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Fire in subtropical grasslands in Southern Brazil: effects on plant strategies and vegetation dynamics

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PREFACE

The thesis is written as a cumulative PhD thesis. Chapters 1 to 5 are independent papers that were and will be submitted for publication in different scientific journals. Moreover, an introduction and a conclusion with an integrating discussion join considerations of the different chapters. In order to facilitate reading, tables and figures were inserted into the text. References about papers in preparation were referred according to the chapter. References in text and in the bibliography were all formatted in the same way. Enumeration of tables and figures was conducted separately for each chapter.

In addition to English and German summaries, a summary in Portuguese was written at the end of the thesis, briefly presenting the contents of each chapter.

INTRODUCTION

(Morro Santana, Porto Alegre)

> *"…A comienzos de primavera la pampa se muestra en todo su esplendor cuando florecen centenares de especies de gramíneas, semejando la estepa un mar de pasto policromo que se agita a impulsos del viento…"*
>
> *(Cabrera & Willink 1973)*

Campos grasslands in southern Brazil: a present and past overview

Grasslands comprise one-fourth of total vegetation of Earth's plant cover (Kucera 1981), covering African savannas, steppes and prairies from North America, South America and Eurasia, and other partly anthropogenic meadows and pastures (Jacobs *et al.* 1999; Kucera 1981). They are often controlled by climate and biogeochemical factors, playing an important role on the global carbon cycle (Parton *et al.* 1996) and supporting a high variety of herbivores and other animal species (Jacobs *et al.* 1999). Floristic diversity of grasslands varies broadly (Sala *et al.* 2001). Some grassland physiognomies are within ecosystems considered to be hotsposts of biodiversity, such as the Cerrado vegetation (Myers *et al.* 2000).

In South America a large spectrum of grassland physiognomies can be found: from Pampas, situated mostly in Argentina and with high plant diversity, between 32° and 38°S (Bredenkamp *et al.* 2002) until the Andean alpine formations like the Llanos with a poorer flora (Barthlott *et al.* 1996). The tropical savannas, as described by Sarmiento ("tropical vegetation where certain forms of grasses dominate and where seasonal droughts and frequent fires are normal ecological factors", 1984), cover large areas of South America, from Venezuela until the northern part of south Brazil.

In Brazil, grassland physiognomies are represented in all biomes in more or less extent (Fig 1., see new vegetation classification, IBGE 2004).. Unfortunately, due to anthropogenic pressure, the areas of natural grasslands have decreased in the last decades. The Cerrado biome, the savanna physiognomies still have ca. 24% (grasslands and shrublands, MMA 2007), whilst the Mata Atlântica biome has less than 5% of the total remaining area *(Campos de Cima da Serra,* Highland grasslands, MMA 2007). Nowadays, the Pampa biome still has 23% of its native grassland cover. However, 48% of its total area has already been changed (MMA 2007), mostly in soja and maize plantation and more recently, in plantation of exotic tress such as *Pinus* spp. and *Eucalyptus* spp (Overbeck et al., 2007).

According to Cabrera and Willink (1973) the Brazilian subtropical grasslands (*Campos*) belongs to the "Provincia Pampeana", which covers from 30° to 39°S in Argentina, Uruguay and the southern part of Brazil. The *Campos* grasslands cover about 40% of the Rio Grande do Sul State (Boldrini 1997; Nabinger *et al.* 2000). Its flora is very rich in plant species with estimations of 3000 (Boldrini 1997) to 4000 species (Klein 1975), showing the highest number of species from the Andean element, as described by Rambo (1951).

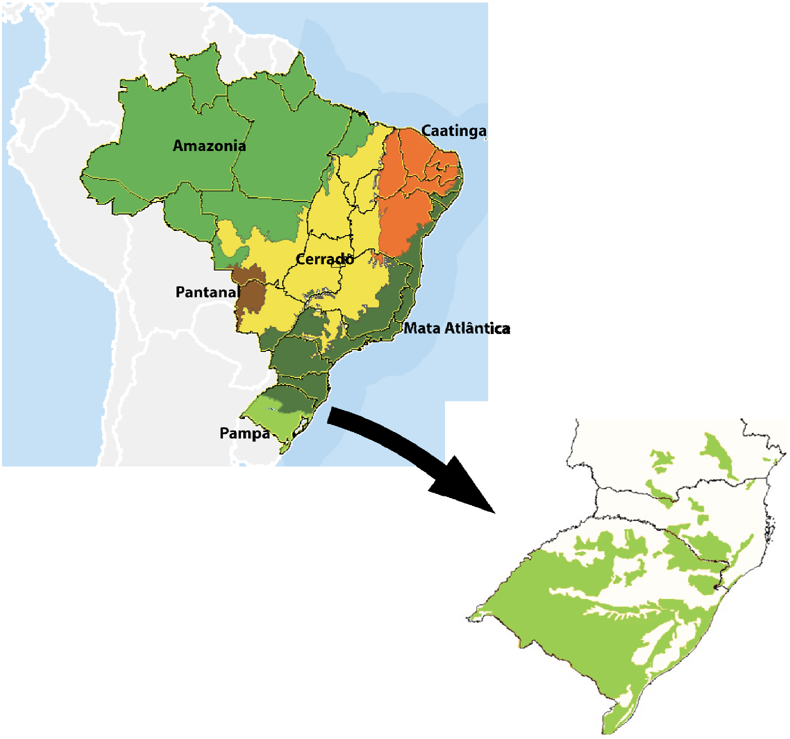

Fig 1. Brazilian biomes and location of Campos grasslands (part of Mata Atlântica and Pampa Biome, modified from IBGE 2004 and Pillar et al 2006).

Campos grasslands are found throughout the entire state of Rio Grande do Sul: in the north part, areas with grasslands can be found until up to 950 m in association with Araucaria forest (Pillar & Quadros, 1997, Boldrini 1997), belonging to the Mata Atlântica Biome (Fig 2a and b). Vast areas in central and southwestern part of the State are dominated by grasslands rich in species, where cattle grazing is the principal economic activity and management (Bioma Pampa, Fig 2c and d, Boldrini 1997, Nabinger *et al* 2000).

Lindman (1906) was one of the first naturalists to describe the *Campos* vegetation. At that time, he already observed the existence of grasslands in a climate propitious to forest. Several authors discussed the fact that the *Campos* are relict from a drier period (Klein 1960; 1984; Rambo 1942; 1953; 1956). Some authors, like Pawels (1954) proposed that climate was a determinant factor on formation of plant communities and the expansion of forests over *Campos* was not happening, because the climate was still not humid enough. Kuhlman (1954) pointed the not well-drained soil as major determinant for the presence of grasslands. Rambo (Rambo 1953; 1956) concluded, however, that *Campos* vegetation was older than forests. In addition, woody species and the Araucaria forest were invading grassland areas, changing the grass-dominated landscape to a shrubland.

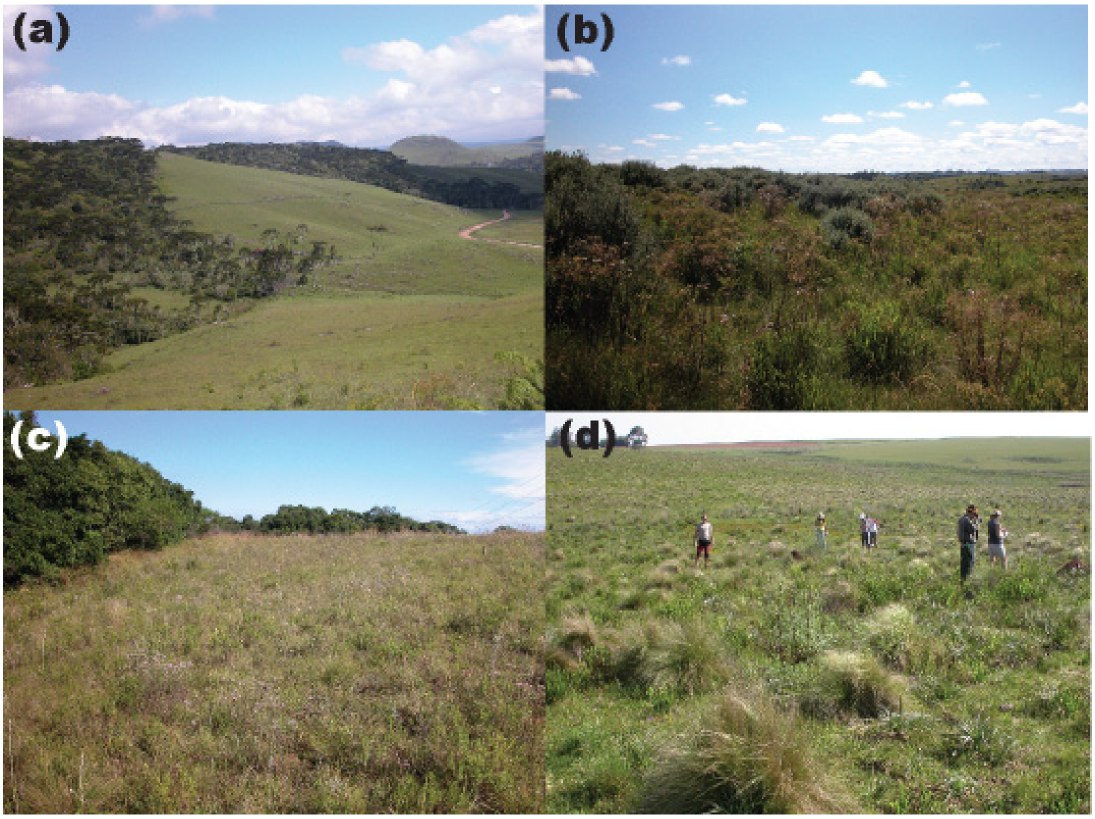

Fig 2. (a) - *Campos* grasslands in contact with Araucaria forest (forest-grassland mosaics, São José dos Ausentes) and **(b)** - excluded from disturbance in northern part of Rio Grande do Sul (near Cambará do Sul). **(c)** – *Campos* grasslands in central part of the state (Morro Santana) and **(d)** – in southern Rio Grande do Sul (Bagé), with typical "barba-de-bode" grass (*Aristida jubata*, Picture Ilsi Boldrini).

Several palynological studies confirmed the hypothesis from Rambo about the grasslands. During the Late Glacial, grasslands were dominant in the southern part of South America, which is an evidence for colder and drier climates (Behling *et al.* 2002). Grasslands prevailed throughout the Late Glacial and Holocene (Behling 1997; Behling and Pillar 2007). The northern part of the State of Rio Grande do Sul (highland grasslands) was probably treeless (Behling and Pillar 2007). The same tendency of climate could be found in palynological studies in the central Argentinean Pampa, where dry grasslands dominated at 10,500 B.P (Prieto 1996). Araucaria forest expansion began after 1000 B.P (Behling 2002; Behling *et al.* 2004), reflecting a more humid climate. Charcoal records could also be found in these studies, which confirm the occurrence of fire. Fire began to be more frequent at ca. 7400 cal yr BP, changing floristic composition (Behling and Pillar 2007; Behling *et al.* 2004).

Besides its high diversity, with approximately 500 Poaceae species and 600 Asteraceae species (Boldrini 1997; 2002; Matzenbacher 2003), the *Campos* grasslands are economically important for local people. According to Nabinger *et al* (2000), the region is the basis for the tradition of beef cattle livestock production, which began with the colonization of the area (XVII century, Pillar & Quadros 1997). The continuous and extensive system of cattle farming in

Southern Brazil is frequently considered to maintain plant diversity and grassland diversity (Nabinger *et al.* 2000).

It is common the use of fire in natural pastures to improve forage quality during winter times, in order to promote sprouting of palatable species. Fires are often set in August, when there is a high quantity of dead biomass (Heringer and Jacques 2002a). However, the use of fire is polemic, since winter burns can lead to a decrease in C3 species (Llorens and Frank 2004) and it favours caespitose grasses over rhizomatous or stoloniferous (Jacques 2003). Cattle browse less intensively some caespitose grasses, as for example *Andropogon lateralis, Aristida jubata*. *Paspalum notatum* (rhizomatous species), on the other hand, is a typical grass species covering vast areas of pastures in central areas of *Campos* grasslands in Rio Grande do Sul, with high forage value (Boldrini 1997). In pasture areas, forage species (e.g. *Paspalum plicatulum* and *Paspalum nicorae*) can be found under protection of *Eryngium horridum* (rosette species, Apiaceae, Fidelis *et al*, under review) for example, an undesirable plant for farmers, decreasing the quality of pastures. Because of this, from an economic point of view, the use of fire for *Campos* vegetation is not recommended, although there are few studies about its effects on vegetation dynamics.

The role of fire on vegetation dynamics and plant strategies in Campos vegetation: what do we know so far?

Plants responses to fire will be determined by the way plants persist through fires and the timing of regeneration in relation to it (Bond 2004). Individuals' survival is determined by several plant characteristics, such as life history, anatomy, physiology and behaviour (Whelan 1995), depending mostly on the degree of bud protection, survival of stem and root cambial tissue (Bond 2004; Bond and van Wilgen 1996).

In *Campos* grasslands, few are the studies about the effects of fire on vegetation dynamics and plant strategies. Eggers and Porto (1994) studied the effects of fire on native *Campos* grasslands structure and diversity. They observed that many species could rapidly resprout after fire, whilst others disappeared from the area. A species with high capacity to regenerate after fires, with sometimes more than one rosette is *Eryngium horridum*. Population biology studies showed the positive effect of fire on increasing and maintaining populations of this rosette species, which is considered a weed by local farmers (Fidelis *et al.* 2008). Unfortunately, there are few studies about effects of fire on plant population biology in *Campos* grasslands.

Fine scale diversity is high, with 34 species in plots of 0.75 m^2 in these grasslands and their dynamics is influenced by fire (Overbeck *et al.* 2005). The longer the intervals of fire, the lower the number of plant species (Overbeck *et al.* 2005; 2006a). Although fire seems to play an important role in *Campos* grasslands, little is known about regeneration strategies after fire events.

Efforts were made in order to classify plants into fire life forms related to fire. Overbeck and Pfadenhauer (2007) adapted Raunkiaer life form system (for description of life forms, see Raunkiaer 1934) and applied to *Campos* species. They concluded that regeneration attributes (capacity to resprout, for example) should be used together with the life form system in order to reach a better functional classification for *Campos* species. There is a lack of information about life form and plant strategies, which complicates the application of such system in Brazilian *Campos*.

As a conclusion, there are few studies about vegetation responses to fire events in *Campos* vegetation in southern Brazil. The above cited studies (except for Eggers and Porto 1994), used sites with different fire histories. Eggers and Porto (1994) only emphasized changes in vegetation cover and plant diversity. No studies were conducted in order to understand the importance of vegetation regeneration after fires and the relative importance of regeneration strategies. There are no data about fire behaviour (i.e. fire temperatures, flame height, fire spread, fuel load and fire intensity) and its effect on vegetation regeneration.

Nowdays, less than 0.5% of *Campos* vegetation are under legal protection in conservation units in Brazil (Overbeck *et al.* 2007). Moreover, these protected areas are usually excluded from any kind of disturbance, leading to the loss of grassland physiognomy and diversity. Recently, scientists are joining discussions with the Brazilian federal government about the conservation of priority areas and the elaboration of new laws about vegetation management and conservation. As showed by earlier studies, *Campos* grasslands need disturbance to maintain their characteristic features. Therefore, studies about new management practices (including the use of fire or mowing) are of crucial importance for the elaboration of management plans for conservation units of *Campos* grasslands.

Aims and justification of the thesis

Rambo (1953; 1956) already noticed that the climate of southern Brazil is more typical for forests (subtropical humid, with no pronounced climatic fluctuations), although grasslands cover more than half of the area. As mentioned before, grasslands were previously present under drier conditions. Therefore, their existence until nowadays may be related to other factors than climate. It is thus, hypothesized that disturbance (fire and grazing) is one of the major factor influencing plant diversity and vegetation dynamics. Disturbance destroys partially or totally aboveground biomass (Grime 1979), opening free spaces in the vegetation allowing for the establishment of species, they can rapidly regenerate without direct competition with dominat species. ("regeneration niche", Grubb 1977). Many species show adaptations to disturbance (e.g. belowground reserve organs, protected buds) and can rapidly regenerate after disturbance events. Consequently, disturbance events are regularly required for the maintenance of plant diversity, influencing process such as recolonization of open areas, regeneration of individuals, competition and, hence, the coexistence of species in the same area. Disturbances and not climatic factors are hypothesized to allow the existence of grasslands with high species richness in the region.

Since this region has an important value for cattle raising, several studies have focused the effects of grazing on vegetation dynamics, mainly with economical objectives (for more details, see Nabinger *et al.* 2000 and references therein). There studies contributed a lot for the understanding of grassland dynamics and mainly for the description of community structure and composition.

In order to complete this knowledge about *Campos* grasslands dynamics, this thesis will focus principally on the effects of fire. Fire is a polemic issue, since Brazilian environmental legislation forbids its use in natural vegetation (see Código Florestal 1969). In addition, even within the scientific community, the use of fire as a management tool is polemic and very criticized, due to mostly the lack of both scientific short- and long-term studies about the effects of fire on forage species, plant diversity and vegetation dynamics. This thesis will evaluate the effects of fire with mowing, because it could be an alternative for the use of fire. Mowing also removes aboveground biomass and opens gaps, increasing the availability of new microsites for species establishment. Nevertheless, quantity and type of nutrients input are different and may affect vegetation responses.

The main objectives of this thesis are:

1) Describe fire behaviour in subtropical grasslands (*Campos*) and fire variables, such as temperature, fuel load, combustion, flame height and fire intensity.

2) Analyse the bud bank density under different disturbance types and frequencies. Furthermore, the belowground organs will be classified and compared between areas.

3) Evaluate the effects of fire on population biology of chosen species of different functional groups (forbs and shrubs) and with different regeneration strategies (seeder and resprouters).

4) Analyse the importance of the different regeneration strategies in subtropical grasslands (seeder vs. resprouters) under different treatments: fire and mowing; and

5) Investigate the effects of fire and mowing on vegetation regeneration and dynamics, pointing out the effects on vegetation recovery and species richness in post disturbance environment.

The experimental part of this thesis (except objective 2) was conducted on Morro Santana, Porto Alegre (Rio Grande do Sul, Fig 3). It belongs to a granitic chain of hills in Porto Alegre, being the highest one (311 a.s.l.). The climate in this region is subtropical humid (Köppen Cfa), with mean temperatures of 22°C in the warmest months. Total annual precipitation is well distributed all over the year (about 1300 mm/year, Livi 1999). Soils are dystrophic red-yellow argisols, corresponding to acrisols, alisols and umbrisols (according to FAO classification, García-Martinez 2005). Grasslands are found at the top and northern slopes of the hill and can. Poaceae, Asteraceae, Rubiaceae and Leguminosae are the most important botanical families found in this area (Aguiar *et al.* 1986). These grasslands are under strong anthropogenic pressure. Fires are set usually during summer periods, occurring randomly and not with the same frequency and intensity. Local people, who live in illegal settlements around the area, set the fires to protect against animals or only due to esthetical reasons. In the northern part of the state, farmers set fire on vegetation during winter to enhance resprouting of forage species. As a consequence, many scientists pointed out the negative consequence of declining of C_3 species (Llorens & Frank 2004).

