefolium* Baill.	n	c	s	0	0	0	0.17

(continued)

Familiy	Species	RT	SG	GF	Border	Group 1	Group 2	Group 3
Euphorbiaceae	*Croton thermarum* Müll.Arg.	n	c	s	0	0	0	0.04
	Sebastiania brasiliensis Spreng.	n	f	t	0.25	0	0	0
	Sebastiania serrata Müll.Arg.	s	f	t	0.17	0	0	0
Fabaceae	*Calliandra tweedii* Benth.	s	b	s	0.17	0	0	0
	Collaea stenophylla Benth.	s	c	s	0	0	0.08	0.08
	Mimosa parvipinna Benth. in Hook	s	c	s	0.25	0.04	0	0.58
Lamiaceae	*Hyptis mirabilis* Briq.	s	c	s	0.17	0	0	0
Malvaceae	*Pavonia hastata* Cav.	s	c	s	0.33	0	0.13	0.13
Meliaceae	*Trichilia clausseni* C.DC.	n	f	t	0.17	0	0.00	0
Myrsinaceae	*Myrsine coriacea* (Sw.) R.Br.	n	f	t	0.50	0	0	0
	Myrsine guianensis (Aubl.) Kuntze	n	f	t	0.17	0	0	0.04
	Myrsine umbellata Mart.	n	f	t	0.58	0	0	0
Myrtaceae	*Campomanesia aurea* O.Berg	s	c	s	0.42	0	0	0
	Eugenia dimorpha Berg	s	b	t	0	0	0	0.04
	Eugenia uniflora L.	n	f	t	0.08	0	0	0
	Myrcia palustris DC.	s	f	t	0.33	0.13	0	0.13
	Myrciaria cuspidata O.Berg	s	f	t	1.00	0.08	0.04	0.17
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	n	f	t	0.08	0	0	0
Rubiaceae	*Guettarda uruguensis* Cham. & Schltdl.	n	f	t	0.08	0	0.04	0.04
	Psychotria carthagenensis Jacq.	s	f	s	0.33	0	0	0
Rutaceae	*Zanthoxylum rhoifolium* Lam.	s	f	t	0.08	0	0	0
Salicaceae	*Casearia decandra* Jacq.	n	f	t	0.25	0	0	0
Sapindaceae	*Cupania vernalis* Cambess.	n	f	t	0.08	0	0	0
	Dodonaea viscosa Jacq.	n	b	s	1.92	0.04	0	0.08
	Matayba elaeagnoides Radlk.	s	f	t	0.17	0	0.08	0.08
Solanaceae	*Cestrum strigilatum* Ruíz & Pav.	s	b	s	0.08	0	0.04	0.04
Styracaceae	*Styrax leprosum* Hook. et Arn.	n	f	t	0.17	0	0	0
	Symplocos tetrandra Mart.	s	f	t	0.17	0	0	0
	Symplocos uniflora Bedd.	s	f	t	0.92	0.08	0.08	0.13
Verbenaceae	*Lantana camara* L.	r	b	s	0.17	0	0	0

CHAPTER 4

Ecosystem effects and responses: trait-based analysis of plant functional types in burned grassland

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Abstract

Question: How does plant functional type (PFT) composition change in relation to post-fire vegetation development in burned grassland?

Location: Regularly burned grassland in Porto Alegre, RS, Brazil (30°03' S, 51°07' W; max. elevation 311m a.s.l.)

Methods: 108 grassland plots (0.25m²) were sampled in two consecutive years in areas with different time elapsed since the last fire. In addition to species identity, 12 plant traits were recorded, including morphological traits and sprouting ability after fire. The trait set was analyzed using the numerical approach presented by Pillar & Sosinski (2003), identifying PFTs maximally associated to time since fire.

Results: High congruence values given by the analysis indicated definition of meaningful PFTs. Traits related to biomass development (such as height of plant, leaf length, proportion of dead biomass) were the most important in defining PFTs. Reproductive activity was indicative of recently burned areas, while presence of non-sprouting species was not related to time since fire. Longer unburned areas were dominated by PFTs formed by caespitose grasses, while recently burned areas presented a greater spectrum of different plant types.

Conclusions: Morphological attributes facilitated interpretation of vegetation development in the studied grassland. While it is not so easy to distinguish between reaction and effect traits for many plants, the link between the two trait sets was very clear: caespitose grasses are the PFT responsible for flammability of the system, thus allowing for the cyclic development of vegetation in relation to frequent burns.

Keywords: caespitose grasses, fire, life-form, morphology, numerical analysis, PFTs, plant form, southern Brazil

Abbreviations: PFT: Plant Functional Type, PCoA: Principal Coordinates Analysis

Introduction

In the past two decades, investigations of plant communities on the basis of species assemblages have been complemented by the analysis of plant functional types (PFTs). The main reasoning was that by grouping plants into functional types, better predictions for vegetation responses under changes in climate or disturbance regime can be made (e.g. Woodward & Cramer 1996, Smith *et al.* 1997). Even though the idea to define PFTs allowing for classification of vegetation on a global scale in a functional sense, e.g. by common core lists of attributes (Weiher *et al.* 1999), was appealing, it has been accepted that a generic functional classification will not be able to address plant responses to specific environmental conditions (Lavorel *et al.* 1997, Campell *et al.* 1999). Only when defined in relation to a specific question ("function") will a PFT really be functional (e.g. Pillar & Orlóci 1993, Steffen 1996, Gitay & Noble 1997). Ways of optimal identification of PFTs differ depending on the specific question and vegetation types. Under the deductive approach (Woodward & Cramer 1996), traits (or, synonymously, attributes) considered to be purposeful for prediction of plant response to an environmental factor are selected *a priori*. The inductive approach, in contrast, aims at sampling of a broad array of traits, which are then subjected to quantitative analysis in order to find the subset of traits most relevant for the environmental function in question. Under this procedure, selection of traits to be sampled will have to be made on the basis of hypothesis on processes in the plant community, i.e. contains a deductive element as well. The necessity of considering different traits not in an isolated way, but to define PFTs on the basis of co-occurring plant attributes ("character syndromes") has been recognized (Pillar & Orlóci 1993, Gitay & Noble 1997, Lavorel *et al.* 1999). One possible approach for this is the definition of plant types by numerical analysis, resulting in combinations of different trait states that maximize correlation with one or more environmental variables (Pillar & Sosinski 2003).

The environmental factor "fire" has been addressed in a number of functional type classifications of plants, e.g. dividing species into sprouters and non-sprouters, resisters and endurers, seeders and non-seeders or into groups dominating different phases of post-fire vegetation development, i.e. in classifications related to post-fire regeneration and reproductive strategies or temporal niche differentiation (e.g. Noble & Slatyer 1980, Keeley *et al.* 1981, Bond & van Wilgen 1996, Pausas 1999, Bond & Midgley 2001), in general following a deductive approach. Often, these models are applied not to entire communities, but to illustrate and contrast opposed strategies, or their use is restricted to analysis of specific groups of plants, most frequently woody species (e.g. Pausas 1999, Bellingham & Sparrow 2000, see also Vesk & Westoby 2004). In communities subject to frequent fires, plants should be adapted to fire or, to be more precise, the current fire regime, allowing for rapid post-fire vegetation recovery. For example, for South Brazilian grassland, it has been shown that species composition will not change as a consequence of a fire event, while absence of fire over several years leads to a decline in abundance of herbaceous species due to competitive pressure of the

caespitose grasses (Overbeck *et al.*, submitted (b)). Other grassland systems may be characterized by a fast temporal sequence of different plant types after fire (e.g. Ghermandi *et al.* 2004), allowing for clear definitions of PFTs in the community. In both cases, community structure in grassland will change drastically after a burn, as live and dead biomass are being consumed by fire, leaving open soil, dead remains of plants, e.g. charred woody plant parts, and some basal structures, e.g. from tussock grasses. Soon thereafter, plant biomass will start to cover the open soil through sprouting from underground plant parts and seed germination.

In this study, we hypothesized that plant morphological attributes – considered to be surrogates for function (Barkman 1988) – are plastic between different stages of post-fire vegetation development in response to changed resource availability and changed competitive hierarchies, and thus would serve for the definition of PFTs in relation to fire. Based on a set of 12 traits sampled in plots with different time since fire in regularly burned grassland in Porto Alegre, RS, Brazil, we defined PFTs in relation to time since fire by numerical analysis, applying the method of Pillar & Sosinski (2003). We discuss practicability and interpretational value of morphological traits in view of plant response to fire and the influence of vegetation structure on flammability (response and effect traits *sensu* Lavorel & Garnier 2002).

Methods

Study area and field sampling

In large parts of southern Brazil, grassland can be found despite climatic conditions allowing for forest vegetation. Grasslands are thought to be relicts from the late Pleistocene with cooler and drier climate, stabilized by recurrent action of fire or through grazing (e.g., Rambo 1953, Klein 1975, Pillar & Quadros 1997, Behling *et al.* 2004). Under exclusion of fire and grazing, slow advancement of forest vegetation over grassland takes place (Oliveira & Pillar 2004). Fire most likely has been present in southern Brazil since early in the Holocene (Behling *et al.* 2004), most probably as a tool in hunting by indigenous people (Kern 1994), even though natural fires should have occurred as well. Today, the largest part of the grasslands that has not been transformed into agricultural land or plantations of exotic forest species is used for cattle production. Only few areas underlie no formal land management, among them our study site on Morro Santana, in Porto Alegre, RS, Brazil (30°03' S, 51°07' W, max. alt. 311m a.s.l.). The hill is covered by a mosaic of forests (Atlantic forest) and grasslands. The species-rich grasslands, with a species pool of about 450 to 500 species in the grassland area of ca. 220 ha (Overbeck *et al.* submitted (a)), are subject to frequent (average fire frequency: approx. 3 years) fires caused by local population.

Six pairs of transects (distance between transects in each pair approximately 5m) were installed from the forest border into the grassland, in areas differing in slope, aspect, degree of shrub encroachment and time since the last fire. In October 2002, one transect in each of the pairs was subjected to an experimental burn. In two of the transects, situated in areas that had burned 10 months

before, the fire did not spread due to lack of continuous biomass. This left us with four transects burned in our experiments (group 1), four transects burned almost a year before (group 2), and four transects burned three or more years before (group 3). Additionally, one of the transects from group 3 burned after the first survey, allowing us to directly test for differences in species and PFT composition before and after the fire (group 0). Vegetation description (more details below) was conducted in Jan./Feb. of 2003 (i.e. 3-4 months after the controlled fire) and in Nov./Dec. of 2003 (1 year after the fire; see. Tab. 1).

Table 1. Months since last fire for the different transect groups and survey periods.

Group	1st survey (Jan-Feb 2003)	2nd survey (Nov-Dec 2003)
0	>36	8-9
1	3-4	13-14
2	~12-13	~22-23
3	>36	>46

Each transect consisted of seven contiguous large plots of 4.5m by 4.5m. Within large plots #3, #5 and #7 (#3 being the third from the forest border, #7 the farthest), three contiguous plots of 50cm by 50cm were marked. In each of these plots, cover values were estimated for all species using the Londo (1976) decimal scale. Species populations in each plot were described by the attributes presented in Table 2 (for the purpose of this study, the term population refers to a species population in a plot).

Table 2: Traits used for description of plants in burned grassland on Morro Santana, Porto Alegre, RS, Brazil.

Nr	Attribute	Code	States
1	height of plant	hp	continuous (in dm)
2	length of leaves	ll	continuous (in dm)
3	dead biomass	db	ordered: in % cover, in 10% classes
4	basal architecture	ba	ordered: 1 – solitary, 2 – multistemmed, 3 - caespitose
5	stem structure	st	ordered: 1 – rosette or semirosette, 2 – unbranched stem, 3 - brached stem
6	plant habitus	hb	ordered: 1 – graminoid, 2 – forb, 3 – suffrutescent forb, 4 – liana, 5 – shrub, 6 – tree
7	inclination	in	ordered: 1 – prostrated, 2 – semierect, 3 - erect
8	leaf texture	te	ordered: 0 – no leaf, 1 – membraneous, 2 – sclereophylleous
9	leaf class	lc	ordered: 0 – no leaf, 1 – fine leaf, 2 – lanceolated fine leaf, 3 – lanceolated broad leaf, 4 – broad leaf (classes based on calculation of the ratio leaf width to leaf length)
10	leaf type	fi	ordered: 0 – no leaf, 1 – non-fibrous leaf, 2 – fibrous leaf
11	Reproductive ability (flowering)	fl	ordered: 0 – without reproductive organs, 1 – with reproductive organs
12	sprouting ability after fire	sa	ordered: 0 – non-sprouter, 1 – sprouter

If a species was present with different states for one or more traits, e.g. with solitary or multi-stemmed individuals or striking differences in leaf size, it was recorded as two distinct populations,

with separate cover values for each. Only height was never considered as an attribute to justify separation into several populations: maximum height for each species in each plot was recorded. The attribute sprouting ability after fire refers to the species and was recorded afterwards, based on further field observations and literature; as a consequence, species that had not been fully identified and where this attribute thus could not be assigned were taken out from the analyses.

Data analysis

For definition of PFTs, we followed the numerical procedure developed by V. Pillar (Pillar & Orlóci 1993, Pillar 1999, Pillar & Sosinski 2003), using the polythetic option implemented in SYNCSA software (Pillar 2004b). For details on the method, see Pillar & Sosinski (2003). In short, the algorithm is based on three data matrices: matrix **B** describing populations by the traits, **W** describing the communities by population performances (cover values), and **E** describing community sites by one or more environmental variables. A matrix correlation $\rho(\mathbf{D}, \mathbf{D})$ between community distances (**D**) described by trait-based plant types (pooled populations in **W**) and community distances (**D**) described by the environment (**E**) is calculated and used as a measure of congruence between variation in community composition and variation in the environment. At each iterative step of a recursive algorithm aiming at maximizing the correlation $\rho(\mathbf{D}, \mathbf{D})$, a subset of traits is extracted from matrix **B** and the resulting population by traits matrix is subjected to polythetic cluster analysis of the populations. The partition level that leads to the population pooling in **W** maximizing the correlation $\rho(\mathbf{D}, \mathbf{D})$ indicates the optimal number of PFTs for the subset of attributes considered. Using the polythetic algorithm, we tested all possible combinations of the initial trait set. Chord distances (Orlóci 1967) were used for **D** and Euclidean distances for **D**. Before the analyses, we pooled the population data to one plot of 0.75m^2 within each large plot, taking the mean value for the environmental factors where they differed between the three plots. The above-mentioned analytic procedure was applied to different data sets:

1) Data from all pooled plots from the first survey data (matrices **B** and **W**), and time since fire as environmental variable (**E**, Table 1), aiming at describing PFTs in relation to fire history.

2) Data from both surveys for matrices **B** and **W**, separately for the four treatment groups, using time since last fire (Table 1) as environmental variable, aiming to describe short-term dynamics in PFT composition in each group. For these analyses, we did not pool plots, as this would have lead to a very small number of plots in group 0.

After identification of attributes maximizing the correlation $\rho(\mathbf{D}, \mathbf{D})$ and the resulting optimal PFTs as groups of populations described by these attributes, vegetation composition in plots was described by the performance of the PFTs, in a PFT by plot contingency table. We subjected this data matrix to ordination by Principal Coordinates Analysis (PCoA), using chord distance as resemblance measure and calculated the correlation coefficient of the environmental variables to the ordination axes (see, e.g., Podani 2000 for ordination method). For comparison with PFT composition, species data

likewise was subjected to ordination by PCoA. Differences in PFT composition between treatment groups were tested by multivariate analysis of variation with randomization testing (Pillar & Orlóci 1996). Numerical analysis of PFTs, ordination procedures and calculations of correlations were conducted with the application SYNCSA 2.2 (Pillar 2004b) and analysis of variance with MULTIV 2.3.10 (Pillar 2004a).

Results

Species data

In the 108 plots, a total of 2075 populations belonging to 198 morpho-species (170 identified species) was sampled in the first and a total of 2326 populations belonging to 188 morpho-species (178 identified species) in the second survey. Of these populations, twelve and nine (for first and second survey, respectively) could not be identified and thus were taken out from the analyses. Ordination of species data did not show a separation of treatment groups for either of the two surveys, i.e. species distribution did not reflect fire history (Fig. 1A). Correlation of fire to the first ordination axes was only –0.08 and 0.06 for axis 1 and 2, respectively, and congruence between variation in species composition and time since fire was only 0.11. Species composition thus can be considered independent of single fire events (see also Overbeck *et al.*, submitted (a)).

Analysis of PFTs – all plots from the first survey

Dead biomass (*db*), height of plant (*hp*) and leaf length (*ll*), i.e. traits related to plant biomass development, and leaf class (*lc*) were represented in the five solutions with the highest congruence values to time since last fire. Sprouting ability (s*a*), flowering (*fl*) and leaf texture (*te*) were other attributes that entered into the five trait subsets best defining PFTs in relation to time since fire, with congruence values from 0.53 to 0.60 (Tab. 3) for pooled plots of $0.75m^2$. The traits *hp*, *ll*, *lc* and *db* were the ones determining the highest congruence when only using one trait for defining PFTs (Tab. 4). Sprouting ability (*sa*) showed a very low congruence. The optimal number of groups formed for each trait subset was low (Tab. 3).

Even though congruence was slightly lower, we selected solution number 3 as the optimal solution, as it included the traits reproductive activity (*fl*) and sprouting ability (*sa*), both supposed to be directly linked to the action of fire. The ordination diagram of plots based on this solution gave a clear separation of the three plot groups based on time since fire along axis 1 (Fig. 1B), with plots from group 3 packed closer together than plots from groups 2 and especially 1, which occupied a larger part of the ordination space, thus indicating greater heterogeneity of plant types in more recently burned grassland.

Table 3: The five trait subsets showing the highest values (only optimal number of PFTs presented). See Tab. 2 for explanation of trait codes.

Nr.	Congruence	Number of groups	Optimal subset of traits					
1	0.60	5 groups	db	hp	ll	lc	sa	
2	0.59	3 groups	db	hp	ll	lc		
3	0.58	7 groups	db	hp	fl	ll	lc	sa
4	0.55	9 groups	db	hp	fl	ll	lc	te
5	0.53	6 groups	db	hp	ll	lc	te	

Table 4: Maximum congruence values for each trait when used alone in calculation of correlation. See Tab. 2 for explanation of trait codes.

Trait code	hp	ll	lc	db	ba	te	fl	fi	hb	in	lc	sa
Congruence	0.30	0.23	0.23	0.21	0.19	0.15	0.13	0.13	0.09	0.07	0.04	-0.05
Number of groups	13	9	5	5	2	3	2	2	6	3	2	2

Time since fire had a correlation of –0.85 to the first ordination axis (R=0.09 and R=0.10 for axis 2 and 3, respectively). Of the seven PFTs formed by the solution, three showed high correlations to the first ordination axis: PFT1 represented solitary scapose forbs with short leaves and no dead biomass, and PFT2 multi-stemmed grasses, with longer leaves and bearing reproductive organs; both of these types were correlated positively to axis 1 (PFT1: R=0,85, PFT2: R=0.64). PFT4, associated with unburned plots (R=-0.99 to first axis), represented tall grasses with fine long leaves and high percentage of dead biomass (Tab. 5). All three groups (defined by time since fire) differed significantly from each other when subjecting the PFT-composition to multivariate analysis of variance with randomization testing (p<0.001).

Table 5: PFTs revealed by the selected solution of the ranking process (#3, Tab. 3) using the full data set from the first survey, and correlations to ordination axis (Fig. 1B). See Tab. 2 for description of trait codes.

PFT #	db	hp	fl	ll	lc	In	fi	st	hb	te	ba	sa	relation to...	PFT characterization
1	1	2	0	1	2	2	1	2	2	2	1	1	post-burn (0.85)	medium-height solitary scapose forb, semierect, not flowering, no dead biomass
2	2	2	1	2	2	2	2	1	2	2	2	1	post-burn (0.64)	multistemmed, medium-height flowering grass, little dead biomass
3	1	1	0	0	3	2	1	2	3	2	1	0	(axis 3)	small solitary scapose suffrutescent forb, not flowering, non-sprouting
4	3	3	0	3	1	2	2	1	1	2	2	1	pre-burn (-0.99)	multistemmed grass with a high percentage of dead biomass, broad leaves
5	6	2	0	0	3	3	1	2	4	2	1	1	(axis 6)	solitary liana, high percentage of dead biomass
6	1	2	1	0	3	1	1	2	3	2	1	0	(no axis)	solitary non-sprouting forb, flowering, no dead biomass
7	1	14	0	0	3	3	1	3	5	2	1	0	(axis 5)	solitary high shrub, no dead biomass
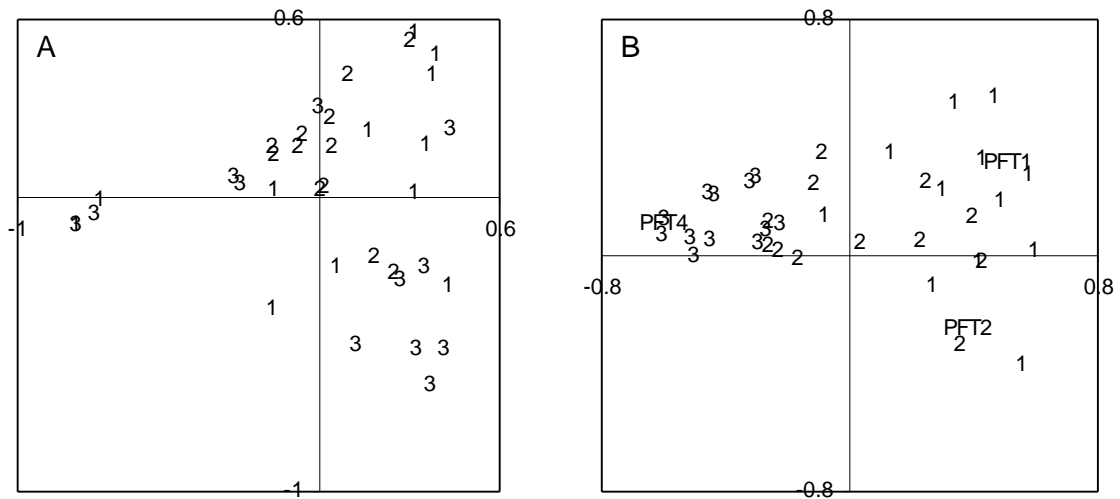
Figure 1: Ordination diagram (PCoA; Chord distance as resemblance measure), of plots from the first survey, depicting in A) composition defined by species and in B) by PFTs according to solution 3 of the ranking process (Tab. 3). Plots are labeled according to treatment group (1: recently burned, 2: burned one year before, 3: burned more than 3 years before). In A) axes 1, 2 and 3 (not shown) explained 15.8%, 11.9% and 10.2%, respectively, in B.) 70.7%, 16.5% and 7.7%, respectively. PFTs in diagram B are depicted when correlation to one of the first two axes was higher than 0.4.

Analysis of PFTs – data from the first and the second survey

For plots from group 0 (burned between the two surveys), congruence of PFT-based community composition and time since last fire was high (congruence around 0.95 for the first five solutions; Tab. 7). Again, traits related to biomass production (*hp*, *ll*) and reproduction (*fl*) were important. However, some traits related to physiognomic plant form also entered into the subsets, such as *hb*, *lc*, *te*. Reproductive activity could always be found in the trait subsets, in contrast to sprouting ability. The ordination of plots based on PFTs of the first solution revealed a very clear separation of plots from the two survey periods along the first axis (Fig. 2A). While only one PFT (PFT2) was clearly associated with plots from the first survey, unburned for more than three years, four different PFTs showed positive correlation to the first ordination axis, i.e. were characteristic of recently burned plots (see Tab. 6 for description of these types). Only one PFT (PFT6, solitary scapose sprouting forbs) was related to axis 2, and apparently could be found in plots from both surveys.

Table 6: PFTs revealed by the solution of the ranking progress with highest congruence for plots from group 0. Out of the 9 PFTs formed, only the five PFTs showing correlation above 0.4 to the first ordination axis of the ordination in Fig. 2A are given. See Tab. 2 for explanation of trait codes.