Difficulties in conducting fire experiments in Brazil

Since fire is a polemic issue in southern Brazil, several difficulties were faced in order to implement experiments. Experiments were carried out in a private area (belongs to the Universidade Federal do Rio Grande do Sul) and its access is not controlled. Therefore, people from surrounding settlements can freely reach the experimental area.

Environmental authorities from Porto Alegre (Secretaria do Meio Ambiente – SEMA) required an official request for fire experiments. The authorization came after approximately 13 months. Therefore, observations after fire and mowing experiments could not be performed for longer than one year (it was originally planned for two years).

Local people access the area and collect medicinal plants, e.g. "carqueja" (*Baccharis trimera*) and "macela" (*Achyrochline satureoides*) for personal use and also to sell in local markets. Even though experimental plots were located far from pathways, people sometimes found the markers and pulled them off or destroyed part of the plots.

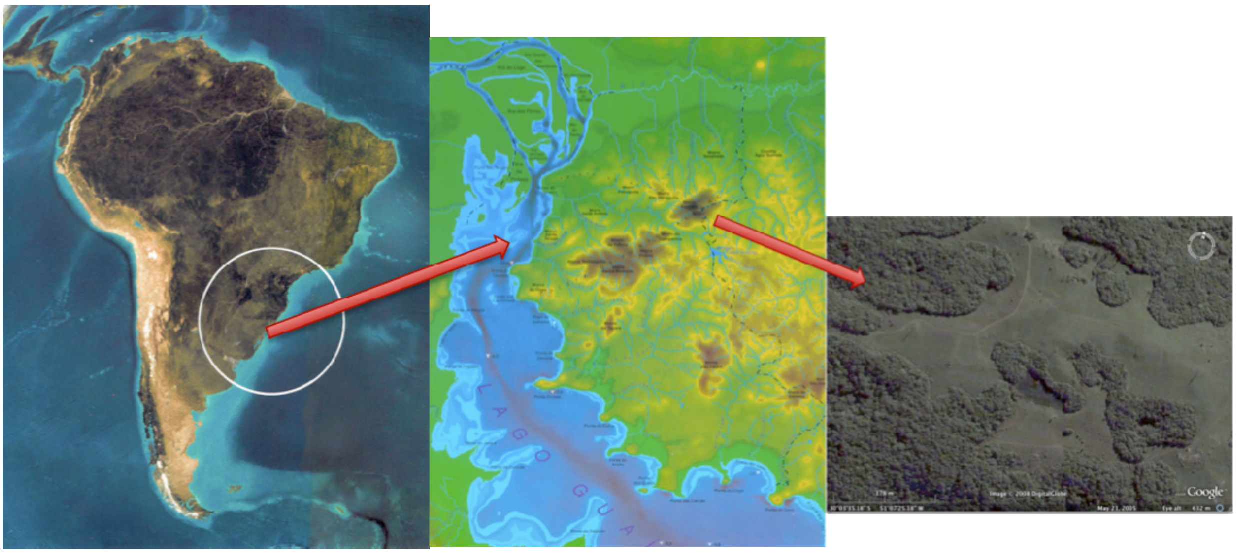

Fig 3. Location of study area, Morro Santana, in Porto Alegre, southern Brazil (modified from Menegat *et al* 2002)

After fire experiments, burned and mowed plots were more visible and as a consequence, two plots had their markers removed. Data loggers left on the area in order to sample microclimate data (temperature, PAR and air moisture) were destroyed (see Fig 4a) and therefore, this part of the PhD projected was interrupted.

In October 2007, a fire took place in the area, set probably by locals. People set fire with different purposes, such as to clean the area or kill animals (snakes). Unfortunately, this fire took place before the last observation (one year after experiments) and burned nearly 75% of the study area at the top of the Morro Santana (Fig 4b). All control plots were totally destroyed. Fire did not affect plots burned in the experiments, but singed two burned plots (Fig 4c). Mowed plots were more affected by fire, since it burned litter and also singed vegetation (Fig 4d). Because of this, these plots (26 of a total of 42) could not be used for last observations. Since control plots were completely destroyed, plots before experiments (at T0) were considered “controls”.

Organization of the thesis

This thesis is divided in introduction, five chapters and conclusions. Due to the lack of data about fire behaviour, fire experiments were conducted and the results are summarized in Chapter 1. Data about fire temperature in different heights, fuel load, flame height and principally fire intensity that were missing for these grasslands could be evaluated. Since it was observed that, several species could resprout after fire events, not only the seed bank, but also the bud bank might have a great importance on vegetation regeneration. Therefore, Chapter 2 is about the relevance of the bud bank for vegetation dynamics and regeneration. It compares the bud bank size in grasslands under different management (grazing and fire) and also under different fire frequencies. In addition, it describes the belowground organs found in these grasslands, pointing out their relation with the management. The main topic of this thesis is the effect of fire (and also mowing) on vegetation regeneration. Besides, effects of fire were also investigated for population biology of chosen species from different functional groups and strategies (forbs x shrubs, seeders x resprouters), which is summed up in Chapter 3. The two following chapters summarize the effects of fire and mowing on plant community. Chapter 4 focuses the importance of seeders and resprouters. It compares the relevance of these strategies under two different managements (fire and mowing) and in grasslands under different fire frequencies (frequently burned and excluded since six years). The effects of fire and mowing on vegetation regeneration and dynamics are examined in Chapter 5. Finally, the conclusion summarizes the most important results and general conclusions about the importance of fire in *Campos* grasslands are elucidated

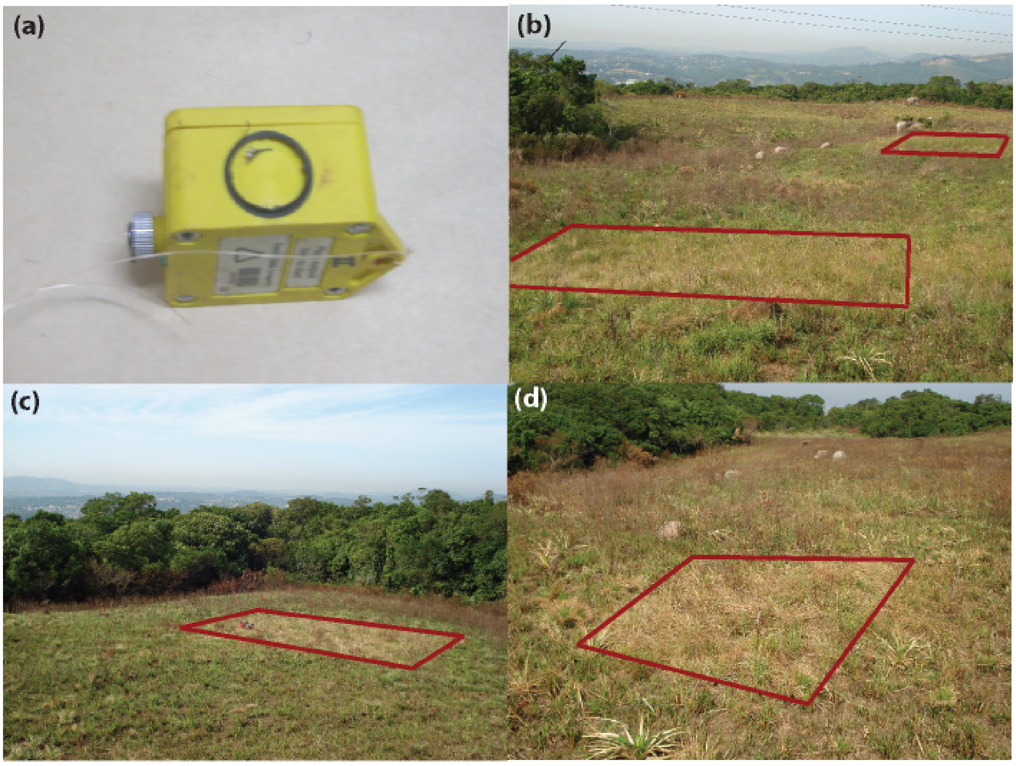

Fig 4. **(a)** – Data logger for air temperature with destroyed sensor, **(b)** – study area (Morro Santana) after two weeks of burning (October 2007) with remaining plots from fire experiments, **(c)** – burned and **(d)** – mowed plot singed by fire.

This study is the final part of a larger cooperation project between the Vegetation Ecology (Technische Universität München) and the Laboratory of Quantitative Ecology (Universidade Federal do Rio Grande do Sul) about the study of the subtropical grasslands (*Campos*) and the mosaic forest-grassland in southern Brazil. This successful cooperation resulted in seven PhD theses, seven Master Theses and Diplomarbeit, and several publications. It involved an interdisciplinary group of researchers (Vegetation Ecology, Quantitative Ecology, Soil Ecology, Landscape Ecology and Forest and Environmental Politics) and financial agencies from both countries: DAAD and DFG (Germany) and CAPES (Brazil). In addition, a part of this thesis (Chapters 4 and 5) is also integrated to a Brazilian project from EMBRAPA (Brazilian Agricultural Research Corporation) about the sustainability and conservation of *Campos* grasslands in southern Brazil.

References

Aguiar L. W., Martau L., Soares Z. F., Bueno O. L., Mariath J. E. & Klein R. M. (1986) Estudo preliminar da flora e vegetação de morros graníticos da Região da Grande Porto Alegre, Rio Grande do Sul, Brasil. *Iheringia* **34**, 3 - 38.

Barthlott W., Lauer W. & Placke A. (1996) Global distribution of species diversity in vascular plants: towards a world map of phytodiversity. *Erdkunde* **50**, 317-28.

Behling H. (1997) Late Quaternary vegetation, climate and fire history from the tropical mountain region of Morro do Itapeva, SE Brazil. *Palaeogegraphy, Palaeoclimatology, Palaeoecology* **129**, 407 - 22.

Behling H. (2002) South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogegraphy, Palaeoclimatology, Palaeoecology* **177**, 19 - 27.

Behling H., Arz H. W., Pätzold J. & Wefer G. (2002) Late Quaternary vegetational and climate dynamics in southeastern Brazil, inferences from marine cores GeoB 3229-2 and GeoB 3202-1. *Palaeogegraphy, Palaeoclimatology, Palaeoecology* **179**, 227 - 43.

Behling H. & Pillar V. D. (2007) Late quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. *Philosophical Transactions of the Royal Society B* **362**, 243-51.

Behling H., Pillar V. D., Orlóci L. & Bauermann S. G. (2004) Late Quaternary *Araucaria* forest, grassland (campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogegraphy, Palaeoclimatology, Palaeoecology* **203**, 277 - 97.

Boldrini I. I. (1997) Campos do Rio Grande do Sul: caracterização fisionômica e problemática ocupacional. *Boletim do Instituto de Biociências da Universidade Federal do Rio Grande do Sul* **56**, 1 - 39.

Boldrini I. I. (2002) Campos sulinos: caracterização e biodiversidade. In: *Biodiversidade, conservação e uso sustentável da Flora do Brasil* (eds E. L. Araújo, A. N. Noura, E. V. S. B.

Sampaio and J. M. T. Carneiro) pp. 95-7. Sociedade Botânica do Brasil, Universidade Federal Rural do Pernambuco, Recife.

Bond W. J. (2004) Fire. In: *Vegetation of Southern Africa* (eds R. M. Cowling, D. M. Richardson and S. M. Pierce) pp. 421-46. Cambridge University Press, Cambridge.

Bond W. J. & van Wilgen B. W. (1996) *Fire and plants*. Chapman ¨Hall, London.

Bredenkamp G. J., Spada F. & Kazmierczak E. (2002) On the origin of northern and southern hemisphere grasslands. *Plant Ecology* 163, 209 - 29.

Cabrera A. L. & Willink A. (1973) *Biogeografia de America Latina*. Secretaria General de la Oganización de los Estados Americanos, Washington, D.C.

Eggers L. & Porto M. L. (1994) Ação do fogo em uma comunidade campestre secundária, analisada em bases fitossociológicas. *Boletim do Instituto de Biociências* 53, 1 - 88.

Fidelis A., Overbeck G., Pillar V. D. & Pfadenhauer J. (2008) Effects of disturbance on population biology of a rosette species *Eryngium horridum* Malme in grasslands in southern Brazil. *Plant Ecology* 195, 55-67.

García-Martinez P. (2005) Caracterización química y física de los suelos del Morro Santana (Porto Alegre, Rio Grande do Sul, Brasil). In: *Chair of Soil Sciences*. Technische Universität München, Freising-Weihenstephan, Germany.

Grime J. P. (1979) *Plant Strategies and vegetation processes*. John Wiley and Sons, Chichester, UK.

Grubb P. J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Review* 52, 107 - 45.

Heringer I. & Jacques A. V. A. (2002) Acumulação de forragem e material morto em pastagem nativa sob distintas alternativas de manejo em relação às queimadas. *Revista brasileira de Zootecnia* 31, 599-604.

Jacobs B. F., Kingston J. D. & Jacobs L. L. (1999) The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden* 86, 590 - 643.

Jacques A. V. A. (2003) A queima das pastagens naturais - efeitos sobre o solo e a vegetação. *Ciência Rural* 33, 177 - 81.

Klein R. M. (1960) O aspecto dinâmico do pinheiro brasileiro. *Sellowia* 12, 17 - 44.

Klein R. M. (1975) Southern Brazilian phytogeographic features and the probable influence of upper Quaternary climatic changes in the floristic distribution. *Boletim Paranaense de Geociências* 33, 67 - 88.

Klein R. M. (1984) Aspectos dinâmicos da vegetação do sul do Brasil. *Sellowia* 36, 5 - 54.

Kucera C. L. (1981) Grassland and fire. In: *Fire regimes and ecosystem properties* (eds H. H. Mooney, N. L. Bonnicksen, N. L. Christensen, J. E. Lotan and W. A. Reiner) pp. 90-111. United States Forest Service.

Kuhlmann E. (1954) Vegetação campestre do Planalto meridional do Brasil. In: *Aspectos da geografia riograndense* (ed C. N. d. Geografia) pp. 39 - 55. Serviço gráfico do Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Lindman C. A. M. (1906) *A vegetação do Rio Grande do Sul*. Universal, Porto Alegre.

Livi F. P. (1999) Elementos do clima: o contraste de tempos frios e quentes. In: *Atlas ambiental de Porto Alegre* (eds R. Menegat, M. L. Porto, C. C. Carraro and L. A. D. Fernandes) pp. 73 - 8. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre.

Llorens E. M. & Frank E. O. (2004) El fuego en la provincia de La Pampa. In: *Fuego en los ecosistemas argentinos* (eds C. Kunst, S. Bravo and J. L. Panigatti). Instituto Nacional de Tecnología Agropecuaria, Santiago del Estero.

Matzenbacher N. I. (2003) Diversidade florística dos campos sul-brasileiros: asteraceae. In: *54o. Congresso Nacional de Botânica* pp. 124-7, Belém, Pará.

Ministério do Meio Amebiente (MMA). (2007) Mapeamento de Cobertura Vegetal dos Biomas Brasileiros. Technical Report, Ministério do Meio Ambiente – Probio. http://www.mma.gov.br/portalbio. Acessed in May 2008.

Müller S. C. (2005) Padrões de espécies e tipos funcionais de plantas lenhosas em bordas de floresta e campo sob influência do fogo. In: *Department of Ecology* p. 135. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Myers N., Mittermeier R. A., Mittermeier C. G., Fonseca G. A. B. & Kent J. (2000) Biodiverity hotspots for conservation priorities. *Nature* **403**, 853-8.

Nabinger C., Moraes A. d. & Maraschin G. E. (2000) Campos in Southern Brazil. In: *Grassland Ecophysiology and Grazing Ecology* (eds G. Lemaire, J. Hodgson, A. d. Moraes, C. Nabinger and P. C. F. Carvalho) pp. 355-76. CAB International.

Overbeck G. E., Müller S. C., Fidelis A., Pfadenhauer J., Pillar V. D., Blanco C., Boldrini I. I., Both R. & Forneck E. D. (2007) Brazil´s neglected biome: the Southern Campos. *Perspectives in Plant Ecology and Systematics* **9**, 101-16.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science* **16**, 655-64.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. *Brazilian Journal of Biology*.

Overbeck G. E. & Pfadenhauer J. (2007) Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora* **202**, 27-49.

Parton W. J., Coughenour M. B., Scurlock J. M. O., Ojima D. S., Gilmanov T. G., Scholes R. J., Schimel D. S., Kirchner T. B., Menaut J.-C., Seastedt T. R., Garcia-Moya E., Kamnalrut A., Kinyamario J. I. & Hall D. O. (1996) Global grassland ecosystem modelling: development and test of ecosystem models for grassland systems. In: *Global change: effects on Coniferous forests and grasslands* (eds A. I. Breymeyer, D. O. Hall, J. M. Melillo and G. I. Ågren) pp. 229 - 69. John Wiley & Sons Ltd., London.

Pawels G. (1954) Algumas notas sobre a distribuição do campo e mata no sul do país e a fixidez do limite que os separa. In: *Aspectos da geografia riograndense* (ed C. N. d. Geografia) pp. 32 - 8. Serviço Gráfico do Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro.

Prieto A. R. (1996) Late quaternary vegetational and climatic changes in the Pampa grassland of Argentina. *Quaternary Research* **45**, 73-88.

Rambo B. (1942) *A fisionomia do Rio Grande do Sul*. Editora Unisinos, São Leopoldo.

Rambo B. (1951) O elemento andino no Pinhal Riograndense. *Anais Botânicos do Herbário Barbosa Rodrigues* **3**, 7 - 39.

Rambo B. (1953) História da flora do Planalto Riograndense. *Anais Botânicos do Herbário Barbosa Rodrigues* **5**, 185 - 232.

Rambo B. (1956) A flora fanerogâmica dos Aparados riograndenses. *Sellowia* **7**, 235 - 98.

Raunkiaer C. (1934) *The life forms of plants and statistical plant geography*. Claredon Press, Oxford.

Sala O. E., Austin A. T. & Vivanco L. (2001) Temperate grassland and shrubland ecosystems. *Encyclopedia of Biodiversity* **5**, 627-35.

Sarmiento G. (1984) *The ecology of neotropical savannas*. Harvard University Press, Cambridge.

Whelan R. J. (1995) *The ecology of fire*. Cambridge University Press, Cambridge.

Chapter 1

FIRE BEHAVIOUR IN BRAZILIAN *CAMPOS* GRASSLANDS

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Abstract: Fire has long been used as a management tool in many countries. In Brazil, it is forbidden, although some ecosystems are recognized to be fire-dependent. Brazilian *Campos* grasslands are rich in species and the maintenance of its diversity and physiognomy is dependent on disturbance (e.g. fire and grazing). Nevertheless, there are no studies about fire intensity, temperatures and responses of vegetation to fire events in these grasslands. Here we aim to describe fire behaviour, using fourteen experimental burn plots in Porto Alegre region (Morro Santana, 30º02'S to 30º04'S and 51º06'W to 51º09'W, 311m a.s.l.). Two sites under different fire histories were chosen to locate the plots: frequently burned and excluded since six years. Experimental burning was performed during summer. The following parameters were measured: air temperature and air moisture, vegetation height, wind speed, fuel (fine, coarse), fuel moisture, fire temperatures (soil level and at 50 cm), ash, residuals, flame height, fire duration; burning efficiency and fire intensity were later calculated. Fuel load varied between 0.39 to 1.44 kg/m^2 (fine fuel ranged from 0.27 to 1.01 kg/m^2 and coarse fuel from 0.05 to 0.43 kg/m^2). It correlated positively with both fire temperatures and fire intensity. Fire temperatures ranged from 47°C (50 cm above soil surface) to 537.5 °C (at soil surface), being higher in the excluded site. Fire intensity was low compared to grassland elsewhere (36.5 to 319.5 kW/m), differing significantly between sites. Fine fuel was the best variable to explain fire intensity. Our results on fire behaviour in subtropical grasslands provide support for management and fire risk prediction. Further, they would help environmental authorities to avoid wild fires of high intensity and temperatures in conservation areas.