PFT #	ba	db	fi	fl	hp	in	lc	ll	st	hb	te	sa	relation to..	description
1	2	2	1	0	1	3	2	1	2	2	2	1	post-burn (0.78)	small erect multistemmed scapose forb, not flowering, medium height, medium percentage dead biomass
2	3	3	2	0	3	2	1	3	1	1	2	1	pre-burn (-0.99)	tall caespitose grass, high percentage dead biomass
3	1	1	1	0	2	3	3	0	2	5	2	1	post-burn (0.43)	solitary shrub
4	1	1	1	0	1	1	3	0	2	2	2	1	post-burn (0.62)	small creeping solitary scapose forb
5	2	3	2	1	2	2	1	2	1	1	2	1	post-burn (0.90)	multistemmed semierect graminoid, high percentage dead biomass, flowering

For plots burned right before the first survey (group 1), the ranking process indicated lower congruence of PFT-based composition to time since last fire than for group 0 (maximum value: 0.59; Tab. 7). Traits maximizing congruence for plots of group 1 were similar to those of group 0, but the trait flowering (fl) now did not appear in the optimal traits subset. Plots from group 1 still were clearly separated along the first ordination axis (Fig. 2B). Only two PFTs showed high correlations with the first ordination axes, and both represented medium high caespitose grasses: PFT 6, negatively correlated to axis 1 (R=-0.92), was characterized by a no dead biomass, while PFT 16, with a high positive correlation to axis 1 (R=0.90) characterized plants with a high percentage of dead biomass. Other PFTs revealed in the analysis showed high congruence to the second ordination axis with little explanatory power.
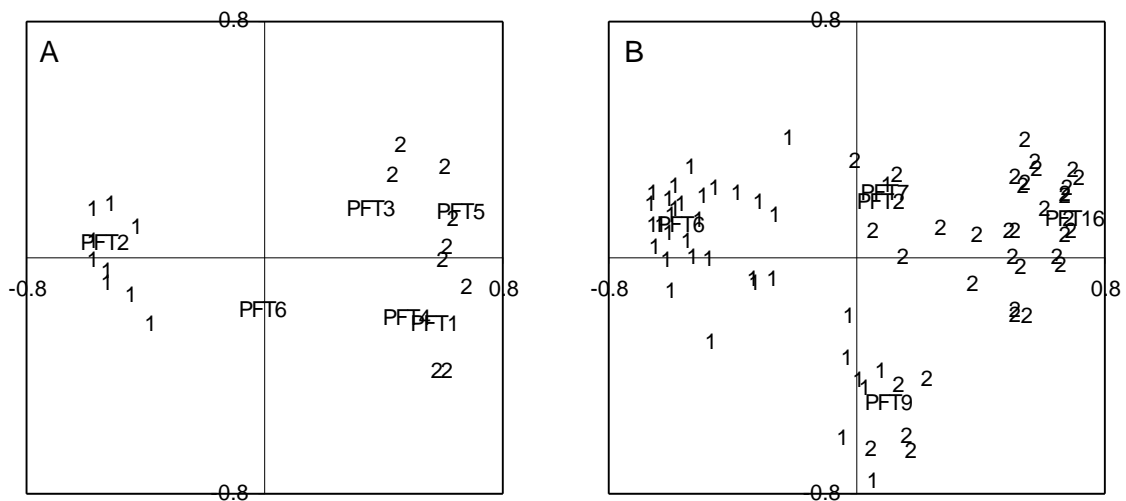
Figure 2: Ordination (PCoA; chord distance as resemblance measure) of data from both surveys, based on PFT composition. A) plots of group 0 (burned between surveys); B) plots of group 1 (burned before first survey), both using the trait subsets maximizing the correlation (Tab. 7). Plots are coded according to survey period 1 and 2. PFTs shown when correlated with 0.4 or more to axis 1 or 2. Explanation of ordination axes: A) 78.7%, 11.5% and 7.0%; B) 41.1%, 13.1%, and 11.2%, for axes 1,2 and 3 (not shown), respectively.

Maximum congruence for plots burned one year before the first survey (group 2) was 0.30, with *ba*, *db*, *ll*, *hb* the traits identified for definition of 20 PFTs (Tab. 7). For plots unburned for more than 3 years before the first survey, congruence was very low: the best solution, with *db*, *hp*, *te* as attributes defining PFTs, gave a maximum congruence of only 0.11, indicating almost no differences in PFT composition in respect to time since last fire (Tab. 7). For groups 0, 1, and 2, difference in PFT composition was highly significant ($p<0.001$) between the two survey dates. For plots of group 3, despite the low correlation coefficient, differences between the two surveys still were significant ($p<0.01$).

Table 7: Congruence and optimal trait subsets for the data from surveys 1 and 2, separately for each treatment groups (see text). See Tab. 2 for trait codes. Below presentation of the five best solutions for each group, the correlation of time since fire (survey period) to the first two ordination axes and the significance of survey dates compositional differences (based on PFTs) tested by multivariate analysis of variance are given.

Group 0 – burned between the two surveys			Group 1 - burned experimentally		
Congruence	n groups	optimal trait subsets	Congruence	n groups	optimal trait subsets
0.954818	9 groups	fl hp in lc ll hb te	0.587452	23 groups	ba db fi ll te sa
0.950836	27 groups	fi fl hp hb te	0.583505	28 groups	ba db ll hb te sa
0.950128	15 groups	fi fl ll hb te sa	0.57902	23 groups	ba db ll hb te
0.949486	15 groups	fl ll hb te	0.578922	20 groups	ba db fi ll te
0.949284	26 groups	fi fl hp hb sa	0.576363	14 groups	ba db ll te sa
Corr. with time since fire: axis 1: 0.99, axis 2 –0.25:, axis 3: 0.07			Corr. with time since fire: axis 1: 0.88, axis 2: 0.12, axis 3: -0.24		
Sign. level between survey dates: $p<0.001$			Sign. level between survey dates: $p<0.001$		

Group 2 - burned one year before			Group 3 - burned 3 years or more before		
Congruence	n groups	optimal trait subsets	Congruence	n groups	optimal trait subsets
0.304664	20 groups	ba db ll hb	0.111975	5 groups	db hp te
0.302257	24 groups	ba db ll hb sa	0.10854	2 groups	db hp
0.300918	26 groups	ba db ll hb te	0.108293	8 groups	ba db hb
0.300074	27 groups	ba db fi ll hb sa	0.107273	13 groups	ba db hb te
0.299803	22 groups	ba db fi ll hb	0.104837	16 groups	db fi lc hb te
Corr. with time since fire: axis 1: 0.58, axis 2: -0.15, axis 3: 0.26			Corr. with time since fire: axis 1: 0.38, axis 2: 0.06, axis 3: 0.01		
Sign. level between survey dates: $p<0.001$			Sign. level between survey dates: $p<0.01$		

Discussion

Use of morphological plant traits in relation to fire in grassland

The traits we sampled can be classified into traits related to plant growth and biomass development (*ht*, *ll*, *db*), plant architecture (*ba*, *st*, *in*) and rather fixed morphological plant characteristics (*hb*, *te*, *fi*, *lc*). Sprouting ability (*sa*), the only trait described at the species level, reflects plant strategy for post-fire recolonization, and *fl* reproductive activity. Only the morphological characteristics and sprouting ability are relatively constant for any species (the latter actually may differ between young and old individuals of the same species; however, we assigned the trait per

species). Traits related to plant growth/biomass development and to plant architecture are clearly plastic, i.e. may differ between plants of the same species or even within a single plant in the course of its life cycle or be dependent on environmental heterogeneity. Morphological traits are related to ecological functions, as they reflect adaptations to environmental conditions (Barkman 1988), however, they may not all be interpreted as readily as the "core traits" identified by Weiher *et al.* (1999), which characterize plant strategies in relation to the challenges for dispersal, establishment and persistence. In order to study PFT composition in relation to fire in grassland, principally traits allowing for flammability and spread of a fire and those allowing for post-fire vegetation recovery (effect traits and response traits *sensu* Lavorel & Garnier 2002) are important. After fire, recolonization of a burned area ("response") will occur through sprouting from surviving plant parts or through seed germination. The trait sprouting ability – "negatively" defining obligate seeder species – should sufficiently reflect these two main strategies when working on the community level, integrating seed dispersal and plant establishment into the principal strategy types sprouters and non-sprouters (e.g. Bond & van Wilgen 1996). A more detailed classification, e.g. as proposed by Lloret & Vilà (2003), was not possible in this study due to very limited information on seed-related regeneration mechanisms in the flora studied. Traits characterizing plant morphology and architecture are not necessarily response traits of plants as such, but rather may characterize response of the community to fire, as they could – in our study, this was not the case – indicate massive post-fire establishment of single species, species groups and thus PFTs absent or almost absent in longer unburned vegetation, i.e. the fire followers found in Mediterranean-type shrubland (e.g. Christensen & Muller 1975, Keeley *et al.* 1981) or some grassland (e.g. Ghermandi *et al.* 2004) communities. Having established or regained cover in a burned area, a plant must persist; for this, a number of attributes principally related to space acquisition and occupation, competitive ability, disturbance response and reproduction has been proposed (Weiher *et al.* 1999). These traits are of importance for any plant individual in any community, but too general when searching for PFTs in response to a specific factor. Furthermore, they cannot be considered a response to fire, but are related to resource availability, competition levels and other factors acting upon the community. Considering the importance of community flammability for plant types related to fire (effect traits), traits focusing on plant morphology and architecture should be adequate, as they allow for a description of vegetation structure which defines fuel distribution (Bilbao *et al.* 1996). In grassland, dead biomass from caespitose grasses with its high surface-to-area ratio constitutes the principal fuel, as live biomass acts as a heat sink before being sufficiently dry for combustion (Bond & van Wilgen 1996), and under productive conditions, i.e. sufficient moisture supply, can accumulate fast enough to allow for yearly burns (Bond *et al.* 2003).

Plant functional types in burned grassland in southern Brazil

The PFTs formed by the analyses describe combinations of different trait states in relation to the factor fire, combining effect and reaction traits. The values given in the description of a PFT by

traits (e.g. Tab. 5 and 6) are mean values of the attribute states from plants that entered into this group; therefore, they are abstract representations of real plants, giving a simplified view reduced to the important differences in trait composition in the community in relation to the environmental factor used for the analyses. Analysis of all plots with data from the first survey and analyses of the two surveys, conducted separately for all treatment groups, lead to the same conclusion: diversity of functional types is highest in recently burned plots, and decreases with time since fire. Longer unburned plots are more similar in their PFT composition, as they all show high dominance of caespitose grasses, while burned plots show higher species number and diversity (Overbeck *et al.*, submitted (b)), and, due to lower competitive pressure in early post-burn vegetation, permit the coexistence of a variety of plant types. While we did not test this formally, PFT diversity thus seems to be a consequence of species diversity, as a larger number of species allows for a larger set of attribute combinations (Montalvo *et al.* 1991). The important effect of caespitose grasses and accumulated litter on dominance structure in grasslands is well established in the literature: growth of highly productive and competitive tussock grasses leads to thinning out principally of small herbaceous species in the community (e.g. Collins 1987, Leach & Givnish 1996). On the one hand, densely packed leaf sheets and dead material at the base serve as principal protection of buds in caespitose grasses, thus allowing for sprouting after fire (e.g. Sarmiento 1992). On the other hand, accumulation of dead biomass inhibits plant growth because of shading, not only affecting neighboring plants (e.g. Facelli & Pickett 1991), but also the tussock grass itself (e.g. Silva *et al.* 1990, Silva *et al.* 1991, Morgan & Lunt 1999). Due to these effects, absence of fire over periods as short as three years in the studied grassland leads to a sharp decline in species richness (Overbeck *et al.* 2005 (b)). The plant traits leading to the highest correlations (Tab. 3) underline this situation: dead biomass, height of plant and leaf length all are traits 1) directly related to plant growth and biomass accumulation and 2) clearly distinguishing caespitose grasses/graminoids from other plants. The trait leaf class may be considered here as well, as almost all caespitose grasses showed fine leaves, in contrast to forbs and shrubs, where a broad spectrum of leaf forms (from fine to broad leaves) can be found. The two other traits in the solution selected by us for definition of plant types, sprouting ability and flowering, also can be directly related to the action of fire as response traits characterizing vegetation recovery after fire. Increased flowering activity after fire is well known for many grassland ecosystems (e.g. Daubenmire 1968, Vogl 1974, Lunt 1994, Bond & van Wilgen 1996), and was clearly related to recently burned plots in our study. PFTs representing non-sprouting species did not show any correlation to the main trends of variation in a PFT-based ordination of plots (Fig 1B); their presence in plots from the first survey – only a small proportion of species in South Brazilian grassland are obligate seeders (Overbeck *et al.*, unpubl.) – was associated to a third ordination axis with low explanation (7.7%), and no relation to fire. The data of the two survey dates analyzed separately for each treatment group directly characterized vegetation development through time after a burn. Differences in PFT composition and in attribute state distribution were the most pronounced in plots of group 0, burned between the two surveys (Fig 2A;

Tab. 6). Unburned plots were characterized by large caespitose grasses with fine leaves and a large amount of dead biomass, whereas after the burn, similar to the results discussed above, a variety of plant types could be found, many of them flowering. In plots from group 1, congruence was already a lot lower, indicating that differences between the two years were not as drastic anymore. Basal architecture, dead biomass, leaf length and leaf texture now were the most important traits, entering all of the five best solutions, and reflecting increased dominance of caespitose grasses (basal architecture types: caespitose) and accumulation of dead biomass. In plots of group 2, burned a year before, with even lower congruence, the traits basal architecture, dead biomass, leaf length and habitus entered all traits subsets, allowing for the same conclusion. Low congruence for plots of group 3 indicated that three years after fire, a relatively stable state with little changes in plant type composition is reached, with high dominance by caespitose grasses and large amounts of litter and dead biomass.