Keywords: fire intensity, fire temperatures, fuel load, management, southern Brazil

Introduction

Subtropical grasslands (*Campos)* in southern Brazil are one of the less known ecosystems worldwide, covering ca. 13.7 million ha, and their conservation has been neglected (Overbeck *et al.* 2007). Although its flora is very rich in species and endemism (estimations about 3000 plant species, (Boldrini 1997), only less than 1% of the total area is under legal conservation. Moreover, the legal protected areas adopted a management strategy that is not the most effective. Areas are fenced and totally excluded from any kind of disturbance, leading to shrub encroachment (Oliveira and Pillar 2004) and thus, loss of both plant species diversity and physiognomy.

Disturbance is a major factor influencing *Campos* grassland dynamics. Both grazing and fire maintain grasslands diversity and physiognomy by the removal of aboveground biomass and consequently opening gaps in vegetation, which allows other species to establish. According to Bond *et al*. (2005) savannas and grasslands are fire-dependent ecosystems, since the dominance of grasses and shrubs are dependent on burnings. Additionally, they argued that such fire-dependent ecosystems are not a result of only recent anthropogenic burnings, but have existed since a long time.

In *Campos* grasslands in southern Brazil fire is present since the beginning of the Holocene, likely due to the use of fire by indigenous populations coupled with a seasonal climate, as supported by abundance of charcoal particles in peat profiles (Behling and Pillar 2007; Behling *et al.* 2004). Nowadays, fire is lit by farmers to eliminate accumulated dead grass biomass and unwanted species (mostly shrubs) and thus to increase forage quality. Fire is carried out usually at the end of winter, which enhances resprouting of many species, but decreases C_3 grasses (Llorens and Frank 2004, Nabinger *et al.* 2000). The combination of these two practices (fire and grazing) is very common in Brazilian subtropical grasslands, despite fire being prohibited as a management tool by federal and state environmental legislation (Código Florestal 1965).

Fire affects plant population and community in several ways. Vegetative reproduction is mostly stimulated by fire events (Pfab and Witkowski 1999; Whelan 1995) and plays an important role on plant population dynamics. Germination rates of serotinous seeders are probably increased by fire (Stokes *et al.* 2004). However, the effect on seedling recruitment has been shown to be either positive (Satterthwaite *et al.* 2002) or negative (Hoffmann 1996). Although recent ecological studies on Brazilian subtropical grasslands have confirmed the positive effect of fire on plant diversity (e.g. Overbeck *et al.* 2005) and in impeding the establishment of woody species (e.g. Müller *et al.* 2007), nothing is known about fire temperatures and fire behaviour for these ecosystems and, consequently, their effect on plant communities.

Peak fire temperatures and duration are important variables for survival of plant tissues (Whelan 1995). Most studies adopt temperatures above 60°C as lethal for plant tissues (see for example Whelan 1995, Bilbao *et al.*, 2006). The longer plants are exposed to temperatures higher than 60°C, the more detrimental are the effects of fire. Bova and Dickinson (2005) stated that flame residence time was a better variable than fire intensity to predict tissue necrosis in oaks and chestnuts, demonstrating the importance of heat flux duration for plant survival. On the other hand, seed dormancy in many plant species (especially legumes) is broken by high temperature exposures (Auld and Denham 2006; Herranz *et al.* 1998; Martin *et al.* 1975; Rivas *et al.* 2006; Tarrega *et al.* 1992; Williams *et al.* 2003; 2004).

Though fire temperatures may influence plant mortality and germination, fire intensity is the most important variable to analyse fire effects on plant community (Stocks *et al.* 1997) and plant population dynamics (Whelan 1995). According to Trollope *et al*. (2002), fire intensity was shown to correlate with other fire parameters (e.g. rate of spread, temperature, and flame height) and is easily measured. Other variables can also influence fire behaviour such as fire frequency, season, climate, wind speed and direction, slope and fuel. Fuel load is the total amount of dry biomass, that means, the total amount of heat energy available for release during fires (Whelan 1995), being considered one of the most important parameters influencing fire behaviour (Trollope *et al.* 2002).

Our objective in this study, based on experimental burning carried out in natural grassland in Porto Alegre, southern Brazil, is to evaluate fire parameters (fire intensity, fuel load, rates of fire spread, burning efficiency, consumed fuel, fire peak temperatures and duration) and to study their relationship. These parameters are important to determine fire behaviour and to infer its effects on the ecosystem. No similar studies have been carried out for *Campos* grasslands in Brazil so far.

Material and Methods

Study area

The experimental burnings were carried out on natural grassland located on Morro Santana (near Porto Alegre, 30º02'S to 30º04'S and 51º06'W to 51º09'W, 311m a.s.l.). The climate in this region is subtropical humid (Köppen classification Cfa), with a mean temperature of 22°C (Livi 1999). The soils are characterized by a horizon A rich in clay; Acrisol is the predominant soil type (Streck *et al.* 2002). Grasslands undergo frequent anthropogenic fires occurring in intervals of three to five years in small patches, and a mosaic is produced with patches burned in different years. These grasslands are very rich in species (450 to 500 plant species in an area of 220 ha), with high fine-scale diversity (Overbeck *et al.*, 2005, 2006a). The vegetation is composed of a matrix of caespitose grasses (e.g. *Elionurus muticus*, *Aristida flaccida* and *Andropogon lateralis*) and a large number of small forbs (mainly from Asteraceae, Leguminosae and Rubiaceae) (Overbeck *et al.* 2006a). When fire is excluded there is an increase in shrub cover, being some species fire sensitive (Müller *et al.* 2007).

Two sites on Morro Santana were chosen for this study: frequently burned grassland – FB (last fire occurrence in summer 2005) and excluded from fire since six years - E. The excluded site is characterized by the dominance of two shrubs (obligate seeders belonging to Asteraceae): *Baccharis leucopappa* and *Heterothalamus psiadioides.* The frequently burned site shows a higher cover of forbs and the presence of small shrubs. Grass cover is high at both sites, but higher on FB.

Methods

Seven plots (25 m^2) were randomly established in each site. To avoid fire spread into the vegetation outside plots, firebreaks (2 m width) around each plot were set up. Since these grasslands usually burn during summer period, fire experiments were carried out in December 2006 and January 2007 with assistance of local fire brigade. Due to logistic problems and climate factors, the experimental burnings were performed in two different days (three weeks of difference between sites): plots in site FB were burnt in December 2006 and plots in site E were burnt in January 2007. Fires were ignited with a torch, always set to spread with the wind direction (head fire).

Air temperature and relative air moisture were measured before and during fire experiments using two TinyTag data loggers (Gemini data loggers, TGP-4500, every 5 seconds) approximately 2 m away from the plots. In addition, wind speed (m/s) and number of dry days before the experiment was also registered.

In order to estimate fuel load (kg/m^2), aboveground biomass in all plots was sampled immediately before burns in three quadrats of 0.04 m^2 per plot. The biomass was separated in coarse (stems and crowns) and fine (leaves and culms). Fuel moisture (expressed on a dry weight basis) was determined after samples were oven dried at 70°C during 72 hours. After fire, ashes and residual uncombusted materials were sampled (three quadrats of 0.04 m^2 per plot), dried and weighted.

Fire measurements

To measure fire temperatures, high temperature chromel – alumel thermocouples (unshielded head, type K, stainless steel sheath, and 150 x 3 mm) were used. Cables were placed inside aluminum tubes and additionally wrapped in aluminum foil and anti-fire tape to reduce heat absorption and conduction. Thermocouples were calibrated to measure over the range 0 – 1100 °C. Sensors were placed in two different positions: soil surface (0 cm) and shrubs crown height (50 cm). They were positioned in the middle of the plot and connected to a DL2 Data logger (Delta-T). Temperatures were recorded every 2 seconds.

Standard parameters of fire behaviour were also evaluated: rate of spread (m/s), flame height (m), fire duration (s), burning efficiency (%), and Byram´s fire line intensity (kW/m). Fire intensity was calculated using the equation $I = h*w*r$ (h = heat yield of fuel, w = consumed fuel load, and r = rate of fire spread). Since heat yield of fuel was not measured for subtropical grasslands in southern Brazil, we used 15 500 J/g, a value found in Australia by Griffin & Friedel (1984) and also used for Brazilian Cerrado (Heloísa Miranda pers. comm.). Experiments were carried out between 10:00 and 15:00.

Statistical analysis

To evaluate differences between the two sites in terms of the measured variables, analysis of variance was performed using randomization tests (10000 iterations, Manly 2007). For a better visualization of the results, Principal Components Analysis (PCA, see e.g. Podani 2000 for details on the method) based on correlations was used to reveal the main trends of variation of sampling units (in both sites FB and E) and the measured variables (fire intensity, fuel load, fine fuel, coarse fuel, combustion, temperature at soil level, temperature at 50 cm above soil level, flame height, tussock height, shrub height, air temperature, relative air moisture, ash, and residuals). The stability of axes was tested with bootstrap resampling (1000 iterations, Pillar 1999). General linear modelling techniques were used to determine which variable (the same 14 measured parameters used in the ordination analysis) most influenced fire intensity and to provide the simplest model. The significance of the model was examined by randomization tests (1000). Since experiments were carried out in different dates, environmental conditions may not have been the same and they could have influenced fire intensity. In order to evaluate if these possible biases were relevant, we evaluated, among the weather related variables, which ones statistically differed between treatments; if none of these variables were among the ones that most influenced the fire parameter in the final linear models, the models were deemed not biased by weather conditions during burnings. All statistical analyses used the software MULTIV (Pillar 2005).

Results

Weather conditions

There was a period of 4 to 7 days of no precipitation before fire was set. The highest air temperatures were obtained near midday (between 35°C and 38°C), as well as the lowest air moisture content (38% - 45%). Wind speed varied from 0.37 to 2.0 m/s. According to Table 1, air temperature and relative air moisture were almost the same for both sites, while wind speed was higher in site FB during the fire experiment.

Table 1. Weather conditions before fire experiments in different sites (FB – frequently burned and E – excluded from fire since six years) on Morro Santana, southern Brazil: air temperature (°C), relative air moisture (%) and wind speed (m/s) (means and standard errors).

Site	Air Temperature (°C)	Relative air moisture (%)	Wind speed (m/s)
FB	32.43±0.74	47.18±2.2	0.98±0.22
E	34.9±1.36	54.8±3.2	0.55±0.08

Fuel load and fire temperatures

A continuous grass matrix, with some short shrubs, characterizes site FB, whilst site E shows an increased cover of shrubs. Tussock grasses (33.57±2.91 cm, p = 0.11) and shrubs (82±2.22 cm, p = 0.001) are taller in the excluded site than in the frequent burned site (tussock grasses 27.6±1.79 cm, shrubs 65.2±1.98 cm) (Fig. 1a).

Fine fuel ranged from 0.27 to 1.01 kg/m^2 and coarse fuel from 0.05 to 0.43 kg/m^2. Fuel load varied from 0.39 to 1.44 kg/m^2. The excluded site also had the highest values of fine, coarse and fuel load in comparison to the frequently burned site (Fig 1.b). In addition, both sites showed a higher load of fine than coarse fuel.

Fire temperatures fluctuated from 47°C (50 cm above soil surface) to 537.5 °C (at soil surface). At the soil surface, fire temperatures tended to be higher in the excluded (p = 0.11), as well as temperatures measured at 50 cm above soil surface (p = 0.12, Fig. 1c).

Temperatures at soil surface correlated positively to fine fuel (r = 0.53). Fire temperatures at 50 cm showed a strong positive correlation to fire intensity (r = 0.82), fine fuel (r = 0.68), flame height (r = 0.70), and fuel load (r = 0.66).

Plots in the excluded site burned longer over temperatures of 60°C at both soil surface and above 50 cm (Fig. 2). The highest value of residence time was reached at 50 cm (360 s). At soil surface, residence time was much higher (140 to 330 s) than in the frequently burned site

(15 to 235 s). Residence time was very low (from 5 to 40 s) at 50 cm above soil surface in the frequently burned site.

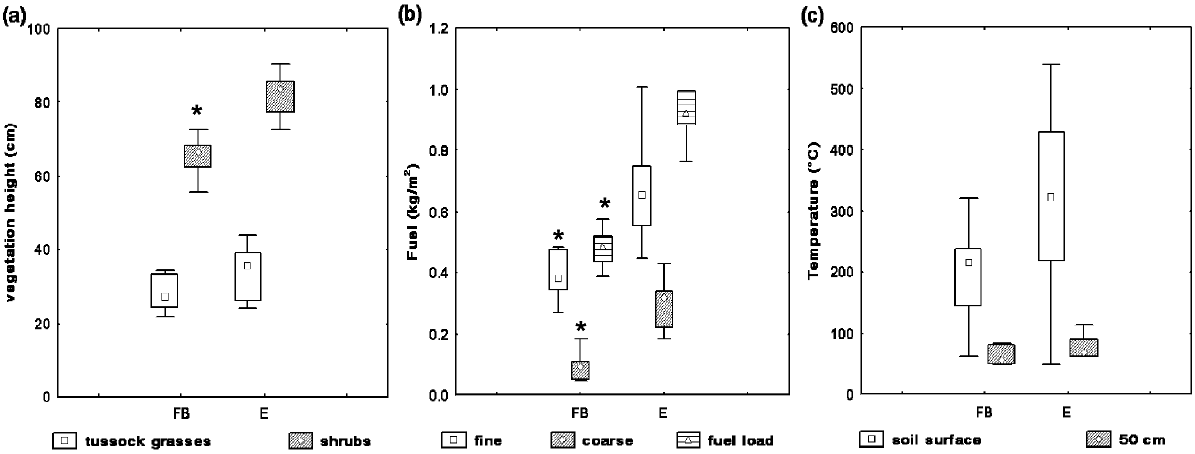

Fig 1. **(a)** Tussock and shrub heights (cm), **(b)** fine and coarse fuel, as well as fuel load (kg/m^2) and **(c)** fire temperatures at the soil surface and 50 cm above surface in sites frequently burned **(FB)** and excluded from fire since six years **(E)** on Morro Santana, southern Brazil. Asterisks mean significant differences between sites (p ≤ 0.05), based on randomization testing. Points between the boxes represent the median, boxes 25%-interquartils, and the t-shaped lines the maximum and minimum values among seven experimentally burned plots

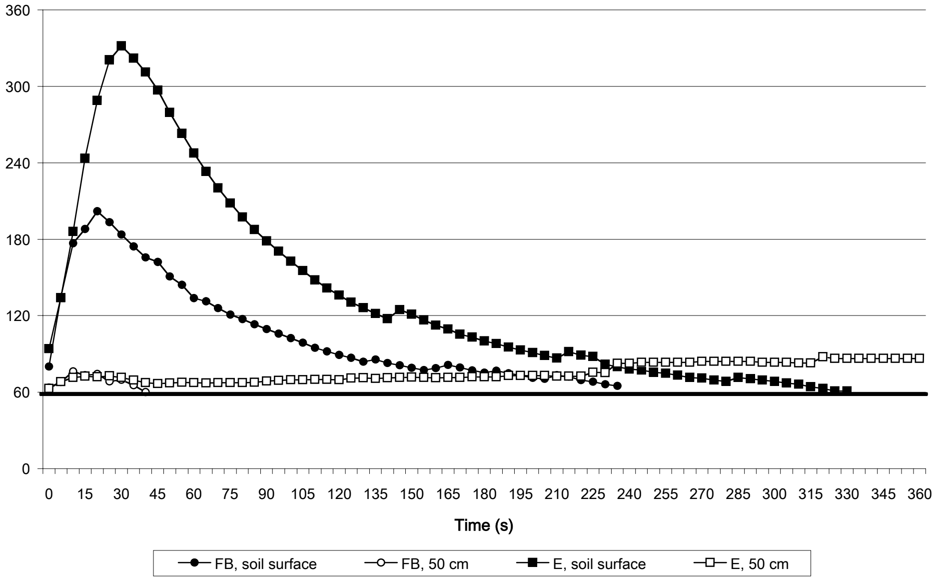

Fig 2. Maximum temperatures (°C) and residence times (s) above 60°C of fire experiments in different areas sites (FB – frequently burned and E - grasslands excluded from fire since six years) and different heights (at soil surface and 50 cm above soil surface) in *Campos* grasslands in southern Brazil. Each point on the curve is the average of seven experimentally burned plots.

Fire intensity

Fire intensity had significant differences between sites, as showed by Table 2 ($p = 0.02$). Values ranged from 36.5 to 319.5 kW/m. Fine fuel showed the highest correlation to fire intensity ($r = 0.86$). Other variables also strongly correlated to fire intensity, temperatures at 50 cm above soil surface ($r = 0.82$), flame height ($r = 0.81$), and shrub heights ($r = 0.59$), and coarse fuel ($r = 0.62$).

Table 2 also shows other variables measured during and after fire experiments. Ashes ($p = 0.02$) and flame height ($p = 0.0006$) were higher in the excluded site, while coarse fuel moisture ($p = 0.03$) was higher in the frequently burned site. Fine fuel moisture (%) showed no significant differences between sites ($p > 0.05$), as well as residuals (kg/m^2), burn efficiency (%) and rate of fire spread (m/s, $p > 0.05$).

Table 2. Means and standard errors of variables measured in experimental burnings in different sites (FB – frequently burned and E – excluded, seven plots each) on Morro Santana, southern Brazil: ashes (kg/m^2), uncombusted residuals (kg/m^2), fine and coarse fuel moisture (%), burn efficiency (%), flame height (cm), rate of fire spread (m/s), residence time above 60°C at soil surface and 50 cm above soil surface (s) and fire intensity (kW/m). Fuel moisture was expressed on a dry mass basis. Probabilities were generated by randomization testing (10000 interactions). Asterisks mean significant differences between sites ($p \leq 0.05$).

variables	FB	E
ashes (kg/m^2)	0.02±0.003	0.05±0.01 *
residuals (kg/m^2)	0.06±0.01	0.08±0.02
fine fuel moisture (%)	44.49±1.46	37.84±4.23
coarse fuel moisture (%)	49.44±3.72	36.21±3.71 *
burn efficiency (%)	93.8±0.84	95.07±0.9
flame height (cm)	36.43±3.96	64.52±5.7 ***
rate of spread (m/s)	0.015±0.002	0.013±0.001
fire intensity (kW/m)	93.52±19.6	179.04±27.5*

* $p \leq 0.05$

** $p \leq 0.01$

*** $p \leq 0.001$

According to the PCA, the two sites were clearly separated (Fig. 3). Almost all measured variables correlated with one of the two axes ($r \geq 0.5$), except for temperatures at soil level, air temperature and relative air moisture. Fuel load, fine fuel, and fire intensity highly correlated to Axis 1 ($r = 0.98$, $r = 0.94$, and $r = 0.89$, respectively), showing that plots of the excluded site had higher values of these variables in comparison to the ones of the frequently burned site. Other variables also showed high correlation to Axis 1, such as flame height ($r = 0.9$), coarse biomass ($r = 0.83$), shrub cover ($r = 0.77$), temperature at 50 cm above soil level ($r = 0.75$) and ash and residual weight (r = 0.57 and r = 0.5, respectively). Air temperature and relative air moisture correlated with Axis 2 (r = -0.88 and r = 0.76, respectively).