All analyses conducted in this study yielded not only one solution, but resulted in a number of solutions with similar correlations and more or less similar trait subsets. Even though the aim of the analysis is to maximize congruence, in case of different solutions with similar congruence coefficients and usually similar trait subsets, the researcher will have to decide which one of these is the most "functional", just as we opted to select a solution with a slightly lower total congruence value in the analysis of the whole data set from the first year, but which included two traits we considered to be of particular importance for our question. This may be considered subjective, but, on the other hand, a high correlation itself does not necessarily indicate a cause-and-effect, i.e. functional, relationship. For the method applied in this study, selection of traits for sampling is crucial. We suggest that, at least in situations where species composition shows no clear response to the environmental factor in question and thus variability within any given species was the issue, traits measured directly in the field should always be preferred for the analysis, as only these will show variation which could be related to variation in environmental variables, as opposed to traits found in screening programs (e.g. Grime *et al.* 1997). The use of principally morphological traits can facilitate investigations in poorly described floras (Díaz *et al.* 2001), such as the one studied by us. Trait selection will always depend on the specific question, and on the balance of work effort and expected results (Skarpe 1996).

Effect and response in fire-prone grassland

Traits linked to disturbance response (post-fire recovery, stimulated reproduction) and ecosystem effects (flammability) have been considered to be largely independent of each other, as the disturbance and resource axes in plant strategy schemes relate to different plant traits (Grime 1979, Leishman & Westoby 1992, Lavorel & Garnier 2002). However, the caespitose growth form with its ability to resprout and regain biomass quickly after a burn and its property to increase flammability of the system in short periods links plant response and ecosystem effect. Flammability is a property of the community (Whelan 1995), and thus no evolutionary attribute, as it is the individual plants which are subject to natural selection (for debate, see Mutch 1970, Snyder 1984; see also Christensen 1985,

Bond & Midlgey 1995). Clearly, flammability-enhancing traits of grasses may be a consequence of other selective pressures, such as drought or grazing: periodic drought, fire, and grazing together will have determined selection processes in grassland evolution and cannot be disentangled easily (e.g. Vogl 1974, Anderson 1982), even though their effects are not identical (Noy-Meir 1995). The unique property of fire in grassland is that only part of the community – the graminoids – is responsible for the flammability, but that all will burn (Zedler 1995). If flammability-enhancing traits have evolved in part of the species present, regeneration traits of all species will reflect increased probability of fire (Schwilk & Ackerly 2001). The prevalence of sprouting as opposed to regeneration by seeds in our system (see Overbeck et al, submitted (b)) may be an indicator for regimes of frequent disturbances, where sprouting species with their strategy of occupying the "persistence niche" (Bond & Midgley 2001) should have an advantage over seeders. If grasslands evolved under climatic conditions unfavorable for forest development at former times, and as the grassland vegetation type in general is associated with a high resistance to drought, grazing and fire, then the presence of any one of the factors fire and grazing should guarantee for the persistence of grassland even in the absence of the original environmental constraint (climate) responsible for its evolution, without the necessity of any evolutionary link between response and effect traits.

The caespitose growth form does not only dominate vegetation structure, species and PFT composition, but, due to its architectural singularity (e.g. Sarmiento 1992, Briske & Derner 2000), promotes fire as an ecosystem process necessary for persistence of the grassland community through a positive feedback cycle between vegetation structure and fire (D'Angelis & Vitousek 1992), i.e. is responsible for the very existence of the vegetation type. Does this mean that trait-based PFT analyses could be substituted by use of the life-form as the "ultimate expression of trade-offs" (Lavorel & Garnier 2002)? Existing theoretical framework for the analysis of plant function and ecosystem processes (e.g. Lavorel & Garnier 2002) seems to be harder to apply to real communities as it suggests at first glance: information on the functions behind traits or the measurable expressions of them is often scarce, "functions" vary in a complex way with environmental conditions or in relation to other traits and cannot always be distinguished easily, neither be readily separated into effect or response nor measured in screening programs. Life form or growth form integrate a set of traits in a non-random and non-independent way (Box 1981) and thus may allow more easily for interpretation of the relationship between plants and environmental conditions than more abstract trait combinations. However, trait-based approaches are needed to deepen our understanding of which properties of plant form are actually functional or responsive to changing environmental factors, and thus which environmental changes may be severe enough to change growth form or life form distribution.

Acknowledgements

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CHAPTER 5

No stimulation of germination by heat found in subtropical grassland species

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submitted to *Plant Ecology*

Abstract

Fire has been shown to stimulate seed germination in a number of fire-prone ecosystems, mainly in shrublands and, though not exclusively, in hardseeded species. Two main mechanisms have been identified: stimulation by charred wood or smoke, or by heat. For nine herbaceous (5 grasses, 1 Cyperaceae, 3 forbs) species from frequently burned South Brazilian grassland, we experimentally tested the effect of heat on seed germination. Seeds were exposed to temperature between 50° and 110°C (to 180°C for two species) for two minutes and subsequent germination was monitored in a germination chamber. None of the species showed increased germination after the treatment, whereas germination ability after the different treatment varied between species. Two of the herbs and the three grasses with the smallest seeds were able to germinate after temperatures of 110°C or higher; the other species showed different temperature limits. The results suggest that while apparently heat effects of fire have not lead to the development of any mechanisms directly stimulating germination, at least some species are resistant to heat and thus are not negatively affected by the passage of a fire.

Keywords: fire, heat, high temperature, Southern Brazil, subtropical grassland

Introduction

Fire is an important factor in many of the world's grassland communities. Plant species differ in their response to fire: some may resist fire entirely, others may have their above ground biomass destructed but will be able to sprout from underground organs after fire, while a third group may have to recover by seed germination (Gill 1981, Whelan 1986, Bond & van Wilgen 1996). A number of studies has linked soil heating during burns to post-fire seedling establishment. Experimental studies on the impact of fire on seed germination have mostly treated the effect of heat on hard-seeded species (e.g. Leguminosae, Cistaceae, Malvaceae, among others) growing in Mediterranean climate ecosystems: the importance of high temperatures, mostly in the range of 80° to 100°C, for breaking of dormancy of these species is well established in the literature (e.g., Christensen & Muller 1975, Mott & Groves 1982, Keeley *et al.* 1985, Thanos & Georghiou 1988, Auld & O'Connell 1991, Keeley & Bond 1997, Hanley & Fenner 1998, Herranz *et al.* 1998, Ferrandis *et al.* 1999, Hanley & Lamont 2000, Keeley & Fotheringham 2000, Hanley *et al.* 2002). On the other hand, species from fire-prone dune fynbos in southern Africa, also thought to be dependent on germination from soil-stored seed after disturbance, did not show stimulated germination rate after heat treatments: post-fire seedling recruitment was a consequence of fluctuating diurnal temperatures due to removal of insulation (Pierce & Moll 1994). Also, heat apparently does not stimulate germination of all hard-seeded legume species (Martin *et al.* 1975). Impact of fire on germination of grass or herbaceous species without hardseededness is even less clear. Keeley & Fotheringham (2000) state that grass species do not form dormant seed banks requiring heat shock for recruitment and Baskin & Baskin (1998a) conclude that grass-seeds in general show a non-deep physiological dormancy, which can be broken relatively easy, e.g. by annual fluctuations in temperature; thus, heat should play no positive role. In contrast, an experiment by Zacharias *et al.* (1988) showed that of five South African grasses, one did in fact experience increased germination after heat treatment. Vilà *et al.* (2001) report high germination rates after experimental heating to 105°C in a C_3 tussock grass. Naveh (1975) cites examples of Mediterranean climate grasses in Israel that showed increased germination rates after being exposed to temperatures of 90° and 105°C. Christensen (1985) notes that it is difficult to find examples of fire-stimulated germination outside of Mediterranean shrublands. This, however, may be linked to the number of studies conducted, and not to the existence or non-existence of heat stimulation in species from other ecosystems or climate regions other than Mediterranean-type shrublands.

Negative effects of soil heating caused by a passing burn, on the other hand, may be just as important for post-fire seedling regeneration patterns than stimulation of germination. Whelan (1986) mentions the importance of seeds to be stored at a site or depth where they will be protected from destruction by heat. For most hardseeded legumes, for example, temperatures of 90° to 110°C for periods of 4 minutes (Martin *et al.* 1975) or of 120°C for 1 minute (Auld & O'Connell 1991) have proven to be lethal.

Fire, present in the region since early in the Holocene (Behling *et al.* 2004), is a common management tool in South Brazilian grasslands and, together with grazing, is considered to be a factor stabilizing these extremely species-rich systems under climatic conditions allowing for forest development (Klein 1975, Pillar & Quadros 1997). Knowledge of effect of fire on plant population biology of grassland species, however, is scarce, if not inexistent. In this study, we tested reaction to heat of seeds of ten dominant herbaceous species collected in a frequently burned grassland in Porto Alegre, RS, Brazil, in a laboratory experiment, simulating the effect of a passing fire on seeds stored in the seed bank.

Material and Methods

Seeds of five Poaceae (all caespitose grasses; five C4, one C3; nomenclature follows IPNI 2004), one Cyperaceae, and three herbaceous species (Tab. 1) were collected at the time of natural seed dispersal of each species in grassland areas on Morro Santana, Porto Alegre, RS, Brazil (30°03' S, 51°07' W, max. alt. 311m a.s.l.). The hill, part of the granitic hill region of Porto Alegre, is covered by a forest-grassland mosaic, with forests predominant on southern slopes and along creeks, and grasslands, underlying frequent anthropogenic fires, characteristic for the top and northern slopes. Grasslands are very rich in species, with a total species pool of approximately 450 to 500 species in an area of 220 ha, and dominance by C4 tussock grasses, e.g. *Elionurus muticus*, *Andropogon lateralis*, *Aristida laevis*. Between tussocks, a large number of often only sparsely distributed herbs can be found, mostly from the Asteraceae, Fabaceae and Rubiaceae, just like grassland shrubs, especially *Baccharis ssp.* (Asteraceae), other Asteraceae and Euphorbiaceae (*Croton ssp.).* In areas unburned for longer periods, these shrubs may become physiognomically dominant, transforming grasslands into low shrublands. *Eryngium ssp.*, large rosettes from the Apiaceae, form dense populations at some patches; the species is considered to be a disturbance specialist profiting from frequent fires because of stimulated vegetative reproduction (Fidelis *et al.*, submitted). Forest borders seem to slowly advance onto the grasslands, but are being pushed back by the grassland fires occurring every three to five years, today usually of anthropogenic origin. At places with rock outcrops, protecting shrubs and trees from fire, small forest nuclei can be found, impeded in their expansion by fire (Müller & Forneck 2004). Floristic composition of the grassland is described in detail in Overbeck *et al.* (submitted (a).

All selected species were abundant in the study area and thus had a sufficient amount of seeds to be collected. Seeds were stored under dry conditions until the start of the experiments. In grasses, the dispersal unit usually is not the caryopsis itself, but a seed enclosed by various spikelet bracts (lemma, palea, glume), e.g. a floret (caryopsis with lemma and palea) or the entire spikelet (Cheplick 2000). As we hypothesized that these adhesive structures might provide for some protection of the caryopsis against heat, we did not use the seed itself, but always the entire dispersal unit like liberated at the time of seed dispersal for the experiments (see Tab. 1). Only in *Aristida laevis*, we cut off the largest part of the long awns, in order to be able to place the seeds into the Petri dishes.