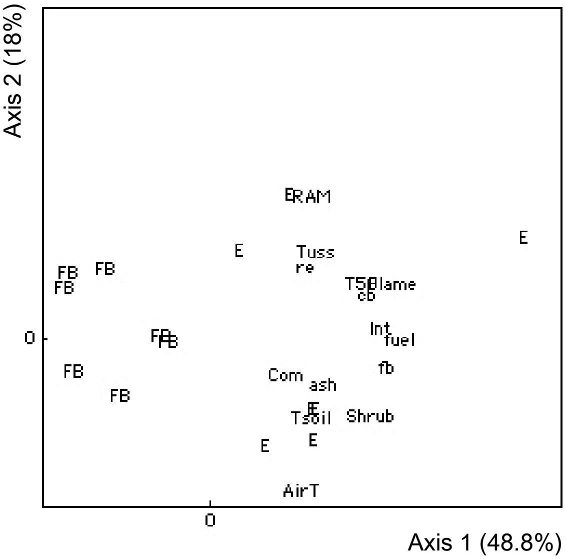

Fig.3. Ordination of plots in frequently burned grasslands (FB) and excluded sites (E) and measured variables (fb – fine fuel, cb – coarse fuel, fuel – fuel load, Int – fire intensity, Tsoil – temperature at soil level, T50 – temperature at 50 cm above soil level, Tuss – tussock height, Shrub – shrub height, ash – ash weight, re – residual weight, Flame – flame height, Com – combustion, AirT – air temperature, and RAM – relative air moisture). The ordination method is Principal Components Analysis (PCA), applied to correlations between variables. Bootstrap resampling (1000 iterations) indicated significance of axis 1 only ($P(ro^o \geq ro) = 0.047$). Only parameters that correlated ($r \geq 0.5$) with one of the axes are showed.

After testing all possibilities with the 14 measured variables, the model that best fit resulted in only one (from 14 tested) variable influencing fire intensity: fine fuel. The following equation was found:

$$\textbf{Fire Intensity} = -36.49 + 324.02(\textbf{fine fuel}),$$

which can be represented by a linear regression (Fig.4). The ß coefficient was found to be significant (p=0.003), as well as the linear model ($R^2=0.71$, p=0.0009).

Discussion

Maximum fire temperatures (both soil and at 50 cm) found in this study were similar to the ones found for Australian grasslands (98°C to 458°C, Morgan 1999) and shrub-woodlands (150°C, Bradstock and Auld 1995), open savannas in Venezuela (198°C to 232°C, Silva *et al.* 1990), heathlands in Scotland (140 to 840°C, Hobbs and Gimingham 1984), mixed prairie in USA (83.3°C to 682.2°C, Stinson and Wright 1969), and Brazilian cerrados (83°C to 330°C, Miranda *et al.* 1993). Bilbao *et al.* (2006) stated that in savanna areas, surface fires are very common and under these conditions, the highest temperatures would be recorded at soil level.

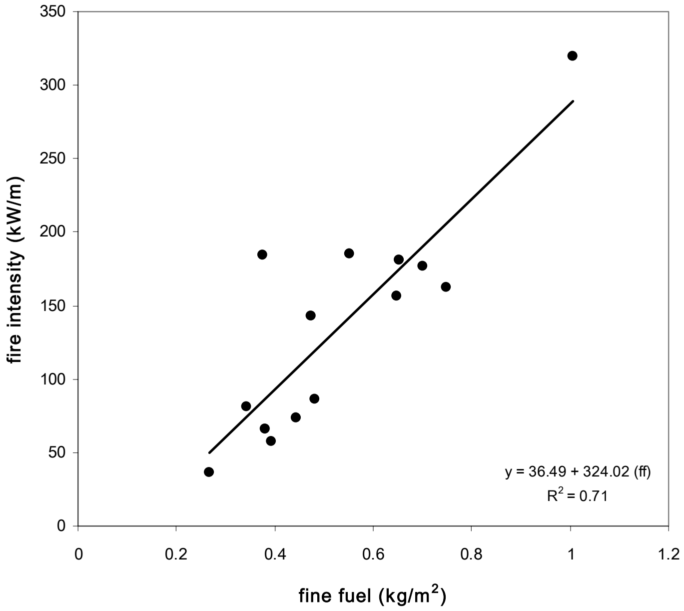

Fig. 4. Regression model of fire intensity (I) on fine fuel (ff) for subtropical grasslands in southern Brazil (R^2=0.71, p= 0.0009).

We found that soil surface temperatures were always higher than that at 50 cm. Temperatures measured at both levels correlated positively with fine fuel, corroborating its importance. There is a great accumulation of fine fuel near soil surface due to the high cover of tussock grasses and forbs. Grasses build up a great amount of biomass, both live and dead. After fire, most forbs were completely consumed, remaining only shrub stems and grass crowns (uncombusted residuals), resprouting after one week (Fidelis *et al.*, Chapter 4). Some forbs, such as *Eryngium horridum* and *Eryngium pristis* (spiny rosette forbs, Apiaceae) were not totally consumed by fire, with their basis remaining and also resprouting very quickly after fire (for more details, see Fidelis *et al.* 2008). Burn efficiency in both sites was very high (ca. 90%), confirming the high flammability of these grasslands, even only after two years since last fire (site FB).

Differences in vertical temperature are determined by the spatial distribution of vegetation (Bilbao and Medina 1996). In the present study, temperatures (both at soil level and 50 cm) tended to be higher in the excluded site. In the latter, there was higher accumulation of biomass (both dead and live) from tussock grasses and almost no bare soil. Fuel load was higher and although this site showed a higher cover of shrub species, fine fuel was the most important component increasing fire temperature.

High temperatures can cause tissue necrosis at different depths (Bova and Dickinson 2005). High temperatures (up to 530 °C) were reached in the present study, mostly in areas excluded since six years. However, according to Bova and Dickinson (2005), the most important factors affecting tissue death are fire intensity and residence time of fire. Our results showed that plants were exposed to temperatures higher than 60°C in average between 23 and 247 seconds, similar to residence time found by Bilbao *et al.* (2006) for the Gran Sabana in Venezuela. Short exposure to high temperatures may have positive effects on vegetation dynamics, mostly on germination of some species. As reported by several studies (for example: Auld and O´Connell 1991; Herranz *et al.* 1998; Rivas *et al.* 2006; Tarrega *et al.* 1992), some species (mostly legumes) need short exposures to high temperatures (above 70°C) to break their dormancy. In south Brazilian grasslands, no relation between high temperatures and increase in germination viability could be found so far (Fidelis *et al.* 2007; Overbeck *et al.* 2006b), but the experiments were conducted mostly with species from Poaceae, Apiaceae and Asteraceae, not with legumes.

Fire intensity was very low compared to other vegetation types (see Table 3). We had to use small plots to facilitate the authorization for the experiment by environmental control agencies. However, the small size of plots may have lead to lower values of fire intensity. Additionally, experiments were performed during the growing season (summer). During this period, dead biomass levels are lower than in winter (Fidelis *et al.,* unpublished data) leading to fires with lower intensities and consequently less damage to vegetation. As showed by the regression model, fine fuel highly influenced fire intensity, showing the importance of accumulated biomass. Further studies using controlled fire experiments during winter and larger plots should be performed in order to confirm or not these low values of fire intensity for the Brazilian *Campos* grasslands.

Nevertheless, fire intensity tended to be higher in the excluded site, where fine and coarse fuels, as well as height of flames and shrub heights were also higher. In this site, there was a dominance of small shrubs (ca. 0.5 to 1 m), but still the lower stratum was continuous, with a high cover of tussock grasses and small shrubs and forbs. Accumulation of dead biomass in this site was higher than in the frequently burned one, contributing to the high burning efficiency and fire intensity. Moreover, fine fuel was the best variable in the regression model for predicting fire intensity. Fine fuel is easy to be measured in the field and can be implemented in models to simulate fire intensity. Since experiments were carried out in different days, we evaluated the influence of environmental parameters on fire intensity and could not find a relation. Only relative air moisture showed a marginal significance in linear models. However, relative air moisture was not significantly different between days and probable have not influenced fire intensity.

Table 3. Comparison of fire intensity and temperature data between different localities and vegetation types.

Local	Vegetation type	Fire Intensity (kW/m2)	Temperature at soil level (°C)	Reference
Africa	savanna	28 - 17905	no data	Trollope *et al.* 1996, Trollope *et al.* 2002, Gambiza *et al* 2005, Govender *et al.* 2006
Australia	savanna	151 - 9214	150	Bradstock and Audl 1995
Australia	grassland	99 - 1147	98 - 458	Morgan 1999
USA	prairie	31 - 11788	83 - 682	Stinson and Wright 1969, Bidwell and Engle 1992, Trollope *et al.* 2002
Scotland	heathland	43 - 1112	140 - 840	Hobbs and Giminghan 1984
Venezuela	savanna	398 - 472	no data	Bilbao and Medina 1996
Venezuela	upland savanna	293 - 2253	48 - 571	Bilbao *et al.* 2006
Brazil	cerrado	2842 - 16394	83 - 330	Miranda *et al.* 1993, Kaufmann *et al.* 1994
Brazil	***Campos* grasslands**	**36 - 319**	**48 - 537**	**present study**

In Brazilian *Campos* grasslands cattle raising is one of the most important economical activities and fire is used to “improve” forage quality (for more information, see Overbeck *et al.* 2007; Pillar *et al.* 2006). Generally, these fires occur at the end of the winter season, in order to decrease the accumulated dead biomass produced by grasses and to enhance resprouting. During winter, live biomass accumulation reaches the lowest values, whilst dead biomass accumulation is nearly the same during summer time (Heringer and Jacques 2002a). Unfortunately, this continuous and intense use of fire (almost every year) may lead to soil erosion and to a decrease in the cover of C_3 grasses, the latter which include several good forage species (Llorens and Frank 2004, Nabinger *et al.* 2000).

Fire as a management tool is still very controversial in Brazil. Its prohibition by state and federal environmental legislation should be reviewed (see Código Florestal 1969 and Behling and Pillar 2007). As showed by our study, fire intensity and temperatures reached during experimental burns were not as high as the ones found in the literature. Vegetation responded fast to fire: after less than one month after fire experiment, some species were flowering, most grasses presented new green leaves and many forb and shrub species showed new sprouts (Fidelis *et al.,* Chapter 4). However, as already mentioned above, such statement should be taken carefully, since many farmers burn during winter, almost annually and combined with grazing. Such practice lead to species richness decrease and changes in vegetation structure (Heringer and Jacques 2002b).

Because of this, further studies on fire behaviour (also during winter) and the effects of fire on vegetation regeneration and diversity should be carried out in order to provide further scientific support for future management practices for both farmers and environmental authorities to maintain the biodiversity of *Campos* grasslands in southern Brazil. Moreover, more studies about fire behaviour would offer support for the elaboration of fire risk prediction systems to help authorities to avoid wild fires of high intensity in conservation areas with *Campos* grassland vegetation.

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References

Auld T. D. & Denham A. J. (2006) How much seed remains in the soil after a fire? Plant Ecology 187, 15-24.

Auld T. D. & O´Connell M. A. (1991) Predicting patterns of post-fire germination in 35 eastern Australian Fabaceae. Australian Journal of Ecology 16, 53-70.

Behling H. & Pillar V. D. (2007) Late quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. Philosophical Transactions of the Royal Society B 362, 243-51.

Behling H., Pillar V. D., Orlóci L. & Bauermann S. G. (2004) Late Quaternary Araucaria forest, grassland (campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. Palaeogegraphy, Palaeoclimatology, Palaeoecology 203, 277 - 97.

Bilbao B. & Medina E. (1996) Types of grassland fires and nitrogen volatilization in tropical savannas of Calabozo, Venezuela. In: Biomass burning and global change (ed J. S. Levine) pp. 569 - 74. MIT Press, Cambridge.

Bilbao B., Méndez C., Delgado-Cartay M. & Moreno J. M. (2006) Fire behavior in experimental savanna burnings in Gran Sabana, Canaima National Park, Venezuela. In: V International Conference on Forest Fire Research (ed D. X. Viegas) pp. 1 - 16, Portugal.

Boldrini I. I. (1997) Campos do Rio Grande do Sul: caracterização fisionômica e problemática ocupacional. Boletim do Instituto de Biociências da Universidade Federal do Rio Grande do Sul 56, 1 - 39.

Bond W. J., Woodward F. I. & Midgley G. F. (2005) The global distribution of ecosystems in a world without fire. New Phytologist 165, 525-38.

Bova A. S. & Dickinson M. B. (2005) Linking surface-fire behavior, stem heating, and tissue necrosis. Canadian Journal of Forest Research 35, 814 - 22.

Bradstock R. A. & Auld T. D. (1995) Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. Journal of Applied Ecology 32, 76 - 84.

Fidelis A., Müller S. C., Pillar V. D. & Pfadenhauer J. (2007) Efeito de altas temperaturas na germinação de espécies dos Campos Sulinos. Revista Brasileira de Biociências 5, 354-6.

Fidelis A., Overbeck G., Pillar V. D. & Pfadenhauer J. (2008) Effects of disturbance on population biology of a rosette species Eryngium horridum Malme in grasslands in southern Brazil. Plant Ecology 195, 55-67.

Griffin G. F. & Friedle M. H. (1984) Effects of fire in Central Australia rangelands. I Fire and fuel characteristics and changes in herbage and nutrients. Australian Journal of Ecology 9, 381-93.

Heringer I. & Jacques A. V. A. (2002a) Acumulação de forragem e material morto em pastagem nativa sob distintas alternativas de manejo em relação às queimadas. Revista brasileira de Zootecnia 31, 599-604.

Heringer I. & Jacques A. V. A. (2002b) Composição florística de uma pastagem natural submetida a queima e manejos alternativos. Ciência Rural 32, 315-21.

Herranz J. M., Ferrandis P. & Martínez-Sánchez J. J. (1998) Influence of heat on seed germination of seven Mediterranean Leguminosae. Plant Ecology 136, 95-103.

Hobbs R. J. & Gimingham C. H. (1984) Studies on fire in scottish heathland communities. Journal of Ecology 72, 223-40.

Hoffmann W. A. (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. Journal of Ecology 84, 383 - 93.

Livi F. P. (1999) Elementos do clima: o contraste de tempos frios e quentes. In: Atlas ambiental de Porto Alegre (eds R. Menegat, M. L. Porto, C. C. Carraro and L. A. D. Fernandes) pp. 73 - 8. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre.

Manly B. F. J. (2007) Randomization, bootstrap, and Monte Carlo methods in biology. Chapman & Hall/CRC, Boca Raron.

Martin R. E., Miller R. L. & Cushwa C. T. (1975) Germination response of legume seeds subjected to moist and dry heat. Ecology 56, 1441-5.

Miranda A. C., Miranda H. S., Dias I. F. P. O. & Dias B. F. S. (1993) Soil and air temperatures during prescribed cerrado fires in Central Brazil. Journal of Tropical Ecology 9, 313-20.

Morgan J. W. (1999) Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology 144, 127-44.

Müller S. C., Overbeck G. E., Pfadenhauer J. & Pillar V. D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. Plant Ecology 189, 1-14.

Nabinger C., Moraes A. d. & Maraschin G. E. (2000) Campos in Southern Brazil. In: Grassland Ecophysiology and Grazing Ecology (eds G. Lemaire, J. Hodgson, A. d. Moraes, C. Nabinger and P. C. F. Carvalho) pp. 355-76. CAB International.

Oliveira J. M. & Pillar V. D. (2004) Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. Community Ecology 5, 197-202.

Overbeck G. E., Müller S. C., Fidelis A., Pfadenhauer J., Pillar V. D., Blanco C., Boldrini I. I., Both R. & Forneck E. D. (2007) Brazil´s neglected biome: the Southern Campos. Perspectives in Plant Ecology and Systematics 9, 101-16.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. Journal of Vegetation Science 16, 655-64.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006a) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. Brazilian Journal of Biology.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006b) No heat-stimulated germination found in herbaceous species from burned subtropical grassland. Plant Ecology 184, 237-43.

Pfab M. F. & Witkowski E. T. F. (1999) Fire survival of the Critically Endangered succulent, Euphorbia clivicola R.A. Dyer - fire-avoider or fire-tolerant? African Journal of Ecology 37, 249 - 57.

Pillar V. D. (1999) The bootstrapped ordination reexamined. Journal of Vegetation Science 10, 895-902.

Pillar V. D. (2005) MULTIV: Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Pillar V. D., Boldrini I. I., Hasenack H., Jacques A. V. A., Both R., Müller S. C., Eggers L., Fidelis A., Santos M. M. G., Oliveira J. M., Cerveira J., Blanco C., Joner F., Cordeiro J. L. P. & Galindo M. P. (2006) Estado atual e desafios para a conservação dos campos. p. 24. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Rivas M., Reyes O. & Casal M. (2006) Influence of heat and smoke treatments on the germination of six leguminous shrubby species. International Journal of Wildland Fire 15, 73-80.

Satterthwaite W. H., Menges E. S. & Quintana-Ascencio P. F. (2002) Assessing scrub buckwheat population viability in relation to fire using multiple modeling techniques. Ecological Applications 12, 1672 - 87.

Silva J. F., Raventos J. & Caswell H. (1990) Fire and fire exclusion effects on the growth and survival of two savanna grasses. Acta Oecologica 11, 783 - 800.

Stinson K. J. & Wright H. A. (1969) Temperatures of headfires in the southern mixed prairie of Texas. Journal of Range Management 22, 169 - 74.

Stocks B. J., van Wilgen B. W. & Trollope W. S. W. (1997) Fire behaviour and the dynamics of convection columns in African Savannas. Witwatersrand University Press.

Stokes K. E., Allchin A. E., Bullock J. M. & Watkinson A. R. (2004) Population responses of Ulex shrubs to fire in a lowland heath community. Journal of Vegetation Science 15, 505 - 14.

Streck E. V., Kämpf N., Dalmolin R. S. D., Klamt E., Nascimento P. C. & Schneider P. (2002) Solos do Rio Grande do Sul. EMATER/RS; UFRGS, Porto Alegre.

Tarrega R., Calvo L. & Trabaud L. (1992) Effect of high temperatures on seed germination of two woody Leguminosae. Vegetatio 102, 139-47.

Trollope W. S. W., Trollope L. A. & Hartnett D. C. (2002) Fire behaviour a key factor in the fire ecology of African grasslands and savannas. Millpress, Rotterdam.

Whelan R. J. (1995) The ecology of fire. Cambridge University Press, Cambridge.