Table 1: Name, family, percentage of dispersal units containing seed, seed weight and type of dispersal unit for the 10 grassland species from subtropical grassland on Morro Santana, Porto Alegre, RS, Brazil, used in the experiments.

Species	Family	Dispersal units containing seed (%)	1000 seed weight (g)	Type of dispersal unit
Andropogon lateralis Nees	Poaceae (C4)	35.7	0.50	entire spikelet
Aristida laevis Kunth	Poaceae (C4)	94.7	0.96	floret[1]
Briza subaristata Lam.	Poaceae (C3)	70.2	0.30	floret
Elionurus muticus (Spreng.) Kuntze	Poaceae (C4)	24.8	1.58	entire spikelet
Leptochoryphium lanatum Nees	Poaceae (C4)	78.2	1.10	entire spikelet
Schizachyrium microstachyum (Ham.) Roseng., B.R.Arill. & Izag.	Poaceae (C4)	78.7	0.12	entire spikelet
Rhynchospora setigera Boeck.	Cyperaceae	100	1.10	seed
Eryngium horridum Malme	Apiaceae	100	1.06	seed with adhesive structure
Eryngium pristis Cham. & Schlecht.	Apiaceae	100	0.69	seed with adhesive structure
Orthopappus angustifolius Gleason	Asteraceae	100	0.42	seed with pappus

[1] For the experiment, part of the awn was removed to be able to place the dispersal unit into the Petri dish.

For all species except *Eryngium horridum* and *E. pristis*, the experimental design consisted of four heat treatments (50, 70, 90, 110°C) and a control (CR) without heat treatment. *E. horridum* and *E. pristis* were studied in a separate experiment. In previous tests (unpublished data), we had found that both species responded with higher germination rates to a one week treatment of dry storage under a temperature of 40°C. Therefore, we conducted this treatment prior to the temperature treatments, which for these two species consisted of 70, 90, 110, 130, 150 and 180°C. For each species, five replicates of 25 dispersal units were placed in an aluminium dish, exposed to the desired temperature in a preheated oven for a period of 2 minutes and then placed in sterilized Petri dishes (diameter 4 cm) with 2 layers of filter paper sterilized by an UV lamp, just as 5 replicates of 25 seeds which had not been given any heat treatment (CR). Dishes were moistured with distilled water and placed in a germination chamber with a constant temperature of 25°C (20°C for the cool-season species *Briza subaristata* and *Rhynchospora setigera*) and a 16/8 hour light/darkness regime (standard light setting in the laboratory used for the experiment). The dishes were checked at least every two days for sufficient moisture. Every three days, emerging seedlings were counted (appearance of cotyledons and/or radicule as criterion for germination) and removed from the Petri dishes. For each treatment, the experiment was stopped when no germination had occurred for more than two weeks. For treatments where no seed at all had germinated after three weeks, we conducted the tetrazolium test to check if seeds were still viable. For this, the moist seeds were cut with a surgeons scalpel, imbibed by 2, 3, 5-triphenyl-tetrazolium chloride (0.1%; Baskin & Baskin 1998b) and evaluated 3 hours later. The test was not applied in the experiment of *E. horridum* and *E. pristis*.

A problem arose from the fact that spikelets of grasses not always contain seeds. As we did not have access to adequate equipment to separate spikelets with a caryopsis from empty ones (i.e., a centrifuge), we opened all seed dispersal units from which no seed had germinated at the end of the

experiment to see if they had contained a seed or not. From these results, we calculated number of dispersal units that actually possessed a seed, and used this value to calculate germination rates. For each species, differences in germination rate between treatments (% germination seeds from dispersal units containing a seed) were tested for significance by univariate analysis of variance with randomization testing (Euclidean distance as resemblance measure, 1000 iterations), using MULTIV 2.3.7 (Pillar 2004).

For each species except for the two *Eryngium* species, *Orthopappus angustifolius* and *Rhynchospora setigera*, where seeds were not protected by removable structures and we thus used the seed as it was, we extracted 25 seeds from their adhesive units, weighted the seeds and calculated weight to 1000-seed-weight.

Results

Elionurus muticus and *Andropogon lateralis* presented low percentages of dispersal units actually containing seeds (Tab. 1); results for these two species thus should be considered with caution. For these species, it clearly would have been better to have used seeds separated from the spikelets, or having separated spikelets with a seed before the experiments. For all other species, percentage of dispersal units with seeds exceeded 70%, thus allowing for interpretation of the results.

Table 2: Germination rates of ten species from subtropical grassland on Morro Santana, Porto Alegre, RS, Brazil, after 2 minute exposure to dry heat, in percent of seeds per 25 dispersal units (see text). After the species name, indication of significant differences between the treatments (n.s.: no significant differences, **: p<0.01, ***: p<0.001; tested by analysis of variance with randomization testing). Germination rates were different when followed by different letters, read for each species.

		Control (no heat)	50° C	70° C	90° C	110° C	130° C	150° C	180° C
A. laevis	***	98% a	96% a	95% a	98% a	1% b	-	-	-
A. lateralis	n.s.	74%	87%	80%	70%	82%	-	-	-
B. subaristata	n.s.	73%	81%	76%	80%	73%	-	-	-
E. muticus	***	61% a	47% ab	30% b	9% c	0% c	-	-	-
L. lanatum	***	77% a	82% a	62% b	0% c	0% c	-	-	-
S. microstachum	n.s.	87%	86%	83%	81%	87%	-	-	-
R. setigera	***	24% a	26% a	26% a	0% b	0% b	-	-	-
O. angustifolius	***	47% a	47% a	47% a	36% a	0% b	-	-	-
E. horridum	***	53% ab	-	57% a	40% bc	38% abc	27%c	0% d	0% d
E. pristis	**	18% a	-	14% a	7% ab	8% a	8% ab	2% bc	0% c

While seeds from no species were stimulated to a higher germination rate by the heat treatment, species differed in their capability to germinate after high temperatures (Tab. 2). *Andropogon lateralis*, *Schizachyrium microstachyum* and *Briza subaristata* showed no difference in germination rates across all treatments. Seeds from *Aristida laevis*, *Orthopappus angustifolius* and *Elionurus muticus* did not germinate after the 110°C treatment. In *A. laevis*, only 5.8% of the seeds of this treatment were shown to still be viable by the tetrazolium test, while in the other two species, all

seeds were dead. Seeds from *Leptochoryphium lanatum* and *Rhynchospora setigera* did not germinate anymore after the 90° or 110°C treatments, with the rate after 70°C already significantly lower than after 50°C and the control treatment for *L. lanatum*. In *R. setigera*, all seeds in the 90° and 110°C treatment were dead, while mortality rates as sown by the tetrazolium test were 92.0% and 96.8% for these two treatments, respectively, in *L. lanatum*. The apparent linear decline in germination rate in *E. muticus* as temperature applied in the treatments increased may be due to chance due to the very small number of seeds actually contained in each replicate and thus will not be considered here. The three grass species with the lightest seeds, *S. microstachyum*, *B. subaristata* and *A. lateralis*, germinated even after the highest temperature treatment, whereas the larger seeded *L. lanatum*, *R. setigera* and *E. muticus* showed no or almost no germination after even the 90°C treatment. *Eryngium horridum* and *E. pristis* showed a relatively gradual decline in germination ability, still showing germination after 130°C and, to a very small extent after 150°C in *E. pristis*.

Discussion and conclusions

Fire leads to short-term heating of the uppermost soil layer. Bradstock & Auld (1995) report soil temperatures of above 60°C in the uppermost three centimeters during burns in Australian bushland. Miranda *et al.* (1993) state a temperature of 55°C in the depth of 1cm during a Cerrado fire in central Brazil, Auld & O'Connell (1991) mention temperatures of above 80°C in the upper two centimeters for fires with medium intensity and Silva *et al.* (1990) report temperatures between 101°C and 111°C in the upper 5mm of soil in a savanna in western Venezuela. Considering this temperature range experienced in the soil during the passage of a fire, all species tested in our study should be able to germinate from the seed bank unless situated in the uppermost soil layer or directly at the soil surface where temperatures will be higher. For none of the species, a temperature of 70°C significantly decreased germination rates, and for most, a temperature of 90°C likewise showed no effect. Only locally, higher temperatures because of fire passing more slowly or being more intense, i.e. because of accumulation of more woody biomass, should be reached, thus causing a negative effect of soil-stored seeds. We conclude that heat effects of fire in South Brazilian grassland should not directly affect germination processes after fire for the species studied, neither positively or negatively, while we do not rule out the indirect effect of higher germination rates due to reduced competition after fire or favorable resource availability facilitating seedling emergence (e.g. Mott & Groves 1982, Bond & van Wilgen 1996). Apparently, in subtropical fire-prone grasslands, heat stimulation of germination does not exist, in contrast to Mediterranean type ecosystems, where heat has been shown to be necessary to break dormancy in hard-seeded species (see references cited above) or to stimulate germination in disturbance specialists (Cruz *et al.* 2003). Germination of three of the grass species after exposure to temperature of 110° C and of the two *Eryngium* species after exposure to even higher temperatures, however, does suggest a physiological resistance to heat, which could be interpreted as an adaptation to fire. Even though not formally tested as we did not have replicates for the seed weight

measurements, our results suggest that germination ability after exposure to heat may be related to seed size, as shown by Hanley *et al.* (2002) for a set of Western Australian Fabaceae. As these authors suggest, this has to be considered in relation to vertical distribution of seeds in the soil: small-seeded species usually will be found in upper soil layers than large-seeded species and thus may be subject to higher temperatures, requiring higher tolerance levels to temperature.

Fire-followers, depending on fire for establishment in vegetation and shown to respond positively to a heat shock (e.g. Ferrandis *et al.* 1999), cannot be found in South Brazilian grassland (Overbeck, submitted (b)); annuals, in many regions an important part of post-fire colonizers (e.g. Keeley *et al.* 1981, Moreno & Oechel 1991, Ghermandi *et al.* 2004), and which in chaparral and fynbos vegetation have been shown to germinate after a stimulus by heat, charred wood or smoke (Christensen & Muller 1975, Keeley & Bond 1997), in fact are largely missing in the region (Boldrini 1993, Garcia *et al.* 2002, Overbeck *et al.*, unpubl.), reinforcing the conclusion that species in this vegetation are not directly stimulated to germinate by fire. It seems important to additionally test hardseeded species (e.g. Leguminosae, a very species-rich family in Brazilian grassland or savannas; e.g. Boldrini 2002, Mendonça *et al.* 2002) for germination response to heat, in order to be able to verify the results obtained in Mediterranean-type ecosystems (see e.g. Keeley & Fotheringham 2000 and references in Introduction). The restriction of such experiments on hard-seeded species, however, may produce a bias in interpreting the role of heat on seed germination in fire-prone ecosystems in general.

Acknowledgments

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CHAPTER 6 (Conclusion)

Fire in grassland – disturbance or management tool?

Introduction

Many of the world's ecosystems are shaped by fire (e.g. Bond & van Wilgen 1996 for an overview), including a large part of grasslands worldwide. In systems subject to frequent burns, fire is considered to be one of the main factors determining biological diversity and vegetation structure (e.g. Sarmiento & Monasterio 1975, Frost *et al.* 1983, Stocks & Trollope 1993, Braithwaite 1996, Silva & Sarmiento 1997, Collins & Steinauer 1998, Higgins *et al.* 2000). In fact, fire is the factor responsible for the very existence of grasslands and savannas in regions where climate allows for forest development (e.g. Sauer 1950, Vogl 1974, Bond *et al.* 2003), such as southern Brazil (Pillar & Quadros 1997).

Together with agents like domestic grazing and burrowing animals, drought, earthquakes, frost, hurricanes, insect outbreaks, lumberjacks and storms, fire is usually considered to be a disturbance (White 1979, White & Jentsch 2001). However, in some studies of systems subject to frequent burns, fire has been called an "intrinsic", "inherent" or "integral" factor (e.g. Naveh 1975, Abrahamson 1984, Scholes *et al.* 1997). Hulbert (1969) and Naveh (1975) explicitly state that fire should not be considered and studied as a disturbance, but as a necessary component for maintenance and preservation of ecosystems with an evolutionary history of fire. The question whether fire should be called a disturbance or not may be considered a purely semantic issue, but, as Grimm & Wissel (1996) have pointed out, concepts act like signposts for scientific work, and also determine the way we perceive and analyse nature, with consequences also for conservation management. The effect of a single fire or the overall fire regime remains the same, whether we consider it a disturbance or not. However, the often polemic discussion of fire as a disturbance, i.e. as an agent "injuring" vegetation or protected areas (de Medeiros & Fiedler 2004), and misconceptions of fire effects have led to neglection of fire as an important factor in ecological studies in grassland and to rejection of fire as a tool for nature conservation purposes in Brazil (Ramos-Neto & Pivello 2000).

Grassland – disturbed by fire?

Defining disturbance

Grime (1979) defines disturbance as any event partially or totally destroying plant biomass. For White & Pickett (1985) "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" can be called a disturbance. For Bazzaz (1983), a disturbance is "a sudden change in the resource base of a unit of the landscape that is expressed as a readily detectable change in population response". Pickett *et al.* (1989) emphasize that a disturbance is "caused by a factor external to the level of interest" and changes the minimal structure of the system, but does not destroy the system as such. In contrast to Grime's classical definition, these three definitions consider that disturbances may act upon a certain hierarchical level or ecosystem property, but can lead to changes or reactions of other ecosystem

components on other levels, thus clearly distinguish between cause and effect. Under all of these definitions, a grassland fire can be considered a disturbance. Biomass is being destroyed; the community structure is being changed from a community with dense aboveground vegetation to a community where aboveground vegetation has been removed and ashes and open soil prevail; populations of plants express variable responses (some may have to re-colonize the site, some may go extinct, others may increase in frequency, some may increase reproductive activity), and structure (e.g. vertical distribution of biomass, litter), resource availability (e.g. light, nutrients, water) and the physical environment (e.g. soil and surface temperatures, water runoff) are clearly changed as direct or indirect consequence of the burn. Still, the grassland remains a grassland, i.e., some of its components and its structure have changed, but not the system's identity.

Effects of fire on individual plants

The fast recovery of grassland and savanna vegetation after fire is the result of plant adaptations (Gill 1981, Tainton & Mentis 1984, Sarmiento 1992, Bond & van Wilgen 1996), just as in other fire-prone ecosystems, for example Mediterranean type shrubland vegetation (e.g. Christensen & Muller 1975, Keeley 1986). When comparing grassland communities subject to fires worldwide, no general pattern of vegetation development after the burn can be found. In some grasslands, species composition in pre- and post-burn communities is essentially the same, e.g. in South Brazilian Campos (*Chapter 2*); in others, different species groups replace each other in a short-term successional process, e.g. in Patagonia grasslands (Ghermandi *et al.* 2004), where early post-fire vegetation is characterized by a "phantom community" of species only present right after a burn, or in páramo (Ramsay & Oxley 1986). However, it needs to be recognized that all of these species are always part of the community, even though not always all present in aboveground biomass. Problems of applying successional theory to grasslands – or other systems underlying frequent disturbances – have been acknowledged (Wallace 1990): not disturbance-free periods, but repeated disturbances and environmental fluctuations shape vegetation (White 1979), and it may be difficult to distinguish processes that appear to maintain the status quo from those that cause successional dynamics (Walker 1982). Certainly, the idea of fire as an agent setting back succession ("class-II disturbance" in the terminology of White & Jentsch 2001) does not serve for grassland or savanna communities.

Technically, Grime's definition of disturbance applies to any plant being affected by a burn. Any loss of biomass of course will have effects of future population growth, as it is largely plant size that determines growth rate and reproduction (Harper 1977). However, not all plants in a grassland community will be affected negatively by a fire. For tallgrass prairie, it has been observed that little mortality as a direct effect of burning occurs, except in annuals, some C_3 grasses, and seedlings of woody species (Gibson & Hulbert 1987, Collins & Steinauer 1998). In many systems, fires are more frequent in the dry season, i.e. when plants are not in their photosynthetic active phase and large parts of aboveground biomass have already died. Even where no dry season exists, e.g. in southern Brazil, a

part of the community will nonetheless be dormant at the time of the fire or will at least have terminated the reproductive cycle. Fires in early spring, for example, will diminish contribution of C_3 grasses, whereas these will benefit from summer burns, at the expense of C_4 grasses (Llorens & Frank 2004). It has been shown for caespitose grasses that removal of aboveground biomass can have positive effect on tiller development and photosynthetic activity (Knapp 1985, Silva *et al.* 1991, see *Chapter 3*). Some species even depend on removal of dead biomass by fire: kangaroo grass *Themedra triandra*, for example, will die after approximately seven years without fire, suffocated by its own biomass (Morgan & Lunt 1999); for other grasses, likewise negative effects of accumulated biomass and shade on vegetative growth and reproduction have been documented (Vogl 1974, Silva *et al.* 1990, Bond *et al.* 2003). Increased reproductive output after fire is known as a common effect of fire in many grasslands: vernal aspect geophytes, for example, will appear principally, in some cases only, after the passage of a fire (Gill 1981, Tainton & Mentis 1984, Miranda *et al.* 2002). Even young trees from environments subject to frequent burns can be remarkable resistant to fire: Hoffmann (2000) reports that many Cerrado trees survive a fire already at the age of less than one year, in contrast to forest pioneer species establishing in grassland areas.

While this compilation of mechanisms of how plants survive or profit from burns is certainly not exhaustive, it does show that at least for a large part of species present in fire-prone ecosystems, fire is indeed a "normal" factor of their environment (White 1979) that has lead to the development of appropriate adaptive strategies, underlining that these species have been exposed to fire throughout their evolutionary history (Harper 1982). While individuals, not species, are affected by fire, some plants even are *dependent* on fire for completion of their life cycle, or profit from fire, e.g. the vernal aspect geophytes mentioned above. Apparently, when we call grassland fire a "disturbance", we do not consider these species which may not be visible or may be too inconspicuous in pre-fire vegetation, but stumble over them only when flowering after a burn.

Fire and community development

Grassland fires must not only be considered to act upon individual plants, but focus can be shifted onto the community level, spanning a longer period of time. A fire affects a grassland area that had not burned for three years, i.e. where sufficient biomass was present to allow for a stand-replacing fire. Soon after the fire, the majority of species will begin to sprout from protected belowground organs (*Chapter 2, 3*), and some species will colonize the burned areas from seeds, not directly stimulated by fire (*Chapter 5*), but profiting from favorable resource availability and lack of competition. Vegetation will recover rapidly, open soil will be covered by plants and plant litter, and about three years after the fire, a state similar to the one before the fire will be reached considering overall species composition, vegetation structure and physiognomy, with sufficient biomass to allow for the next burn (*Chapter 2, 4*). Fire frequency of course may be rather irregular, with fires occurring at different seasons and with different fire intervals, and effects of single fires will depend on

variability of climate, weather and as a result of interactions with other environmental factors (e.g. Collins 1987, Collins & Gibson 1990, Risser 1990, Higgins *et al.* 2000), without, however, major changes in species composition, at least of the "diagnostic species" allowing for characterization of the system as a grassland (Glenn-Lewin & van der Maarel 1992).

Present climatic conditions in southern Brazil are favorable to forest development, and grasslands are constantly subject to shrub encroachment and, if seed sources are present, forest expansion processes (Waechter *et al.* 1984, Oliveira & Pillar 2004, Müller *et al.*, in prep.), which, however, will suffer a setback by every fire event, as forest pioneer trees are killed and shrubs reduced to the ground level (Pillar 2003; *Chapter 3*). In the absence of fire (or grazing), vegetation would change from grassland to woodland or forest, or, to use the terminology used in the definition of disturbance by Pickett *et al.* (1989), the minimal structure would be changed substantially, from an open grassland system to a forest. After a longer period without fire, vegetation physiognomy and structure thus will have changed in a way that spread of fires is no longer possible. This change most likely is permanent, at least when assuming the absence of major climatic changes or catastrophic events. In other words, structure of a grassland system is being maintained by the interaction of the flammable vegetation and disturbances: fire is responsible for long-term stability of the grassland, even though it may cause short term fluctuations in composition and biomass (Archer *et al.* 1996). At least under mesic or humid climate conditions, absence of fire would lead to a shift to another system state, i.e. could be considered a disturbance for the grassland system.

Grassland vegetation as determinant of grassland fire

Fire differs substantially from most other disturbances, as it cannot, at least in systems where it occurs regularly, be considered an exogenous factor acting upon vegetation, such as many disturbances related to extreme weather events or to chemical and physical activity (White 1979). Rather, its action is a direct result of flammability attributes of the vegetation, or, in the words of Gleason (1913, cited in Vogl 1974): "In order to have a prairie fire, there must first have been a prairie". Fire depends on vegetation structure, requiring sufficient amounts of sufficiently dense flammable biomass to carry a burn (Bilbao *et al.* 1996). In grassland and savannas, the herbaceous layer contributes to all or nearly all of flammable biomass, and in productive communities under mesic or humid conditions, fire return intervals can be as low as one year (Bond *et al.* 2003). While grassland systems may be extremely rich in forb species (*Chapter 1* for southern Brazil), it is the caespitose grasses that provide for the principal fuel, principally as a consequence of the accumulation of dead biomass on the plant, with surface/volume ratios of biomass allowing for rapid spread of fire (Bond & van Wilgen 1996). Because of the positive feedback cycle between grasses and fire (D'Angelis & Vitousek 1992), grasses define system structure not only because of their dominance *per se*, but because of their flammability – they are, so to speak, the grassland's ecosystem engineers (Jones *et al.* 1994, Lawton 1994; *Chapter 4*). It should be safe to say that in grassland systems, at least

in systems above a certain productivity level, fires are predictable in the sense that it is certain that they will occur, in an endogenous rhythm (with, of course, some variability) defined by fuel accumulation (White 1979).

Fire as a tool for nature conservation

We can summarized that 1) on the level of the plant species or even individual plant, fire is not a disturbance for at least part of the community, that 2) on the level of the community, a fire event invokes no successional changes but merely population-level fluctuations in relation to temporal niches in post-fire vegetation development and to differences in competitive ranking and that 3) on the long run, fire is a necessary factor for maintenance of grassland or savanna ecosystems where climate supports forest vegetation, and that, as a consequence, under this long-term perspective, absence of fire needs to be considered a disturbance for grasslands. As Jax (1999) has pointed out, a fire always acts upon individual plants or their resource base, i.e. is a concrete event affecting concrete objects. When we talk of the effect of fire "on grassland", we need to consider the grassland to be an assemblage of individuals. When the grassland as a vegetation type is the object of study or interest, fire cannot be considered a disturbance, as it is one of the principal factors defining presence and properties of the system in an interactive process with grassland vegetation, at least under climatic conditions allowing for forest vegetation, such as in southern Brazil (Pillar & Quadros 1997; *Chapter 3*), southern Africa (e.g. Bond *et al.* 2003), or the North American Tallgrass Prairie biome (e.g. Collins *et al.* 1998).

But should fires not be a disturbance when not caused naturally, but set by humans? For southern Brazil, we do not know of any published data on causes of wildland fires. For Cerrado vegetation protected from fire and grazing in Emas National Park, Goiás State, Central Brazil, Ramos-Neto & Pivello (2000) showed that 1 to 2% of lightning strikes caused fires, predominantly in the wet season, burning more than 2/3 of the park's area during a period of 4 years, some parts more than once. A similar situation was found for a Cerrado area in Minas Gerais State, Central Brazil (de Medeiros & Fiedler 2004). Wet season fires usually are extinguished by rain and therefore rather small in extent, creating mosaics of sites burned at different times (Ramos-Neto & Pivello 2000). Lack of natural burns caused by lightings may simply be a result of land use: frequent anthropogenic fires used for range management or lightened for other purposes may have removed flammable biomass to an extent that natural fires are not possible anymore. Fragmentation of the landscape, e.g. by roads, trails or railroads or by agricultural or silvicultural plantations, limits fire spread, thus also lowering fire frequency for any given grassland area (Vogl 1974, Howe 1994, Leach & Givnish 1996). In Brazil, lightning thus could be a more common source for grassland fires than commonly thought, just like in African savannas (Stocks & Trollope 1993) or American prairie, where majority of fires prior to human occupation likewise occurred in the growing season, in contrast to majority of prescribed burns in vegetation management (Howe 1994).