Williams P. R., Congdon R. A., Grice A. C. & Clarke P. J. (2003) Fire-related cues break seed dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia. Austral Ecology 28, 507-14.

Williams P. R., Congdon R. A., Grice A. C. & Clarke P. J. (2004) Soil temperature and depth of legume germination during early and late dry season fires in a tropical eucalypt savanna of north-eastern Australia. Austral Ecology 29, 258 - 63.

Chapter 2

BUD BANK AND BELOWGROUND ORGANS: THEIR IMPORTANCE FOR VEGETATION REGENERATION IN BRAZILIAN *CAMPOS* GRASSLANDS

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Abstract: *Campos* grasslands are ecosystems under constant disturbance (e.g. grazing and fire). Its absence leads to shrub encroachment, loss of plant diversity and grassland physiognomy. Vegetation recover occurs mostly by vegetative regeneration, having the seed bank a secondary role. Therefore, we aim to analyze the importance of bud bank and the belowground organs for vegetation regeneration and maintenance of biodiversity in *Campos* grasslands. Five areas under different disturbance regimes and histories were chosen: grazing (EEAGr), frequently burned (MsFB), excluded from disturbance since six years (MsE), excluded since 15 years (APN15) and since 30 years (ESA30). 20 soil cores (20x20x15 cm, except for EEAGr 20x20x10 cm and 15 samples) were sampled in all areas. Belowground biomass was sorted for different functional groups (graminoids, forbs and shrubs). Organs were classified into bulbs, rhizomes, xylopodium, root tubers and underground stems. Only viable buds were counted. We found a clear decrease in bud bank density the longer the intervals of fire were. Grazed areas showed the highest densities, mostly from graminoids, whilst excluded areas (APN15 and ESA30) had the smallest bud banks. Forbs showed the more drastic decreases in bud bank density in absence of disturbance. Xylopodium structures were typical for areas under influence of recurrent fires (MsFB and MsE) and diversity of belowground systems also decreased with absence of fire. Xylopodia are not typical storage organs. They are structures with a high gemmiferous potential, being present in many shrub and forb species in *Campos* grasslands and Cerrado vegetation in Brazil. Our results show the importance of considering the bud bank analyses in studies of vegetation regeneration and mechanisms of maintenance of biodiversity in *Campos* grasslands, since most of species have the capacity to resprout after biomass removal. The long intervals between disturbances would lead to a loss of regeneration capacity of many species (mostly forbs). Consequently, there would be a loss of plant diversity in these areas and even if disturbance occurs, vegetation regeneration will not reach its potential.

Keywords: disturbance, fire, grazing, southern Brazil, xylopodium

Introduction

Subtropical grasslands (*Campos*) in southern Brazil are ecosystems under constant disturbance, mainly grazing and fire (Overbeck *et al.*, 2007). They are very rich in species (ca. 3000 plant species, Boldrini, 1997), but there is a decrease in species richness, when areas are excluded from disturbance (see Overbeck *et al.*, 2005). Mechanisms of maintenance of plant diversity are not well known, but the constant removal of aboveground biomass and consequently, opening of new gaps for recruitments might play a crucial role. According to Fidelis *et al.* (Chapter 4), resprouters mainly recolonize newly open areas and seedling establishment is very rare. Such results were also observed for tallgrass prairie, where 99% of new recruits were resprouters, with very few seedlings (Benson and Hartnett, 2006).

Resprouters have a lot advantages over seedlings, namely more successful persistence after establishment (Midgley, 1996), faster growth, use of space and resources (Bond and Midgley, 2001; Vesk and Westoby, 2004) and competitive advantage (Vesk and Westoby, 2004b). Moreover, there are clear evidences that resprouting ability is related to disturbance frequency in different ecosystems (Midgley, 1996; Bond and Midgley, 2001; Vesk and Westoby, 2004a).

The relative high importance of resprouter in grassland ecosystems leads one to a main question: where do these resprouters come from? The bud bank plays, in this case, nearly the same function as the seed bank for seedling recruitment: it maintains plant propagules (seeds and buds) in a dormant way, until environmental conditions are optimal for stem development. Knapp and Smith (2001) highlighted the high capacity of grassland ecosystems to rapid responses in annual net primary production, which might be linked to its rapid capacity of recover mainly from the bud bank.

Harper (1977) was the first one to give significance to the bud bank, defining it as hidden populations of dormant meristems located on rhizomes, corms, bulbs, bulbils and tubers. Klimesová and Klimés (2007) extended Harper´s definition as “all buds that can be potentially used for vegetative regeneration”. Moreover, they distinguished the bud bank according to vertical distribution (above- and belowground bud bank) and seasonality (seasonal or perennial).

Besides its great importance for vegetation regeneration, few studies included the evaluation of the bud bank as a tool, such as in annually burned and unburned grasslands (Benson *et al.*, 2004), precipitation gradient (Dalgleish and Hartnett, 2006; Hartnett *et al.*, 2006), and succession studies (Lee, 2004).

Viable buds and reserves are needed for a plant to be able to resprout (Vesk and

Westoby, 2004). Several belowground organs are bud-bearing, such as bulb, corms, rhizomes and contain carbohydrate storage needed for growth (Chapin III *et al.*, 1990; Suzuki and Stuefer, 1999). Although some studies have analyzed bud bank densities, studies about the diversity and frequency of bud-bearing organs are lacking.

Because of this, we aim to evaluate the bud bank and belowground organs frequency of five areas under different disturbance histories (grazing, frequently burned, exclusion since six years, exclusion since 15 years, and exclusion since 30 years) in *Campos* grasslands in southern Brazil. Our hypothesis is that the longer the intervals of disturbance are, the smaller the bud bank and belowground organs frequency is. Bud bank of different functional groups (graminoids, forbs and shrubs) would show the same tendency, except for shrubs, since the exclusion from fire and grazing of these grasslands lead to the increase of shrub species and cover.

Materials and Methods

Study area

The study was carried out in four different areas in southern Brazil: on Morro Santana, Porto Alegre (Granitic Chain Hills, 30°03' S, 51°07' W; 311 m a.s.l.), Experimental Station of the Universidade Federal do Rio Grande do Sul, Eldorado do Sul (Central Depression, 30°05´S and 51°40´W, 20-70 m a.s.l), Ecological Station of Aracuri, Muitos Capões (Araucaria Plateau, 28°13´S and 51°10´W, 900 m a.s.l), and Aparados da Serra National Park (Araucaria Plateau, 30°04´S and 51°06´W, 720 m a.s.l).

Morro Santana belongs to a granitic chain of hills in southernmost part of Brazil, being characterized by a subtropical humid climate (Köppen classification Cfa), with mean temperatures of 22°C and mean annual precipitation of 1350 mm (Livi, 1999). Soils are dystrophic red-yellow argisols, corresponding to acrisols, alisols and umbrisols (according to FAO classification, García-Martinez, 2005). Most of grasslands are located on the top and northern slopes (Aguiar *et al.*, 1986), forming a mosaic with Atlantic forest. There is no presence of cattle since many years and therefore, fire is the major disturbance occurring in grassland areas, with return intervals of 2-5 years. Fires are mostly set by locals, although it has been present throughout the past 1200 years (Behling *et al.*, 2007). Plant diversity is very high, with a great number of species belonging to Poaceae, Asteraceae, Leguminosae and Rubiaceae (Overbeck *et al.*, 2005; 2006). Two sites in this area were chosen for this study: frequently burned grassland (last fire occurred two years before bud bank analysis) and excluded from fire since six years. The first area is characterized by a continuous grass matrix and forb species, with the presence of several small grassland shrubs. The excluded area shows a higher percentage of shrub cover, mainly from *Heterothalamus psiadioides*, *Eupatorium ligulaefolium* and *Baccharis leucopappa*. Despite the high cover of shrub species, a grass matrix and forb species are still present.

Experimental Station of the Universidade Federal do Rio Grande do Sul (EEA/UFRGS) has a subtropical humid climate (Cfa) and an annual precipitation between 1300 and 1700 mm (Boldrini, 1997). Soils are red dystrophic argisols and planosols. These grasslands have been managed since many years with cattle grazing. Therefore, one finds a formation of a fine-scale mosaic of intensively grazed and ungrazed patches. Tall tussocks (e.g. *Aristida jubata, Andropogon lateralis*), *Eryngium horridum* (a spiny rosette species) and unpalatable shrubs (e.g. *Baccharis trimera*) compose the ungrazed patches, whilst intensively grazed patches consist usually of certain prostrated and rhizomatous species, such as *Paspalum notatum* and *Axonopus affinis* (Focht and Pillar, 2003). Only grazed patches were considered for this study.

The Aparados National Park is also located at the Araucaria Plateau, having thus, the same climatic conditions (Cfb climate, with a mean temperature of 16°C and annual precipitation between 1500-2250 mm, IBAMA 2004). Three main vegetation types can be found at the park: Atlantic rainforest, Araucaria forest and grasslands, forming a mosaic of forest and grassland. Fire also plays an important role in these grasslands, being already recorded in palynological studies at about 6500 ^{14}C BP (Behling *et al.*, 2004). Although Brazilian politics for nature reserves does not allow the use of fire, fire occurs regularly set by farmers from surrounding areas. The chosen area for this study has been excluded from fire and cattle grazing since 15 years. Tussock grasses dominate the area (almost 80 cm tall), with isolated shrub individuals (mostly *Baccharis uncinella*).

The Ecological Station of Aracuri is located on the Araucaria Plateau, with a humid temperate climate (Cfb) and mean temperatures of 16°C. During winter, temperatures can reach -8.5°C and frost can occur. Annual precipitation is very high (1750 mm). Soils can be described as dystrophic brown latosols (Waechter *et al.*, 1984). When the station was created (1981), the predominant vegetation type was a shrubland dominated by *Baccharis* species (mostly *Baccharis articulata*, not taller than 0.5 m). Before its creation, the area was used for cattle mostly, and the exclusion took place before the ecological station creation in 1978 (João André Jarenkow pers. comm.). After nearly 30 years of exclusion, many woody species individuals can be observed established in the shrubland up to 2.5 meters. *Baccharis uncinella* and other grassland shrub species are the dominant species. Although a typical grassland physiognomy cannot be observed at Aracuri, the lower stratum from the shrubland still has several typical grassland species. Therefore, the chosen study area represented the shrubland that was formerly grassland before exclusion in 1978.

It is really difficult to find areas with the same management and mostly, with the same disturbance history. There was a decrease of almost 35% of the natural areas of grasslands in the southernmost part of Brazil, mainly due to changes in land use (soja bean plantations and afforestation with exotic tree species, Pillar *et al.*, 2006; Overbeck *et al.*, 2007). Because of this, we chose these four areas, although they are under different altitudes and latitudes.

Bud bank analysis

20 soil samples of 20x20x15 cm were randomly collected from each study site, except in the grazed area, where 15 soil samples (20x20x10 cm) were collected. In this area, soil is very compact and roots and other belowground organs do not grow deeper than 10 cm in average (pers. obs.). As a result, 95 samples were obtained in areas under five different managements: frequently burned (last fire two years ago, MsFB), exclusion since six years (MsE), excluded since 15 years (ANP15), exclusion since 30 years (ESA30) and grazed grasslands (EEAGr). Since tall shrubs dominate grasslands in ESA30, we sampled only areas with shrub height ≤ 1.0 m. All samples were obtained during summer. In the field, they were accommodated in plastic bags. At the laboratory, all belowground biomass was sorted into different functional groups (graminoids, forbs and shrubs). When there was no aboveground biomass and correct identification of groups was not possible, sample was considered indetermined and buds were not counted.

Belowground organs were washed and fixed in FAA 70 (formalin-acetic acid-alcohol, Johansen 1940), dehydrated in a graded ethylic series and finally, conserved in alcohol 70%. Buds were identified and counted with the help of a stereomicroscope. When identification was difficult, anatomical sections were executed and buds were visualized in a microscope.

In addition, belowground organs were identified and classified, but we used only samples from MsFB and ESA30. Anatomical sections were performed, in order to verify if the organs were roots or stems and based on that, a more specific classification was used: bulb, corm, tuberous roots, underground stems, xylopodium, rhizophores and rhizomes. Since bulb and corm have the same function, they were grouped for the statistical analyses. Moreover, it is difficult to differentiate rhizophores from rhizomes. Therefore, they were also grouped for the analyses. For more detailed discussion about underground system used for Brazilian Cerrado, see Appezzato-da-Gloria *et al.* (2008).

Statistical analyses

The statistical analyses used the total number of belowground buds/m^2 and number of belowground buds/m^2 for each functional group. For belowground organs, we tested differences in number of organs/m^2 between areas. In order to verify differences between both management history and functional groups, analysis of variance using randomization tests were performed (10000 iterations), applied to Euclidean distance (Podani, 2000). Randomization tests were chosen, since there is no restriction about normal distribution of data (for more details, see Manly, 2007).

For a better visualization of data, ordinations were performed using Principal Coordinates Analysis. We used the number (total and for each functional group) of belowground buds/m^2 for samples in each study area. For belowground organs analysis, we used the frequency of belowground organs for samples in each study area. Euclidean distance was applied for both analyses between samples and bootstrap resampling was performed in order to verify ordination axes stability (1000 iterations, Pillar, 1999). The software MULTIV (Pillar, 2005) was used for statistical analyses.

Results

Bud bank analysis

The bud bank showed significant differences between study areas. The largest bud bank was found in grazed areas (average of 2408.3 buds/m^2, see Fig. 1), and the smallest one in areas excluded since 30 years (average of 289.29 buds/m^2). One can observe a clear decrease in number of buds/m^2 as larger the intervals since last fire are ($p \leq 0.05$). The bud bank from MsFB and MsE did not differ significantly ($p = 0.91$) as well as the bud bank from ANP15 and ESA30 ($p = 0.55$).

The number of buds also varied according to the functional group. The graminoid bud bank was larger in grazed areas (Fig. 2a), whilst forb bud bank was larger in areas EEAGr, MsFB and MsE. There was a decrease in bud number in areas ANP15 and ESA30 (Fig. 2b). The bud bank of shrubs was very small in all areas, showing no significant differences ($p \leq 0.05$, Fig. 2c).

One can see this pattern in Fig. 3. Samples from EEAGr (grazing) and most of the samples from MsFB are at the left hand side of the ordination. Samples from MsE, ANP15 and ESA30 are found almost together at the right hand side. Samples at the left side of the diagram are highly correlated whit total number of buds and graminoid and forb buds, which are mostly correlated with Axis 1 ($r = -0.99$, $r = -0.65$, and $r = -0.55$, respectively), whilst samples at the up side had more shrub buds, since it correlated positively with Axis 2 ($r = 0.86$).

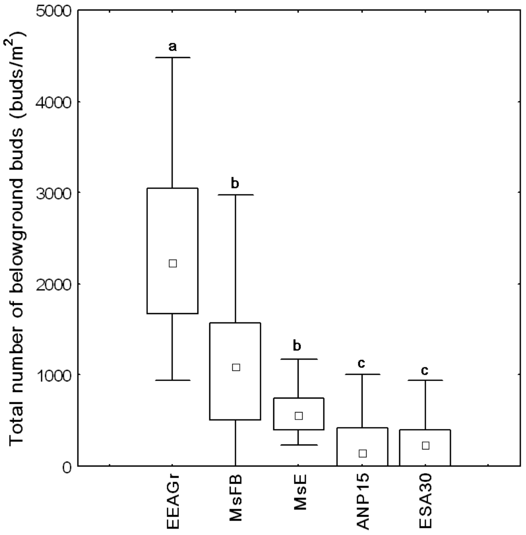

Fig 1. Total number of belowground buds (bud/m²) at the different study areas: **EEAGr** – Experimental Station, grazing; **MsFB** – Morro Santana, frequently burned; **MsE** – Morro Santana, six years exclusion; **ANP15** – Aparados National Park, 15 years exclusion; and **ESA30** – Ecological Station of Aracuri, 30 years exclusion. Different letters mean significant differences (p ≤ 0.05), based on randomization tesing. The squares between the boxes represent the median, boxes 25%-interquartils, and the t-shaped lines the maximum and minimum values.

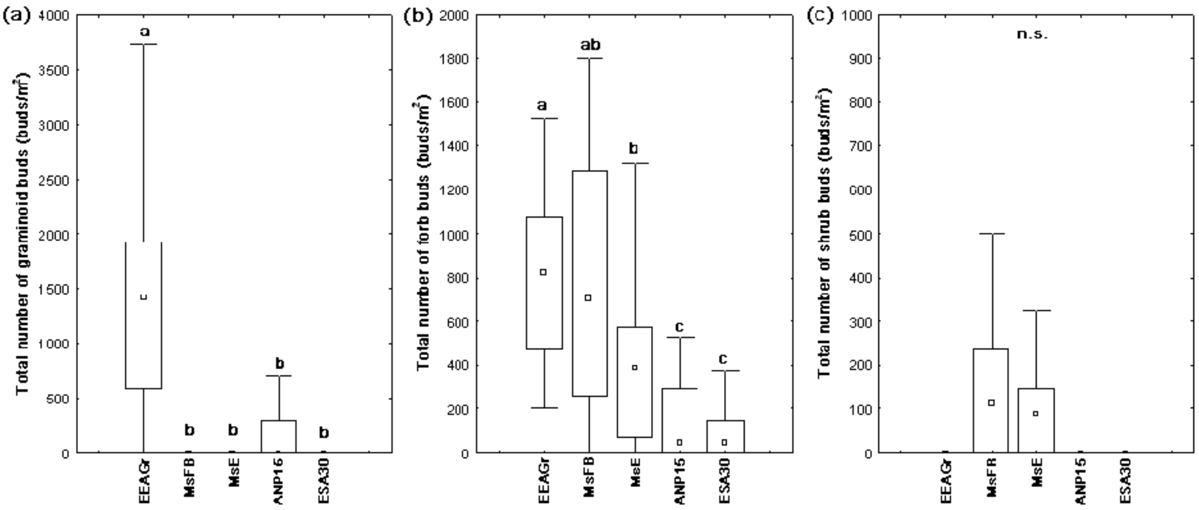

Fig. 2. Total number of belowground buds (buds/m²) according to the functional groups **(a)** graminoids, **(b)** forbs, and **(c)** shrubs at the different study areas: **EEAGr** – Experimental Station of the UFRGS, grazing; **MsFB** – Morro Santana, frequently burned; **MsE** – Morro Santana, six years exclusion; **ANP15** – Aparados National Park, 15 years exclusion; and **ESA30** – Ecological Station of Aracuri, 30 years exclusion. Different letters mean significant differences (p ≤ 0.05), based on randomization testing. The squares between boxes represent the median, boxes 25%-interquartils, and the t-shaped lines the maximum and minimum values.

Belowground organs

A higher diversity and number of belowground organs (Fig. 4) could be found in the MsFB area. There was an obvious decrease in belowground organs composition and number in the ESA30 (p = 0.001, Fig. 5). Higher number of xylopodia and tuberous roots were found in frequently burned grasslands (p = 0.001), whilst underground stems (no storage organs) showed a higher number in excluded grasslands (ESA30, p ≤ 0.05).