As discussed above, protection of South Brazilian grassland areas from fire will lead to substitution of grassland vegetation by forests (e.g. Oliveira & Pillar 2004), resulting in substantial losses of biodiversity due to the high species richness of South Brazilian grassland (Boldrini 2002, *Chapter 1*). For the study area on Morro Santana where field work for this thesis was conducted, plans for establishment of a nature preservation area exist, calling for elaboration of conservation aims and a corresponding management plan. If maintenance of biodiversity was one of the principal objectives of the future reserve, the mosaic of forest and grassland, with different stages of shrub encroachment caused by differently sized patches with different time since fire, needs to be preserved, allowing for high between-patch or landscape level diversity, and, with a proper management, high within-patch diversity in grasslands (see *Chapter 2*). Considering the importance of fire in the evolutionary history of the grasslands (Anderson 1982), fire should be a factor maximizing plant species diversity, even though identification of the "optimal" fire frequency and season for conservation purposes (see Hobbs & Huenneke 1992), just as understanding of vegetation patterns and processes in South Brazilian grassland ecosystems in general, clearly requires more and longer-term studies at more sites – research on fire in South Brazilian grassland is only at its beginning.

Fire should be considered as a management tool not only in our study area on Morro Santana, but in other grassland areas as well, e.g. in National Parks of southern Brazil, where grasslands likely will disappear within the next decades as a result of the current policy of fire exclusion. Actions need to be taken to preserve natural grassland vegetation in Rio Grande do Sul with its high plant diversity, before it is entirely replaced by agriculture or *Pinus* plantations outside the limits of protected areas, or has turned into forest within them.

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SUMMARY

Effect of fire on vegetation dynamics and plant types in subtropical grassland
in southern Brazil

Large parts of southern Brazil are characterized by presence of grasslands, often in mosaics with forests, despite large-scale climatic conditions allowing for forest development. Based on palaeoecological and phytogeographical data, grasslands today are considered to be relicts from cooler and drier climatic conditions during glacial and warmer and drier conditions during early post-glacial times, stabilized until today by fire and grazing. Dynamics between forest and grassland, however, are poorly understood, just as only few studies on the ecology of South Brazilian grassland exist. The presented thesis analyzes the effect of fire on species dynamics and plant functional type composition of South Brazilian Campos grassland, based on field work conducted principally on Morro Santana, Porto Alegre, RS, Brazil. Grasslands on the hill, ungrazed and subjected to frequent fires by local population, are found predominantly on the top and the northern slope, whereas forests cover the other slopes. The species pool of the grassland areas on Morro Santana can be estimated to contain approximately 450 to 500 vascular plant species and thus the studied grassland, like grassland vegetation in southern Brazil in general, is very species-rich, even though this high biodiversity and conservational value of Campos vegetation so far have not been recognized adequately.

Caespitose grasses with the C_4 pathway are the most important plant species group in terms of dominance, while a large number of mostly sparsely and irregularly distributed forbs contributes to grassland diversity, mostly occurring in low frequencies and showing patchy distribution patterns. Areas exposed to the north differ from areas on the top of the hill both in species composition and in soil properties, principally due to shallower soil in the latter; however, no strong relation between soil properties and variation in vegetation composition seems to exist. In the studied grassland, fire exerts an important role for spatio-temporal small-scale diversity. Species number and small-scale dynamics are highest about 1 year after a burn, when competitive interactions are reduced and recruitment possibilities are high in early post-fire environmental with favorable resource conditions. With more time since fire, caespitose grasses increasingly dominate the grassland structure, leading to lower contribution of forbs, even though overall community composition does not seem to be greatly affected by fire on a larger spatial scale over areas of different fire history. Apparently and in contrast to other fire-prone systems, no clear group of fire-following species exists; richness can be attributed to regular burns increasing spatial heterogeneity and lowering dominance.

The community seems to be adapted to the current fire regime and may have evolved under the influence of fire, as can be concluded from the grassland's life-form spectrum and the capacity to either resist a fire or resprout after a fire in the largest part of the species. Caespitose grasses resist

fires with their protected meristems. Most forbs are either resprouting hemicryptophytes or geophytes, and the largest part of the shrubs, whose high cover values characterize South Brazilian grassland physiognomy, resprouts readily after fire. In contrast to savannas, e.g. Brazilian Cerrado, almost no trees can be found in the grasslands; those that are present are pioneer species from nearby forests and do not survive fires unless at sites protected from fire. Interestingly, therophytes are almost absent, which most likely is a result of the region's climatic conditions.

Grasslands under climate favorable for forest development in general show high productivity and usually the tendency to turn into shrublands or forests in the absence of fire. Caespitose grasses and other graminoids can be considered the plant type responsible for the persistence of grasslands, as it is their biomass that allows for flammability, leading to cyclic vegetation development with recurrent burns. While the majority of species present shows efficient mechanisms of post-fire recolonization by resprouting, stimulation of germination by heat does not seem to play a role in the studied grassland. However, seeds of many species seem to tolerate higher temperatures in the soil. In general, germination from seeds was not observed to be of importance for post-fire (re-)colonization.

Fire can hardly be considered to be a disturbance in the studied grassland, as it is the factor responsible for persistence of the open vegetation type, even though some plants may be affected negatively by a fire event. Today, most fires in southern Brazil are anthropogenic, but this is a consequence of land management and does not necessarily mean that natural fires would not occur. The common consideration of fire as a disturbance has led to neglection of fire as a management tool in Brazil and to exclusion of fire from areas protected for nature conservation, thus causing to successional processes from grasslands to shrubland and forest. Together with transformation into agri- or silvicultural plantations, continuation of the policy of fire exclusion threatens persistence of South Brazilian grasslands and thus biodiversity. Fire should be considered as a tool for nature conservation in Campos grasslands in southern Brazil.

ZUSAMMENFASSUNG

**Einfluss von Feuer auf Vegetationsdynamik und Pflanzenfunktionstypen
der Grasländer Südbrasiliens**

Weite Teile Südbrasiliens sind von Grasländern (*Campos*) bedeckt, obwohl die aktuellen klimatischen Bedingungen die Ausbildung von Wäldern ermöglichen. Auf Grundlage paläoökologischer und phytogeographischer Daten nimmt man heute an, dass es sich bei den Grasländern um Relikte aus kühleren und trockeneren Bedingungen des letzten Glazials bzw. aus wärmeren und trockeneren Bedingungen des frühen Postglazials handelt, die durch Beweidung und Feuer bis in heutige Zeit stabilisiert sind. Die Wald-Grasland-Dynamik ist bislang kaum untersucht, ebenso wie nur wenige Studien zur Ökologie der südbrasilianischen Grasländer existieren. Vorliegende Arbeit analysiert den Einfluss von Feuer auf die Vegetationsdynamik und die Zusammensetzung funktionaler Pflanzentypen im südbrasilianischen *Campos*. Die Geländearbeiten wurden auf dem Morro Santana, einem der granitischen Hügel um Porto Alegre, RS, durchgeführt, einem Gebiet mit unbeweideten Grasländern, die frequenten, weitgehend anthropogenen, Feuern unterliegen und sich vorwiegend an Nordhängen und Hügelkuppen finden, während die übrigen Hänge von Wäldern eingenommen werden. Die Grasländer am Morro Santana umfassen ca. 450 bis 500 Gefäßpflanzen; das untersuchte Grasland ist somit, wie südbrasilianische Grasländer allgemein, sehr artenreich, wenngleich die hohe Biodiversität der *Campos*-Grasländern bislang jedoch nur wenig Beachtung findet.

Die Flächen werden von C_4-Horstgräsern dominiert, während eine Vielzahl häufig nur relativ spärlich vorkommender krautiger Arten für die hohe Diversität der Grasländer verantwortlich ist. Grasländer am Nordhang des Morros Santana unterscheiden sich von denjenigen in Kuppenlage, sowohl hinsichtlich Artenzusammensetzung als auch standörtlicher Parameter, hauptsächlich aufgrund flachgründiger Boden auf der Nordseite. Es scheint jedoch kein starker Zusammenhang zwischen Variation in der Artenzusammensetzung und Standortsfaktoren zu bestehen. Feuer besitzt im untersuchten Grasland eine hohe Bedeutung für die kleinmaßstäbliche, v.a. auch zeitliche, Diversität. Artenzahl und Vegetationsdynamik sind etwa ein Jahr nach einem Brand am höchsten, da Konkurrenzwirkung im Pflanzenbestand reduziert und gleichzeitig Rekrutierungsmöglichkeiten und Ressourcenverfügbarkeit hoch sind. Mit mehr Zeit seit dem letzten Feuer erlangen Horstgräser zunehmend Dominanz und führen zu einer Ausdünnung vorwiegend der krautigen Arten, wenngleich die Gesamtartenzusammensetzung über größere Gebiete, also in der Regel Flächen mit unterschiedlicher Zeit seit dem letzten Brand beinhaltend, durch Feuer offensichtlich nicht stark beeinflusst wird. Im Gegensatz zu vielen anderen feuergeprägten Vegetationstypen kommt im untersuchten Grasland keine klare Gruppe feuerfolgender Arten vor; die hohe Artenzahl kann

vielmehr durch die frequenten Brände, die die räumliche Heterogenität erhöhen und die Dominanzwirkung einzelner Arten verringern, erklärt werden.

Die Gemeinschaft scheint insgesamt an das gegenwärtige Feuerregime angepasst sein und hat sich vermutlich unter dem Einfluss von Feuern entwickelt. Der Großteil der vorhandenen Arten ist zum Wiederaustreiben nach dem Feuer befähigt. Die dominanten Horstgräser besitzen durch dichte Blattscheiden geschützte oberirdische Meristeme. Krautige Arten sind größtenteils Hemikryptophyten oder Geophyten, und die Mehrzahl der Graslandsträucher, die die Physiognomie der Flächen prägen, kann nach Feuer ebenfalls durch Austrieb aus unterirdischen Speicherorganen ihre oberirdische Biomasse rasch wiedererlangen. Im Gegensatz zum zentralbrasilianischen *Cerrado* oder anderen Savannen finden sich im südbrasilianischen *Campos* praktisch keine Bäume; diejenigen, die vorkommen, sind Pionierarten der Wälder, die Feuer nur an geschützten Standorten überleben können. Therophyten fehlen praktisch völlig, vermutlich auf Grund der klimatischen Bedingungen der Region.

Generell zeigen Grasländer unter Klimabedingungen, die die Entwicklung von baumgeprägten Vegetationstypen zulassen, eine hohe Produktivität und würden sich in Abwesenheit von Feuer zu Wäldern oder zumindest Buschland entwickeln. Somit sind Horstgräser und andere Grasartige für das Vorhandensein der Grasländer verantwortlich, da ihre Biomasse zur hohen Brennbarkeit der Flächen und somit zur zyklischen Vegetationsentwicklung mit häufigen Bränden führt. Während der Großteil der Arten der Grasländer durch die Möglichkeit des raschen Wiederaustreibens gut an häufige Brände angepasst ist, spielt (Wieder-)Besiedlung gebrannter Flächen über Keimung offensichtlich keine wichtige Rolle; insbesondere führt die Einwirkung von Hitze nicht zur Erhöhung der Keimraten, wie aus anderen feuergeprägten Ökosystemen bekannt. Allerdings scheinen Samen des Großteils der Arten die während eines Brandes im Boden auftretenden Temperaturen zu überleben.

Feuer kann für das untersuchte Grasland nicht als Störung aufgefasst werden, da es für die Präsenz der Grasländer verantwortlich ist, auch wenn ein Feuerereignis für einige, aber nicht alle, Pflanzen negative Auswirkungen haben kann. Feuer im südbrasilianischen Grasland sind heutzutage größtenteils anthropogen, aber dies ist vermutlich eine Folge aktuellen Land- und Vegetationsmanagements und bedeutet nicht, dass keine natürlichen Feuer vorkommen können. Die in Brasilien heute gängige Sicht von Feuer als Störung hat dazu geführt, das Naturschutzflächen vor Feuer geschützt werden und Grasländer somit verbuschen und sich zu Wäldern entwickeln. Zusammen mit der großflächigen Umwandlung in land- oder forstwirtschaftliche Kulturen bedroht diese Politik die Grasländer der Region. Feuer sollte als mögliches Instrument des Naturschutzmanagements der südbrasilianischen *Campos* betrachtet werden.

RESUMO

Efeito do fogo na dinâmica da vegetação campestre e em tipos funcionais de plantas nos Campos do Sul do Brasil.

No Brasil meridional, a vegetação campestre estende-se por grandes áreas, muitas vezes em mosaicos com florestas, apesar das atuais condições climáticas serem favoráveis às formações florestais. Com base em dados paleoecológicos e fitogeográficos, as atuais áreas de campo são consideradas relictos de períodos mais frios e secos (durante as glaciações) e mais quentes e secos (início dos períodos pós-glaciais), mantidas estáveis até hoje pelo fogo e o pastejo. A dinâmica entre florestas e campos é, porém, ainda pouco compreendida, assim como também há poucos estudos em ecologia nos campos do Sul do Brasil. Esta tese representa um primeiro passo na compreensão dos efeitos do fogo na dinâmica da composição de espécies e de tipos funcionais nos campos no sul do Brasil, fazendo parte de um amplo projeto de pesquisa sobre a dinâmica entre floresta-campo em relação ao impacto de diferentes distúrbios, conduzido por uma cooperação entre a TUM (Universidade Técnica de Munique, Freising, Alemanha) e a UFRGS (Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil). O estudo foi realizado principalmente na área do Morro Santana, Porto Alegre, RS, Brasil, o qual faz parte de um conjunto de morros localizados na porção mais setentrional do Escudo Cristalino Sul-rio-grandense. As áreas de campo do Morro Santana não são utilizadas como pastagem, porém estão sob influência de queimadas freqüentes, geralmente provocadas por moradores locais.

No Capítulo 1 (**"Composição florística, variação ambiental e distribuição de espécies em um campo queimado no Sul do Brasil"**), descreve-se a composição florística dos campos e os padrões de distribuição das espécies em relação às variáveis do solo, à exposição e à distância da borda florestal, com base em dados obtidos em 48 parcelas de 0,75 m^2. O *pool* de espécies de plantas vasculares para os campos do Morro Santana foi estimado em aproximadamente 450 a 500 espécies. As gramíneas cespitosas formaram o grupo mais importante em relação à dominância, enquanto um elevado número de espécies herbáceas, geralmente com abundâncias menores e distribuição esparsa, contribuiu para a alta diversidade de espécies da área. A maioria das espécies apresentou baixa freqüência e um padrão agrupado de distribuição na área estudada. A análise multivariada dos dados indicou que as parcelas adjacentes à borda florestal claramente diferiram florística e estruturalmente das parcelas do campo. As parcelas com exposição norte diferiram das do topo do morro, tanto pela composição florística quanto pelas variáveis do solo, principalmente devido à menor profundidade do solo no norte. Entretanto, nenhuma relação forte foi detectada entre a variação das propriedades do solo e a variação da composição de espécies na comunidade. A área estudada, assim como a vegetação

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campestre no sul do Brasil em geral, apresenta alta riqueza de espécies, se comparada a outras formações de campo ou savana no mundo. Apesar disso, a alta biodiversidade e o valor de conservação dos campos não têm sido reconhecidos. Na ausência do pastejo, o fogo é um importante fator de manejo para a conservação da vegetação campestre, uma vez que o distúrbio parece ser necessário para manter esse tipo de vegetação aberta, com alta riqueza de espécies.

O papel do fogo na dinâmica das espécies campestres num período de dois anos foi discutido no Capítulo 2 (**"Dinâmica das espécies sob o impacto do fogo em campos subtropicais no Sul do Brasil"**). Foram utilizados os dados das mesmas parcelas descritas acima, para analisar diferenças na composição de cada parcela em dois anos consecutivos de amostragem. Os dados foram analisados separadamente para parcelas recém queimadas (três meses), queimadas há um ano e queimadas há mais de três anos. O foco das análises foi na variação da riqueza de espécies, diversidade, eqüidade e outros parâmetros estruturais da vegetação. Além disso, os dados do Morro Santana, cujos campos estão sujeitos a queimadas freqüentes, foram comparados com dados de um campo excluído de fogo e pastejo, em São Francisco de Paula, RS, na região do Planalto. Nos campos do Morro Santana, o número de espécies e a dinâmica temporal nas parcelas foram maior nas áreas com um ano após o fogo, diminuindo à medida que a cobertura de gramíneas cespitosas aumentava, ou seja, com o tempo transcorrido após o fogo, atingindo maior estabilidade (menor dinâmica temporal), porém menor diversidade, nas áreas com três a quatro anos sem fogo. Nas áreas de campo excluído, as gramíneas cespitosas obtiveram uma dominância ainda maior e, consequentemente, a riqueza de espécies herbáceas foi bem menor. Assim, o evento de uma queimada claramente resultou no aumento da riqueza e diversidade, considerando a escala da parcela, o que foi atribuído à redução das interações competitivas, principalmente pela menor dominância das gramíneas cespitosas, e à maior disponibilidade de locais para o recrutamento de plântulas na comunidade recém-queimada. Como observado no primeiro capítulo, a composição da comunidade em geral parece não sofrer mudanças causadas pelas queimadas. Mesmo que tenha sido observada certa vantagem para pequenas espécies herbáceas nas áreas recém queimadas, não foram observadas espécies exclusivas destas áreas, ou seja, não houve um grupo que dependesse do fogo para a sua presença no sistema. Concluiu-se, portanto, que as comunidades avaliadas estão adaptadas ao atual regime de queimadas, sugerindo que tenham evoluído sob o impacto do fogo.

Estratégias de adaptação ao fogo são discutidas em maior detalhe no Capítulo 3 (**"Estratégias adaptativas ao fogo em campos subtropicais no Brasil meridional"**). Foi avaliada a distribuição das formas de vida, segundo Raunkiaer, e a reação das espécies ao fogo, permitindo uma descrição fisionômica dos campos e uma classificação funcional em relação ao fogo. Para esta última, o sistema de formas de vida foi ampliado após combinar informações sobre a capacidade das espécies em resistir ao fogo, mantendo parte de sua biomassa aérea, ou rebrotando da base após o fogo. Além de usar dados das mesmas parcelas analisadas em Capítulos 1 e 2, foram utilizados dados de parcelas maiores (1,5 x 1,5m; 4,5 x 4,5m) para a descrição do componente lenhoso. As áreas de campo foram

comparadas conforme o tempo transcorrido após a última queimada e em relação à proximidade da borda florestal. Os campos se destacaram pela dominância de gramíneas hemicriptófitas cespitosas resistentes ao fogo, assim como pela presença de muitas herbáceas hemicriptófitas ou geófitas, a maioria das quais tinha capacidade de rebrotar após o fogo. O componente lenhoso, formado principalmente por espécies arbustivas de campo que rebrotam após o fogo, apresentou valores altos de cobertura, mesmo em áreas recém queimadas. Ao contrário do Cerrado brasileiro ou de outras savanas, espécies arbóreas tiveram pouca importância nos campos estudados: a maioria das espécies arbóreas que esteve presente são consideradas espécies florestais pioneiras, sem a capacidade de resistir ao fogo, exceto quando estabelecidas em lugares protegidos do fogo ou próximos da borda, onde o fogo pára. Em geral, espécies sem capacidade de rebrotar tiveram pouca importância na cobertura total da vegetação e apenas duas espécies terófitas foram encontradas. A falta de espécies terófitas nos campos sul-brasileiros merece mais atenção em estudos futuros. Finalmente, a necessidade de estudos comparativos entre áreas de vegetação campestre do mundo, em relação às formas de vida e estratégias das plantas, é reconhecida.

No Capítulo 4 (**"Efeitos e respostas do ecossistema: análise de tipos funcionais de plantas em áreas de campo queimado"**), a composição funcional dos campos foi avaliada através de análises numéricas. Tipos funcionais de plantas (TFPs), associados à história de fogo nas áreas de campo estudadas, foram definidos com base em um conjunto de 12 atributos morfológicos ou fenológicos, sendo um referente à capacidade de rebrote, pelo método analítico apresentado em Pillar & Sosinski (2003). Os altos valores de congruência entre a variável ambiental considerada (tempo após o fogo) e a variação dos dados da vegetação, indicaram TFPs com alto valor explicativo. Atributos relacionados ao desenvolvimento da planta (tais como altura da planta, comprimento da folha e proporção de biomassa morta) tiveram maior contribuição na definição dos tipos funcionais. O estado fenológico reprodutivo foi indicativo de áreas recém queimadas, enquanto a capacidade de rebrote não mostrou-se relacionada com o tempo após o fogo. As áreas não queimadas há mais tempo destacaram-se pela dominância de tipos formados por gramíneas cespitosas, em contraste às áreas recém queimadas cuja vegetação apresentou maior diversidade de tipos funcionais. Estes resultados enfatizam a importância do papel das gramíneas cespitosas no sistema avaliado. A resposta das plantas e o efeito no ecossistema estão interligados pelo tipo funcional das gramíneas cespitosas, pois, como responsáveis pela flamabilidade do sistema, em conjunto com fatores climáticos, conduzem ao desenvolvimento cíclico da vegetação campestre sujeita a queimadas freqüentes. Os demais grupos de plantas contribuem pouco para a flamabilidade, mas a presença do fogo na história evolutiva dos campos tem conduzido à seleção de espécies adaptadas ao fogo.

No capítulo 5 (**"Ausência de estímulo por altas temperaturas na germinação em espécies de campos subtropicais"**), analisou-se um aspecto de adaptação ao fogo, comum em vários tipos de vegetação do mundo sujeitas ao fogo: o estímulo da germinação pelo fogo. Neste trabalho, foi testado o efeito de altas temperaturas, simulando o aquecimento do solo durante a passagem do fogo, na

germinação de sementes de nove espécies (5 gramíneas, 1 cyperácea e 3 herbáceas) presentes na vegetação campestre do Morro Santana. As sementes foram expostas a temperaturas entre 50° e 110°C (180°C para duas espécies) por um período de dois minutos. A germinação foi monitorada após os tratamentos. Nenhuma das espécies demonstrou uma taxa de germinação maior após os tratamentos, porém a capacidade de germinação diferiu entre as espécies avaliadas. Duas espécies herbáceas e três gramíneas germinaram mesmo após o tratamento que expôs as sementes a 110°C ; as demais espécies diferiram entre si quanto aos limites de tolerância ao calor. Os resultados sugerem que não existe nenhum mecanismo aparente que estimule a germinação das sementes expostas a temperaturas elevadas. Entretanto, algumas espécies demonstraram maior resistência ao calor, não apresentando, portanto, risco de prejuízo na germinação pelo aquecimento de suas sementes por ocasião de uma queimada.

No capítulo da síntese final (Capítulo 6; **"O fogo nos campos – distúrbio ou instrumento de manejo?"**), discutiu-se a aplicação do conceito de distúrbio para o fogo em áreas de vegetação campestre, utilizando os resultados dos capítulos anteriores como base na argumentação. O fogo pode ser considerado um distúrbio apenas em relação a um evento específico de fogo que atue sobre indivíduos concretos de plantas. Mesmo assim, alguns indivíduos podem depender do fogo para completar o seu ciclo de vida, portanto, o fogo não representa um distúrbio para todas as plantas de comunidades campestres. Quando as áreas de campo são consideradas numa escala temporal maior, o fogo não constitui um distúrbio, pois o modo como interage com a própria vegetação, o torna um dos principais fatores responsáveis pela presença de vegetação campestre *per se*, especialmente em áreas cujas condições climáticas são favoráveis ao desenvolvimento de florestas. Atualmente, a maioria das queimadas na região dos campos sul-brasileiros resulta de ignição antrópica, mas isso é uma conseqüência do manejo atual do uso do solo e não necessariamente significa que não ocorreriam queimadas naturais. A consideração do fogo como um distúrbio não é somente uma questão semântica, todavia resultou na negligência do uso do fogo como instrumento legal de manejo em áreas de campos naturais no Brasil e na exclusão absoluta do fogo das áreas de unidades de conservação. Considerando a enorme quantidade de áreas de campo que têm sido transformadas em plantações agrícolas ou silviculturais em conjunto com a continuidade da atual política sobre o uso do fogo, que proíbe o uso das queimadas como prática de manejo, a persistência dos campos sul-brasileiros e a biodiversidade da região estão ameaçadas. O fogo deveria ser considerado como um instrumento para a preservação das comunidades de campo nativo no Sul do Brasil.