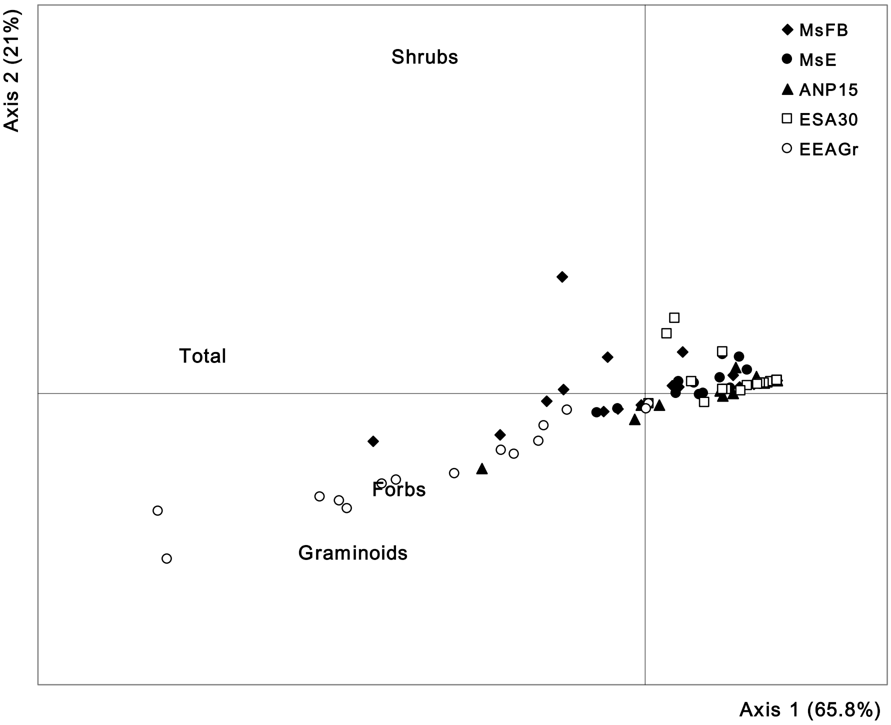

Fig. 3. Ordination of bud bank samples from different study areas: **EEAGr** – Experimental Station of the UFRGS, grazing; **MsFB** – Morro Santana, frequently burned; **MsE** – Morro Santana, exclusion since six years; **ANP15** – Aparados National Park, exclusion since 15 years; and **ESA30** – Ecological Station of Aracuri, exclusion since 30 years. The ordination method is Principal Coordinate Analyses (PCoA), applied to Euclidean distance between sampling units. Bootstrap resampling analysis (1000 iterations) showed no stability for Axis 1 and 2.

Fig. 6 shows the ordination (PCoA) of samples described by belowground organs composition in the different areas. Samples from MsFB could be observed at the left hand side part of the ordination, whilst samples from ESA30 are at the opposite side. Tuberous roots and bulbs correlated negatively to Axis 1 (r = - 0.89 and r = - 0.56 respectively. Xylopodia correlated positively to Axis 2 (r = 0.78).

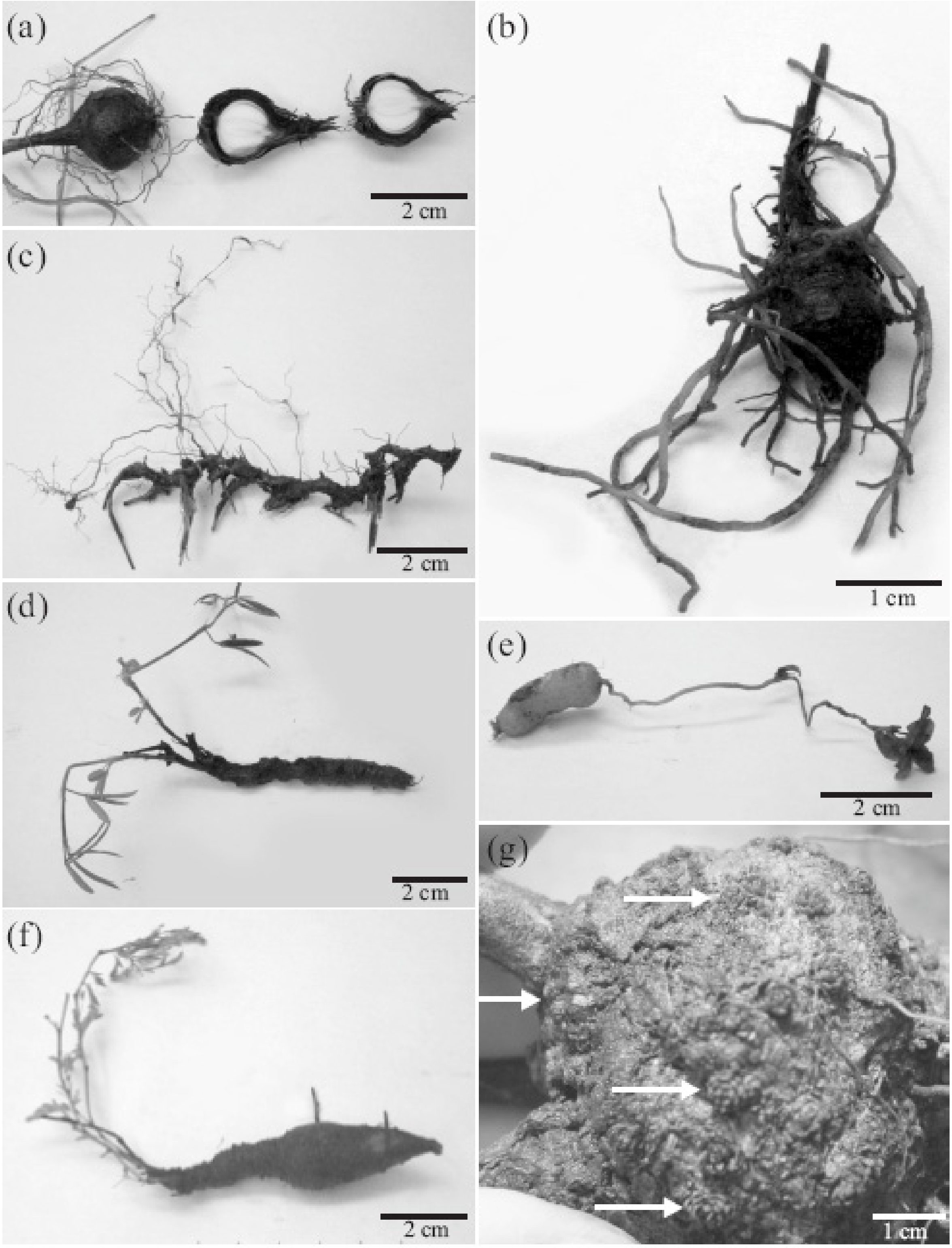

Fig. 4. Different bud-bearing belowground organs: **(a)**- bulb, **(b)** – corm, **(c)** – graminoid rhizome, **(d)** – xylopodium, and **(e)** – tuberous root; **(f)** – xylopodium and **(g)** - details of viable buds of a xylopodium structure**.** White arrows show bud region**.**

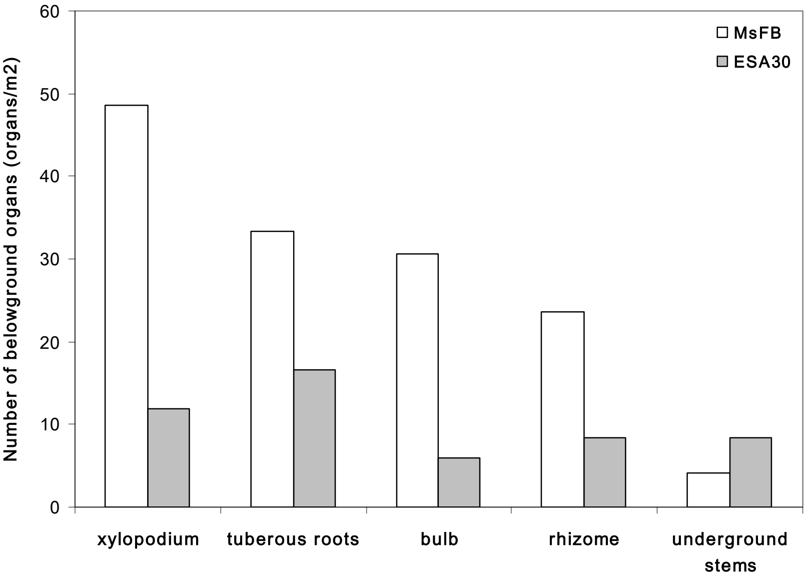

Fig 5. Average number of belowground organs (organs/m^2) at the different study areas: **MsFB** – Morro Santana, frequently burned, and **ESA30** – Ecological Station of Aracuri, exclusion since 30 years.

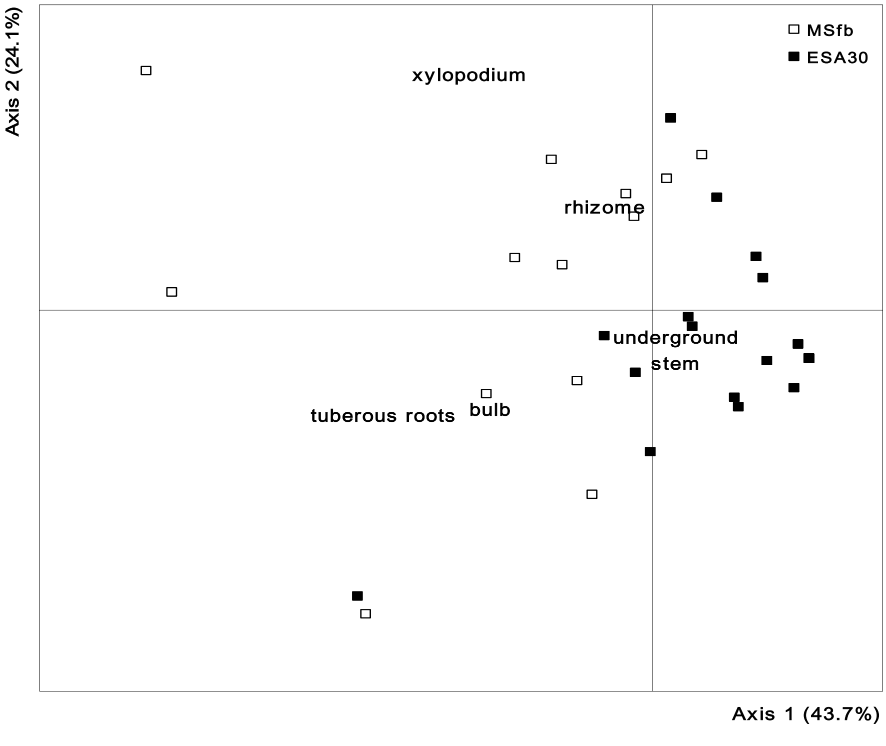

Fig 6. Ordination of belowground organ samples from two different study areas: **MsFB** – Morro Santana, frequently burned; and **ESA30** – Ecological Station of Aracuri, exclusion since 30 years. The ordination method is Principal Coordinate Analyses (PCoA), applied to Euclidean distance between sampling units. Bootstrap resampling analysis (1000 iterations) showed no stability for Axis 1 and 2.

Discussion

Bud bank and disturbance

There is an evident decrease of the bud bank size the longer the intervals of disturbance are, confirming our hypothesis that *Campos* grasslands in Brazil need more or less regular disturbance events, in order to regenerate and maintain biodiversity. Since the most important regeneration strategy in these grasslands is resprouting (see Fidelis *et al.*, Chapter 4), disturbances are needed to stimulate the recruitment of stems from the bud bank.

The grazed area represents the constant disturbed area, although grazing and fire are different types of disturbance. Grazing removes parts of plants, whilst fire removes all aboveground biomass. In addition, plants under grazing suffer of constantly trampling and thus, soil compactness is a characteristic of these areas. Grazed areas showed the largest bud bank, mainly due to the large graminoids bud bank, which is composed predominantly by two species: *Paspalum notatum* and a rhizomatous Cyperaceae. *P. notatum* is a typical rhizomatous grass found in grazed areas in southern Brazil. Rhizomatous and stoloniferous species dominate the pastures landscapes. After exclusion, their dominance decreases and mostly tussock grasses (e.g. *Andropogon lateralis*) replace them (Boldrini and Eggers, 1996; Boldrini and Eggers, 1997). In the grazed areas (EEAGr), the soil seed bank is also dominated by graminoids (Maia *et al.*, 2004). However, seedling establishment is rare (Fidelis *et al.*, unpublished data). Therefore, the bud bank plays an important role on plant regeneration in grazed grasslands.

In burned areas, there is a lack of rhizomatous and stoloniferous graminoid species (Overbeck and Pfadenhauer, 2007). Therefore, at the MsFB, MsE and ESA30, the graminoid bud bank is rare. It shows some importance at ANP15. These grasslands have been excluded from fire since 15, but before that, they were constantly used as extensive pastures. Although it is a National Park, there are still people leaving within the park boundaries and it is common to find some cattle inside the park. The graminoid rhizomes found in this area had no aboveground biomass, but still possessed buds, being probably able to resprout. MsFB and MsE have not been grazed since many years, being fire the major disturbance. ESA30 was also used as pastures before exclusion. However, exclusion time was probably too long and rhizomes found were already under decomposition with no viable buds or could not be found.

Consequently, in order to access the real size of graminoid bud bank in burned areas, one should also survey the aboveground bud bank, since most graminoid are hemicriptophytes and thus, buds are located upper the surface, protected by leaves at the crown basis.

Shrub bud bank was not very important in all areas. Shrubs in grazed and frequently burned grasslands have no importance, since the constant removal of aboveground biomass and competition with grasses and forbs do not allow their successful establishment and persistence. Nevertheless, if areas are excluded, there is an increase of shrubs, leading to shrub encroachment (Oliveira and Pillar, 2004). Because of this, one should expect an increase of the shrub bud bank the longer the intervals of fire were. However, shrub bud bank at ESA30 was very small, probably due to the method used. We chose areas to sample soil cores with shrubs of maximal 1.0 m height. Therefore, several shrub species were not included in this study, underestimating the real size of shrub bud bank.

Forb bud bank seems to be the most affected by disturbance. The longer the intervals of fire, the smaller the forb bud bank is. Such effect is also observed for the aboveground vegetation: in frequently burned areas, the number of forb species and cover is high. If areas are excluded, forbs decrease being outcompeted by tussock grasses and further, by grassland shrubs (Overbeck *et al.*, 2005). On Morro Santana (MsFB and MsE), forbs represented 50% of all species in the area (Overbeck *et al.*, 2006). In addition, Fidelis *et al.*, (Chapter 4) observed that most forb species resprouted from the bud bank, being seedling establishment very rare. Hence, the maintenance of grassland diversity is greatly dependent on a viable bud bank.

Although the aboveground bud bank has not been surveyed, resprouters were observed coming from both above- and belowground (Fidelis *et al.*, Chapter 4). Not all species possess a developed belowground organ with buds and thus, resprouting from buds above or at soil level are also common (Overbeck and Pfadenhauer, 2007). Other studies also reported the importance of bud bank for vegetation dynamics. Benson *et al.* (2004) found a higher total bud bank density in annually burned grasslands: grass:forb bud bank ration was 30-fold greater than in infrequently burned areas. Meristem limitation could only be observed for unburned sites. In addition, they also verified differences between bud and seed bank: grass seed bank densities were lower in annually burned grasslands, whilst in infrequently burned areas the opposite tendency could be observed. This study confirms the results found by Benson and Hartnett (2006) for vegetation regeneration after fire events, where 99% of recruited shoots were result of vegetative regeneration from the bud bank.

The use of bud bank as a tool for studies about vegetation responses to disturbance events should not be neglected. Klimesová and Klimes (2007) recommended studies focusing evaluations of the bud bank, when one is interested in response of plants to disturbance at different levels (individual, populations and community). Its concept can be used across biomes and life forms, in studies about plant responses to disturbance and habitat productivity and competition, in comparisons of vegetative regeneration and regeneration from seeds, and also be used as plant traits in analyses of vegetation dynamics (Klimesová and Klimes, 2007).

As showed by our study, the bud bank was a useful tool to quantify the effects of disturbance (in this case, frequency and the lack of disturbance) on vegetation regeneration potential, since each bud can potentially become a new stem.

Bud bank and vegetation regeneration

Plants are usually divided in two groups according their responses to fire: obligate seeders (have no ability to resprout after loss of biomass) and resprouters (ability to resprout, Hansen *et al.*, 1991; Whelan, 1995). The lower seedling recruitment in comparison to vegetative regeneration in many grassland ecosystems shows the importance of the study of the bud bank (Benson *et al.*, 2004). Resprouters have many advantages on obligate seeders: faster growth, good use of space and resources and occupancy of gaps, effects of disturbance are minimized (Bond and Midgley, 2001; Vesk and Westoby, 2004), competitive advantage (Vesk and Westoby, 2004b) and maintenance of current generation (Bellingham and Sparrow, 2000). For a plant to be able to resprout, meristems and reserves are needed (Vesk, and Westoby, 2004).

The lack of fire leads to a clear decrease of the bud bank. That means, even if areas with more than 15 years of exclusion are burned, one could not guarantee that vegetation regeneration would be the same as in other frequently burned areas. Probably, in these areas, seedling recruitment may play a major role on vegetation regeneration. However, there would be a loss of most grassland species, which are dependent on resprouting. We observed that in excluded areas, where most of belowground organs found with viable buds had no aboveground biomass, remaining “dormant” in the soil. In this case, fire would stimulate stem resprouting. Bonser and Aarseen (2006) pointed out the importance of meristems capacity to hinder development from inactive state in order to preserve resources to be used later for growth and reproduction. But would fire promote the formation of new buds?

We believe that fire would stimulate bud formation as verified by Hayashi and Appezzato-da- Glória (2007) in perennial forbs and Martínková *et al.* (2004) in short-lived forbs. In grazed areas, Lehtilä (2000) demonstrated that, the best strategy would be the gradual activation of buds: few at the beginning of season and gradual activation until its end.

For that reason, the decrease in the bud bank density might be related to both death of buds and belowground organs and the lack of stimulation for the formation of new viable buds. Consequently, the lack of disturbance in *Campos* grasslands would lead to the loss of resprouting ability and therefore, the loss of plant diversity.

Belowground organs

As already above affirmed, resprouters need viable buds and storage. As showed by our study, there was a decrease in number and diversity of belowground organs from the frequently burned to the area excluded since 30 years. Underground stems were more frequent in excluded areas, but all other belowground organs were more frequent in frequently burned areas. Underground stems showed few viable buds, but they were no storage organs.

Xylopodia were the most common belowground organ in frequently burned grasslands. It was first described by Lindman (1906) as a woody underground structure. He firstly observed it in herbaceous species in *Campos* grasslands in southern Brazil. It is also very common in Cerrado vegetation in Brazil (presence in more than 90 genera in herbaceous vegetation from cerrado, Rizzini, 1965) and is described as a woody underground system, which can have a radicular, caulinar (or both) structures, usually with hypocotyl origin. It can be globose, cylindrical or with no defined form (Rizzini and Heringer, 1961; Appezzato-da-Glória and Estelita, 2000). It has been observed that xylopodium formation can be dependent on environmental conditions (e.g. in *Mimosa multipinna*) or genetically determined (e.g. *Clitoria guyanensis*, Rizzini and Heringer, 1961).

Differently from lignotubers, which are typical storage organs originated from cotyledons and with suppressed buds or epicormic strands on the stem (James, 1984; Burrows, 2002), xylopodium is not a typical storage organ (Rizzini and Heringer, 1961; Rizzini and Heringer, 1962; Appezzato-da-Glória and Estelita, 2000; Appezzato-da-Glória *et al.*, 2008). No storage parenchyma tissue, only normal xylem parenchyma, is found in xylopodium structures (Appezzato-da-Glória and Estelita, 2000). It is noticed, however, that these structures can storage water (Braga *et al.* 2006). Nevertheless, they are usually combined with tuberous roots, which possess storage parenchyma tissues (Appezzato-da-Glória and Estelita, 2000; Milanez and Moraes-Dallaqua, 2003), providing thus, the reserve nutrients necessary for plant to resprout after fire or drought events.

Probably the most important function of xylopodium is its high gemmiferous potential, already observed by Rizzini (1962). *Eupatorium ligulaefolium* and *Vernonia nudiflora*, two shrub species with xylopodium, had more than 100 buds/individual in *Campos* grasslands (Fidelis *et al.*, Chapter 3). Buds are irregularly distributed all over the surface of the xylopodium, but mostly found near the surface (Fig 3g, Appezzato-da-Glória *et al.*, 2008). Plants with xylopodium in Cerrado vegetation usually loses its aboveground parts during the dry season and just after the beginning of the rainy season, new sprouts can be observed (Rizzini and Heringer, 1962). In *Campos* grasslands, no loss of aboveground biomass due to drought is observed, since there is no evident dry season.

Storage reserves improve survival and growth when plants face environmental changes (Suzuki and Stuefer, 1999; Bellingham and Sparrow, 2000). They are usually carbohydrates in form of starch (Chapin III *et al.*, 1990). Plants with storage reserves can rapidly regenerate from damage, with a low risk of mortality (Suzuki and Stuefer, 1999). Several studies comparing starch concentration in root and shoots of seeders and resprouters demonstrated that the highest amounts of starch could be found in roots of resprouters. Starch concentration in shoots of seeders and resprouters showed no clear differences (Pate *et al.*, 1990; Bell *et al.*, 1996; Bell and Ojeda, 1999). As a conclusion, xylopodium function is exclusively related to the resprout ability of plants after biomass loss due to mostly fire events, as confirmed by our study (see Fig. 5 and 6).

Other described organs (bulbs, rhizomes and tuberous roots, Fig 3a, c, e respectively) are typical storage organs (Dong and Pierdominici, 1995; Suzuki and Stuefer, 1999). Dong and Pierdominici (1995) also described the potential of rhizomes to store meristems for future regeneration of plants. Viable buds were found in all above cited organs, being more buds found in rhizomes than in tuberous roots and bulbs (data not shown). Bulbs usually showed only one bud/structure. Most bulbs were found with no aboveground parts. However, they are able to rapid allocate nutrients for shoot formation, as observed for *Oxalis* and *Habranthus* species, which quickly appear after fire (Fidelis *et al.*, Chapter 5). These species rapidly emerged after an accidental fire on Morro Santana, already flowering after two weeks (Fidelis and Blanco, in preparation).

Fidelis *et al.* (2006) showed the high importance of belowground biomass in *Campos* grasslands. They found that the ratio between below- and aboveground biomass was near 1 and belowground organs corresponded to about 30% of all belowground biomass. Although the number of belowground organs clearly decreased with fire exclusion, they still could be found with viable buds. Therefore, these belowground systems can survive underground for many years, without allocating nutrients for shoot formation until they are stimulated, as for example by fire. Hence, they have a fundamental role on vegetation regeneration after disturbance events and also on the maintenance of plant diversity in regularly disturbed *Campos* grasslands in southern Brazil.

Conclusions

Campos grasslands in southern Brazil are ecosystems under constant disturbance, mainly due to grazing and fire. Resprouting is the most important strategy, being totally supported by the large bud bank and high frequency of belowground organs with high gemmiferous potential (e.g. xylopodium). The higher the intervals of fire, the smaller the bud banks and the frequency of belowground organs are. Therefore, fire and grazing are important factors for vegetation regeneration and maintenance of plant diversity, since it preserves a viable and large bud bunk. We highly recommend the use of bud bank and belowground organs studies to analyze vegetation regeneration in grassland ecosystems.

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References

Aguiar L.W., Martau L., Soares Z.F., Bueno O.L., Mariath J.E. & Klein R.M. (1986) Estudo preliminar da flora e vegetação de morros graníticos da região da grande Porto Alegre, Rio Grande do Sul, Brasil. *Iheringia* **34**: 3 - 38.

Appezzato-da-Glória B. & Estelita M.F.M. (2000) The development anatomy of the subterranean system in *Mandevilla ilustris* (Vell.) Woodson and *M. Velutina* (Mart. ex Stadelm.) Woodson (Apocynaceae). *Revista Brasileira de Botânica* **23**(1): 27-35.

Appezzato-da-Glória B, Hayashi AH, Cury G, Soares MKM, Rocha R. (2008) Underground systems of asteraceae species from the cerrado. *The Journal of the Torrey Botanical Society* **135**(1): 103-113.

Behling H., Pillar V.D., Müller S.C. & Overbeck G.E. (2007) Late-holocene fire history in a forest-grassland mosaic in southern Brazil: Implications for conservation. *Applied Vegetation Science* **10**: 81-90.

Behling H., Pillar V.D., Orlóci L. & Bauermann S.G. (2004) Late quaternary *Araucaria* forest, grassland (*Campos*), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the cambará do sul core in southern brazil. *Palaeogegraphy, Palaeoclimatology, Palaeoecology* **203**: 277 - 297.

Bell T.L. & Ojeda F. (1999) Underground starch storage in *Erica* species of the Cape floristic region - differences between seeders and resprouters. *New Phytologist* **144**: 143-152.

Bell T.L., Pate J.S. & Dixon K.W. (1996) Relationships between fire response, morpholgy, root anatomy and starch distribution in south-west Australian Epacridaceae. *Annals of Botany* **77**: 357-364.

Bellingham P.J. & Sparrow A.D. (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89(2): 409-416.

Benson E.J. & Hartnett D.C. (2006) The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecology* 187: 163-177.

Benson E.J., Hartnett D.C. & Mann K.H. (2004) Belowground bud banks and meristem limitation in tallgrass prairieplant populations. *American Journal of Botany* 91(3): 416-421.

Boldrini I.I. (1997) *Campos* do rio grande do sul: Caracterização fisionômica e problemática ocupacional. *Boletim do Instituto de Biociências da Universidade Federal do Rio Grande do Sul* 56: 1 - 39.

Boldrini I.I. & Eggers L. (1996) Vegetação campestre do sul do Brasil: Dinâmica de espécies à exclusão do gado. *Acta botanica Brasilica* 10(1): 37 - 50.

Boldrini I.I & Eggers L. (1997) Directionality of succession after grazing exclusion in grassland in the south of Brazil. *Coenoses* 12(2-3): 63 - 66.

Bond W.J & Midgley J.J. (2001) Ecology of sprouting in woody plants: The persistence niche. *Trends in Ecology and Evolution* 16(1): 45-51.

Bonser S.P. & Aarssen L.W. (2006) Meristem allocation and life-history evolution in herbaceous plants. *Canadian Journal of Botany* 84: 143-150.

Burrows G.E. (2002) Epicormic strand structure in *Angophora, Eucalyptus* and *Lophostemon* (Myrtaceae) - implication for fire resistance and recovery. *New Phytologist* 153: 111-131.

Chapin III F.S., Schulze E.-D & Mooney H.A. (1990) The ecology and economics of storage in plants. *Annual Reviews of Ecology and Systematics* 21: 423-447.

Dalgleish H.J. & Hartnett D.C. (2006) Below-ground bud banks increase along a precipitation gradient of the North American great plains: A test of the meristem limitation hypothesis. *New Phytologist* 171: 81-89.

Dong M. & Pierdominici M.G. (1995) Morphology and growth of stolons and rhizomes in three clonal grasses, as affected by different light supply. *Vegetatio* 116: 25-32.

Fidelis A., Müller S., Pillar V.D & Pfadenhauer J. (2006) Efeito do fogo na biomassa aérea e subterrânea dos *Campos* sulinos. In: X. R. G. *Campos*. *Desafios e oportunidades do Bioma Campos frente à expansão e intensificação agrícola*. Pelotas: EMBRAPA - Clima Temperado.

Focht T. & Pillar V.D. (2003) Spatial patterns and relations with site factors in a *Campos* grassland under grazing. *Brazilian Journal of Biology* 63(3): 423 - 436.

García-Martinez P. (2005) *Caracterización química y física de los suelos del Morro Santana (Porto Alegre, Rio Grande do Sul, Brasil).* Master thesis, Technische Universität München Freising-

Weihenstephan, Germany.

Hansen A., Pate J.S. & Hansen A.P. (1991) Growth and reproductive performance of a seeder and a resprouter species of *Bossiaea* as a function of plant age after fire. *Annals of Botany* **67**: 497-509.

Harper J.L. (1977) *Population biology of plants*. London: Academic Press Ltd.

Hartnett D.C., Setshogo M.P. & Dalgleish H.J. (2006) Bud banks of perennial savanna grasses in Botswana. *African Journal of Ecology* **44**: 256-263.

IBAMA. (2004) http://www.ibama.gov.br, accessed in January 2008.

James S. (1984) Lignotubers and burls - their structure, function and ecological significance in mediterranean ecosystems. *The Botanical Review* **50**(3): 225-266.

Johansen D.A. (1940) *Plant microtechnique*. New York: McGraw-Hill Book Company.

Klimesová J. & Klimes L. (2007) Bud banks and their role in vegetative regeneration - a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* **8**: 115-129.

Knapp A.K. & Smith M.D. (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science* **291**: 481-484.

Lee P. (2004) The impact of burn intensity from wildfires on seed and vegetative banks, and emergent understory in aspen-dominated boreal forest. *Canadian Journal of Botany* **82**: 1468-1480.

Lehtilä K. (2000) Modelling compensatory regrowth with bud dormancy and gradual activation of buds. *Evolutionary Ecology* **14**: 315-330.

Lindman C.A.M. (1906) *A vegetação do Rio Grande do Sul*. Porto Alegre: Universal.

Livi F.P. (1999) Elementos do clima: O contraste de tempos frios e quentes. In: R. Menegat, M. L. Porto, C. C. CarraroL. A. D. Fernandes eds. *Atlas ambiental de Porto Alegre*. Porto Alegre: Editora da Universidade Federal do Rio Grande do Sul, 73 - 78.

Maia F.C., Medeiros R.B., Pillar V.D. & Focht T. (2004) Soil seed bank variation patterns according to environmental factors in a natural grassland. *Revista Brasileira de Sementes* **26**(2): 126-137.

Manly B.F.J. (2007) *Randomization, bootstrap, and Monte Carlo methods in biology*. Boca Raron: Chapman & Hall/CRC.

Martínková J., Klimesová J. & Mihulka S. (2004) Resprouting after disturbance: An experimental study with short-lived monocarpic herbs. *Folia Geobotanica & Phytotaxonomica* **39**: 1-12.

Midgley J.J. (1996) Why the world´s vegetation is not totally dominated by resprouting plants; because resprouters are shorter and reseeders. *Ecography* **19**: 92-95.

Milanez C.R.D & Moraes-Dallaqua M.A. (2003) Ontogênese do sistema subterrâneo de *Pachyrhizus Ahipa* (Weed.) Parodi (fabaceae). *Revista brasileira de Botânica* **26**(3): 415-427.

Müller S.C., Overbeck G.E, Pfadenhauer J. & Pillar V.D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology* **189**: 1-14.

Oliveira J.M. & Pillar V.D. (2004) Vegetation dynamics on mosaics of *Campos* and Araucaria forest between 1974 and 1999 in southern Brazil. *Community Ecology* **5**(2): 197-202.

Overbeck G.E., Müller S.C., Fidelis A., Pfadenhauer J., Pillar V.D., Blanco C., Boldrini I.I., Both R., Forneck E.D. (2007) Brazil´s neglected biome: The southern *Campos*. *Perspectives in Plant Ecology and Systematics* **9**: 101-116.

Overbeck G.E., Müller S.C., Pillar V.D. & Pfadenhauer J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science* **16**: 655-664.

Overbeck G.E., Müller S.C., Pillar V.D. & Pfadenhauer J. (2006) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. *Brazilian Journal of Biology*.

Overbeck G.E. & Pfadenhauer J. (2007) Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora* **202**: 27-49.

Pate J.S., Froend R.H., Bowen B.J., Hansen A. & Kuo J. (1990) Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of s.W. Australia. *Annals of Botany* **65**: 585-601.

Pillar V.D. (1999) The bootstrapped ordination reexamined. *Journal of Vegetation Science* **10**: 895-902.

Pillar V.D. (2005) Multiv: Multivariate exploratory analysis, randomization testing and bootstrap resampling.In. Porto Alegre: Universidade Federal do Rio Grande do Sul.

Pillar V.D., Boldrini I.I., Hasenack H., Jacques A.V.A., Both R., Müller S.C., Eggers L., Fidelis A., Santos M.M.G., Oliveira J.M., Cerveira J., Blanco C., Joner F., Cordeiro J.L.P. & Galindo M.P. (2006) *Estado atual e desafios para a conservação dos Campos*. Universidade Federal do Rio Grande do Sul. Porto Alegre, p.24.

Podani J. (2000). *Introduction to the exploration of multivariate biological data*. Leiden: Backhuys Publishers.

Rizzini C.T. (1965) Estudos experimentais sobre o xilopódio e outros órgãos tuberosos de plantas do cerrado. *Anais da Academia brasileira de Ciências* **37**(1): 87-113.

Rizzini C.T. & Heringer E.P. (1961) Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. *Oiton* **17**(1): 105-124.

Rizzini C.T & Heringer E.P. (1962) Studies on the underground organs of trees and shrubs from some southern Brazilian savannas. *Anais da Academia brasileira de Ciências* **34**(2): 235-247.

Suzuki J.-I & Stuefer J.F. (1999) On the ecological and evolutionary significance of storage in clonal plants. *Plant Species Biology* **14**: 11-17.

Vesk P.A. & Westoby M. (2004) Funding the bud bank: A review of the costs of buds. *Oikos* **106**(1): 200-208.

Vesk P.A. & Westoby M. (2004a) Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* **92**: 310-320.

Vesk P.A. & Westoby M. (2004b) Sprouting by plants: The effects of modular organization. *Functional Ecology* **18**: 939-945.

Waechter J.L., Cestaro L.A. & Miotto S.T.S. (1984) Vegetation types in the ecological station of Aracuri, Esmeralda, Rio Grande do Sul, Brazil. *Phytocoenologia* **12**(2/3): 261-269.

Whelan R.J. (1995) *The ecology of fire*. Cambridge: Cambridge University Press.

Chapter 3

POPULATION BIOLOGY AND REGENERATION OF FORBS AND SHRUBS AFTER FIRE IN BRAZILIAN *CAMPOS* GRASSLANDS

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(*Heterothalamus psiadioides* and *Vernonia flexuosa*)

Abstract: Fire is an important factor in several ecosystems. It affects plant population biology of several species. *Campos* grasslands are under constant influence of disturbance, mostly grazing and fire. However, few studies evaluated the effects of fire on plant population biology of grassland species. Therefore, we aim to analyze the effects of fire on population biology of four species, from different functional groups and regeneration strategies: *Chaptalia runcinata* (forb, resprouter, absence of belowground organ), *Vernonia flexuosa* (forb, resprouter, presence of rhizophore), *Eupatorium ligulaefolium* (shrub, resprouter, presence of xylopodium) and *Heterothalamus psiadioides* (shrub, obligate seeder). Seven plots were established in different sites on Morro Santana (Porto Alegre, southern Brazil): frequently burned (FB) and excluded from fire since six years (E). All plots were subjected to controlled burns during summer. Before experiments were conducted, populations were sampled (number of stems, plant height and diameter of rosette plants, presence of flowers/fruits). Further observations were carried out after 90 and 360 days of fire experiments. In addition, we counted the number of seedlings and resprouters recruited after fire. Heat shock experiments were conducted with two species (*H. psiadioides* and *V. flexuosa*), as well as the study of bud bank of chosen species (*E. ligulaefolium* and *V. flexuosa*). The obligate seeder species had all individuals killed by fire and established only after one year. Resprouters, on the other hand, showed new stems immediately after fire. Forb species showed flowering individuals already after two months of experiments. *E. ligulaefolium* and *V. flexuosa* showed only vegetative regeneration from belowground organs and more individuals in excluded sites after one year. Bud bank of *E. ligulaefolium* tended to be larger in sites E, whilst *V. flexuosa* showed an opposite result. High temperatures did not enhance nor killed seeds from both study species. Vegetative regeneration was the most important strategy for all study species, except for *H. psiadioides*, which recruited seedlings only one year after fire. Fire played an important role on population structure and demography and is very important for plant recruitment of studies species

Keywords: obligate seeder, plant population structure, plant recruitment, resprouter, bud bank, heat shock experiments

Introduction

Fire is an important event in many ecosystems. It shapes vegetation, maintains physiognomy and structure, as well as diversity (Bond and Keeley 2005). The effects of fire are dependent on which temperature it reaches, the quantity of available fuel and the nature of biomass (Bond and van Wilgen 1996; Whelan 1995). Fire size, shape and spatial patterns affect recovering and seedling colonization of burned sites (Lavorel *et al.* 1998). Further, shoot recovery and intensity of production of inflorescences might be influenced by fire intensity and temperature, length of recovery period prior to flowering and climatic influences after fire (Bowen and Pate 2004).

Plant populations can be either enhanced (e.g. by promoting vegetative regrowth, increasing germination and seedling recruitment) or damaged (e.g. by increasing mortality) by fire. Plant demography is affected in some aspects, as for example in differences of adult survival and growth (Menges and Dolan 1998) and on the stage distribution of individuals, with high transition rates from vegetative to generative plants (Satterthwaite *et al.* 2002). In frequent burned sites, fire damaged plants and stimulated vegetative regrowth (Pfab and Witkowski 1999).

Germination rates of serotinous seeders are probably increased by fire (Stokes *et al.* 2004). However, seedling recruitment has been shown to have either positive (Satterthwaite et al. 2002) or negative (Hoffmann 1996) correlation with fire events. Moreover, seedlings of seeders are more likely to survive than seedling of resprouters, due to their largest seeds (Lamont *et al.* 1999), faster growth and higher production of aboveground biomass (Bell and Ojeda 1999; Knox and Clarke 2005; Pate *et al.* 1990).

Campos grasslands in southern Brazil are unique ecosystems, maintained mostly by grazing and fire events (Overbeck *et al.* 2007). Unfortunately, plant population studies are scarce (see Fidelis *et al.* 2008). Some studies have demonstrated the influence of fire exclusion on the woody vegetation expansion on grassland and its impact (Müller *et al.* 2007; Oliveira and Pillar 2004), but they did not focus on plant populations.

We aim to study plant population and its responses to fire events in *Campos* grasslands in southern Brazil, focusing mostly on the effects of fire on: 1) plant population demography; 2) plant population structure; and 3) regeneration strategies (sexual vs. vegetative) of four chosen species (Asteraceae) from different functional groups (forbs and shrubs) and with different regeneration strategies (obligate seeders vs. resprouters). Therefore, we conducted field experiments with fire, sampled seeds for heat shock germination experiments in laboratory and analysed the bud bank of chosen species.

Materials and Methods

Study area

The study was carried out in natural grassland sites on Morro Santana, a granitic hill located in Porto Alegre (southern Brazil, 30°03' S, 51°07' W; 311 m a.s.l.). The region is characterized by a subtropical humid climate (Köppen classification Cfa), with mean temperatures of 22°C (Livi 1999). Soils are dystrophic red-yellow argisols, corresponding to acrisols, alisols and umbrisols (according to FAO classification, García-Martinez 2005).

A mosaic of forest and grasslands can be found in the study area, with most of grassland sites located on the top and northern slopes (ca. 220 ha, Aguiar *et al.* 1986). Fire is the major disturbance occurring in grassland, with return intervals of 2-5 years. It has been present throughout the past 1200 according to palynological studies in the area (Behling *et al.* 2007). Nowadays, fires are mostly set by local residents, resulting in a mosaic of distinct species distribution and richness patches in the grassland and maintaining a forest-grassland mosaic (Overbeck *et al.* 2005).

Grasslands are very rich in species. Overbeck et al. (2006a) found 201 plant species, from a pool of 450 to 500. C_4 caespitose grasses are dominant, together with a large number of small forbs belonging to different botanical families (Overbeck *et al.* 2005). Shrubs are present and their importance increases the longer the intervals of fire occurrence are.

Two sites were chosen for this study: frequently burned grassland (FB, last fire occurred two years before experiments) and excluded from fire since six years (E). Site FB is characterized by a continuous grass matrix and still by a large cover of forb species, with the presence of several small grassland shrubs. The excluded site shows a high percentage of shrub cover.

Population biology study

Four species (two forbs and two shrubs) from the same botanical family (Asteraceae) were chosen for this study. Asteraceae is well represented in these grasslands (for more details see Boldrini 1997; Matzenbacher 2003). *Vernonia flexuosa* is a perennial forb, 30-80 cm height with few capitula (ca. 35-50 flowers/capitulum), flowering from October to April (Matzenbacher 2003). It shows large rhizophores (belowground stem system, for more information see Hayashi & Appezzato-da-Glória, 2005) and clonal growth (pers. obs.). *Chaptalia runcinata* (no belowground organ) is a perennial rosette with only one capitulum/individual (flowering from July to September, Cabrera and Klein 1973). *Heterothalamus psiadioides* is an obligate seeder shrub, 50 – 100 cm tall, with numerous flowers and small seeds, flowering from August until

December (Barroso *et al.* 1999). *Eupatorium ligulaefolium* (presence of xylopodium) is a shrub species, 50 – 150 cm tall with numerous capitula (5 flowers/capitulum). It flowers from January until April (Matzenbacher 2003).

Plots (1 x 2 m) were randomly established in the two above-mentioned sites on Morro Santana: frequently burned (FB) and excluded (E). All 14 plots were subjected to controlled burns during summer (December 2006/January 2007). For each plot, the burned area corresponded to 25m^2 to avoid border effects. Fire intensities in each site were 93.52 kW/m for site FB and 179.04 kW/m for site E. Temperatures at soil level varied from 61.6 to 319.11°C (site FB) and from 48.3 to 537.4°C (site E, Fidelis et al., submitted). After fire, nearly all aboveground biomass was consumed (ca. 90% of burn efficiency, Fidelis et al., submitted).

Before controlled burns, all populations were sampled (number of stems, plant height and diameter of rosette plants, and presence of flowers/fruits, T0). Populations were grouped according to following age-state classes: juveniles (individuals ≤ 10 cm height for shrubs species, individuals ≤ 5 cm diameter for forbs) non-flowering (individuals > 10 cm height for shrubs and > 5 cm diameter for forbs) and flowering individuals. Since age-state classes should be the same for all species, we did not consider seedlings or resprouts as a class, because not all species have the capacity to resprout (*Heterothalamus psiadioides*). Instead, we evaluated the regeneration strategy of these species only after fire experiments, considering thus, seedlings and resprouters for the analysis. Observations were carried out after two months (T60) and one year after fire (T360).

Germination experiments

To evaluate the potential capacity of generative regeneration of these species after fire, germination experiments using heat shock treatments were performed for *Heterothalamus psiadioides* and *Vernonia flexuosa*. *Eupatorium ligulaefolium* did not flower during the study period and fewer individuals *Chaptalia runcinata* flowered, thus the number of seeds was not enough for experiments. Seeds were collected on plant canopy from different populations during summer. They were stored in paper bags (room temperature) during 2 months. They were sorted, weighted and measured before germination experiments.

For the experiments, seeds were subjected to different heat shock temperatures during 1 minute: 60º, 80º, 100º, and 120ºC. Each species and treatment had 5 replicates (25 seeds each). Heat treatments used a preheated oven, with insertion and removal of replicates in aluminium dishes. Untreated seeds were used as controls. Both treated and untreated seeds were placed in Petri dishes, with two layers of sterilized filter papers. All dishes were moistened with distilled water and put to germinate during 60 days in germination chamber. Since this study aimed to reproduce real conditions from the field, 20º/30ºC temperature, 12/12 hours dark/light conditions were chosen. Seed were kept moist and observations were performed every three days. When radicle and/or cotyledons could be observed, they were counted and removed from Petri dishes.

Bud bank analysis

The bud bank can be defined as all buds that can become a new shoot, being of crucial importance for vegetative regeneration of some ecosystems (Klimesová and Klimes 2007). In order to evaluate the capacity of vegetative regeneration, the bud bank from a shrub (*Eupatorium ligulaefolium)* and a forb (*Vernonia flexuosa*) was analysed. Three plots (1m^2 each) were established in both sites and all individuals were removed with their belowground organs. Plants were placed in plastic bags and washed later in laboratory. Fresh material was used for the analysis, with help of a stereomicroscopy. Only viable buds were counted. When the bud identification was uncertain, anatomical cuts were executed. Buds were counted per individual and later extrapolated to buds/m^2.

Statistical analyses

We used analysis of variance to verify statistical differences between number of stems, buds in different sites and time since fire experiments. We used the same test to analyze differences between tested temperatures in germination experiments for study species. Randomization tests were used (Pillar and Orlóci 1996) applied to Euclidean distances (10000 iterations), since there is no restriction about normal distribution of data (for more details about method, see Manly 2007). In order to avoid serial correlation due to repeated measures, repeated measures analysis was applied to detect significant differences between times of observation for plant traits (plant height and diameter). There was an accidental fire before the last plant demographic observations and two plots were burnt (from site FB). Therefore, they were not used for statistical analysis at T360. The software MULTIV (Pillar 2005) was used for all statistical analyses (except repeated measures analysis, Statistica 6.0).

Results

Population biology

In general, more individuals were sampled in the frequently burned site, except for *Heterothalamus psiadioides*, which showed more individuals in excluded sites (p = 0.05) before fire experiments. After two months, no individuals of *H. psiadioides* could be observed. One year later, seedlings were found in site E. *Eupatorium ligulaefolium* had more individuals in site FB before fire experiments ($p = 0.018$) and showed the same tendency after experiments (no significant differences). The same pattern could be observed for *Chaptalia runcinata* ($p > 0.05$). *Vernonia flexuosa* tended to show more individuals in site FB before and after two months of fire experiments, but after one year, site E tended to have more individuals ($p > 0.05$). No interactions between time since experiment and site could be observed for any of the study species.

Before fire experiments, populations of both forbs and shrubs showed a higher proportion of non-flowering individuals than juveniles in both sites (Fig. 1). *H. psiadioides* was the only species with flowering individuals, but only in excluded sites (49.24%). After two months of experiments, no individuals of this species could be observed, whilst populations of *E. ligulaefolium* contained a higher proportion of non-flowering individuals in site FB (63.86%) and the opposite result in site E: more juveniles than non-flowering individuals (61.1% and 39.9%, respectively).

Forb species had different patterns. After two months of fire, *C. runcinata* had more juveniles than non-flowering individuals in both sites (55.7% in site FB and 85.71% in site E), whilst *V. flexuosa* showed a higher proportion of non-flowering individuals (72.34% in site FB and 60% in site E). Flowering individuals were present in both species two months after fire. *C. runcinata* showed flowering individuals in both sites, while *V. flexuosa* had only in excluded sites.

H. psiadioides only had new individuals after one year of fire experiments, all juveniles. *E. ligulaefolium* showed well- established populations, most with non-flowering adult individuals in site FB (82.15%) and site E (91.18%), with few juveniles after one year of fire. Populations of *V. flexuosa*, on the other hand, showed a high proportion of juveniles in frequently burned sites (FB, 66.67%), but the same proportion of juveniles and non-flowering individuals in excluded sites (45% for both sites). In addition, after one year of fire, flowering individuals could be observed in excluded sites (10%). *C. runcinata* showed a different pattern: more non-flowering individuals in site FB (55.36%) and more juveniles in site E (59%). No flowering individuals were found at the end of observations.

Both *V. flexuosa* and *E. ligulaefolium* showed only vegetative regeneration. New stems resprouted from belowground organs. No resprouting from epicormic buds could be observed. *C. runcinata* showed 98% of new rosettes arising from vegetative regeneration and only 2% were seedlings after two months. No seedlings could be observed after one year. *H. psiadioides* showed 100% of seedlings emerging after one year of fire experiments exclusively in site E.

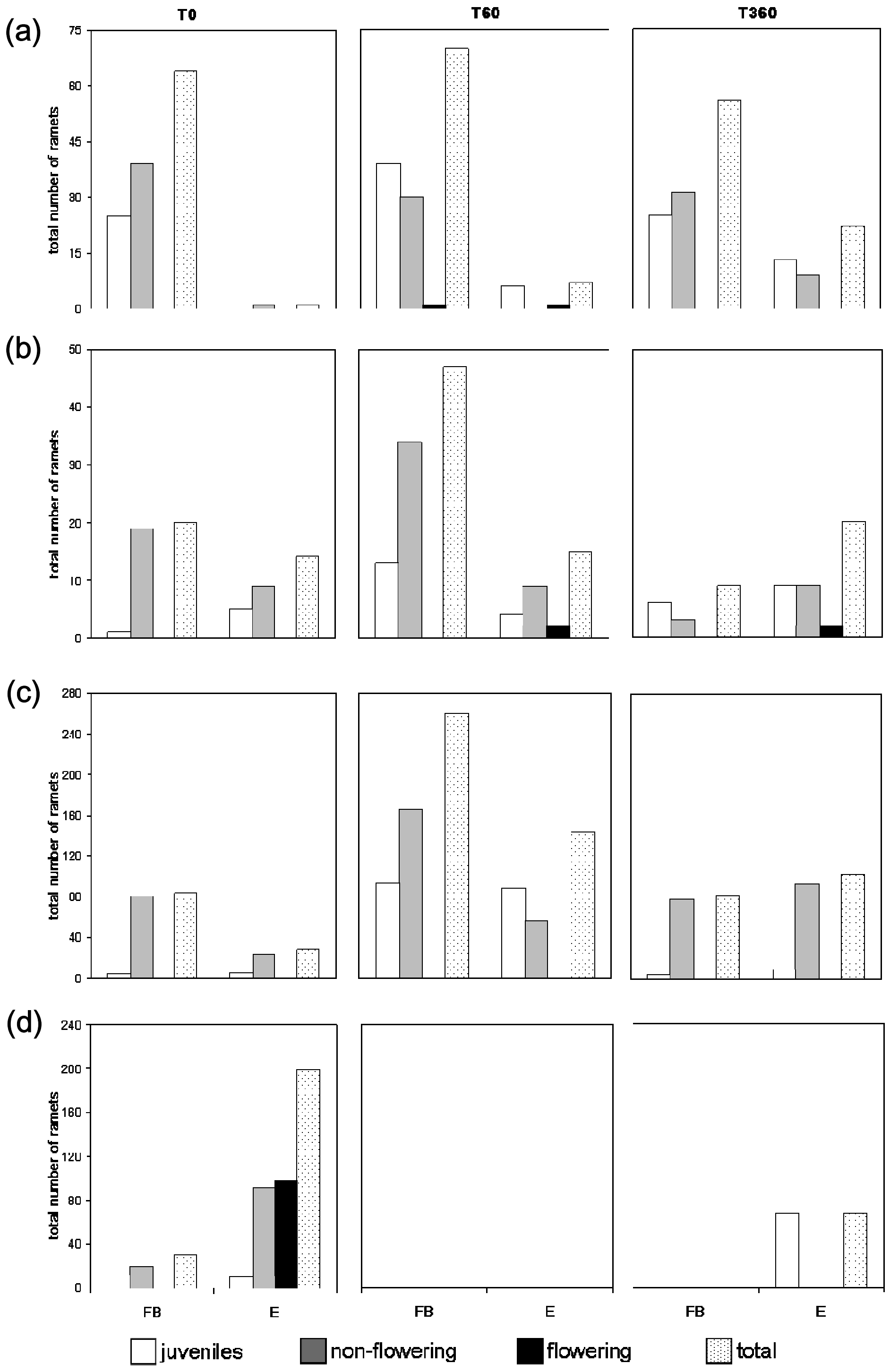

Fig 1. Number of individuals (stems) in different age-state classes (juveniles: individuals ≤ 10 cm height for shrubs species, individuals ≤ 5 cm diameter for forbs; Non-flowering, flowering individuals and total) in site FB (frequently burned) and E (excluded from fire since six years) on Morro Santana, southern Brazil. **(a)** – *Chaptalia runcinata*, **(b)** – *Vernonia flexuosa*, **(c)** – *Eupatorium ligulaefolium* and **(d)** – *Heterothalamus psiadioides*.

E. ligulaefolium also had a higher rate of stem death in site FB than in site E (68% and 29%, respectively). Individuals of *H. psiadioides* showed 34% of stem established between T60 and T360 only.

Plant traits from populations also showed significant differences between sites and time. Populations of *V. flexuosa* individuals tended to be taller in excluded sites before fire experiments than in frequently burned sites ($P > 0.05$). After one year of experiments, individuals were still smaller than before experiments in site FB ($F = 7.73$, $p = 0.01$) and tended to be smaller in excluded site ($p > 0.05$) (Table 2). *C. runcinata* populations were taller in frequently burned sites at T0 ($p = 0.03$). After one year, rosettes showed no significant differences with individuals at T0 in site FB ($F = 0.04$, $p = 0.84$), although in excluded sites they tended to be smaller ($p > 0.05$). Plant diameter showed no significant differences between sites and before and after one year of fire.

Populations of *E. ligulaefolium* had no significant differences in plant height at T0 between sites ($p = 0.47$) and after one year, plants had the same size as before experiments ($F = 1.08$, $p = 0.3$). *H. psiadioides*, however, showed taller individuals in excluded sites than in frequently burned ones ($p = 0.05$). In frequently burned sites, there was no establishment of individuals after fire experiments. In excluded sites at T360, individuals were very small (1.25±1.27 cm).

Heat shock experiments

Heat shock experiments neither enhanced germination nor damaged seeds. There were no significant differences between control and the treatments for all tested species (Table 3). *Heterothalamus psiadioides* showed the highest germination rates (≥ 75%), whilst rates of *Vernonia flexuosa* did not reach 40%. Additionally, seeds from *H.psiadioides* germinated first (after 5 days). *V. flexuosa* had seedlings only after 10 days.

Bud bank analysis

The bud bank of *Eupatorium ligulaefolium* tended to be larger in excluded sites ($p > 0.05$, Fig. 2a). *Vernonia flexuosa*, however, showed the opposite tendency: a larger bud bank in frequently burned sites (no significant differences, Fig. 2b). Stem density followed the bud bank pattern for *V. flexuosa*, but not for *E. ligulaefolium*: there was more stems in frequently burned than in excluded sites ($p = 0.02$).

Table 1. Stem density (stem/m^2), stem establishment (%) and stem death (%) of forbs (*Chaptalia runcinata* and *Vernonia flexuosa*) and shrubs (*Eupatorium ligulaefolium* and *Heterothalamus psiadioides*) in different sites (FB – frequently burned and E – excluded since six years) on Morro Santana, southern Brazil.

Site	Species	Stem density (stem/m^2)			Stem establishment (%)		Stem death (%)	
		T0	T60	T360	T0-T60	T60-T360	T0-T60	T60-T360
FB	*Chaptalia runcinata*	4.86	5.00	4.00	102.94	0	100	20
	Vernonia flexuosa	1.43	3.36	0.64	235.00	0	100	81
	Eupatorium ligulaefolium	6.00	18.57	5.86	309.52	0	100	68
	Heterothalamus psiadioides	2.14	0	0	0	0	100	-
E	*Chaptalia runcinata*	0.07	0.50	1.64	700	328.57	100	-
	Vernonia flexuosa	1.00	1.07	1.43	107.14	133.33	100	-
	Eupatorium ligulaefolium	2.00	10.29	7.29	514.29	0	100	29
	Heterothalamus psiadioides	14.21	0.00	4.86	0	34	100	-

Table 2. Plant height (cm) and plant diameter (only of forbs, cm) from populations of *Chaptalia runcinata, Vernonia flexuosa, Eupatorium ligulaefolium* and *Heterothalamus psiadioides* (means ± SE) in different sites (FB – frequently burned and E – excluded since six years) at different times (T0 – before experiments, T60 –two months, and T360 –one year after fire). Repeated measures analysis was performed for between times. Different small letters mean significant differences between time of observations (rows) and different capital letters mean differences between sites (columns, $p \leq 0.05$), based on randomization testing.

Site	Species	Plant height (cm)			Plant diameter (cm)		
		T0	T60	T360	T0	T60	T360
FB	*Chaptalia runcinata*	4.9±3.65 aA	1.37±0.9a A	4.14±3.79 aA	10.05±2.46	6.61±3.59	8.23±3.89
	Vernonia flexuosa	2.1±1.49 a	1.36±0.85 b	1.89±1.76 b	7.56±3.05 a	10.17±5.00 b	7.34±4.8 ab
	Eupatorium ligulaefolium	35.67±16.15 aA	14.63±10.33 bA	33.96±15.73 aA	-	-	-
	Heterothalamus psiadioides	14.87±7.28 A	-	-	-	-	-
E	*Chaptalia runcinata*	4.2±4.7 aB	1.00±0b A	3.86±3.13 aA	8.07±2.92 a	4.86±0.38 b	7.45±3.96 a
	Vernonia flexuosa	5±0	2.67±3.59	3.75±5.07	15±0 a	13.27±8.58 b	9.15±4.5 c
	Eupatorium ligulaefolium	47.86±34.9 aA	10.20±8.01 bA	31.92±15.54 cA	-	-	-
	Heterothalamus psiadioides	41.93±23.95 aB	-	1.25±1.27 b	-	-	-

Table 3. Seed weight and germination rates of two grassland species under different heat shock treatments in southern Brazil (means ± standard deviation). No significant differences could be found ($p \leq 0.05$).

Species	Weight (g)	Treatments (germination rates %)				
		control	60°	80°	100°	120°
Heterothalamus psiadioides	0.11±0.04	77±8.9	78.4±8	80.8±14.5	89.6±7.8	81.6±8.3
Vernonia flexuosa	1.02±0.1	32±8.9	36.8±10.7	32.8±8.7	38.4±11.5	38.4±11.5

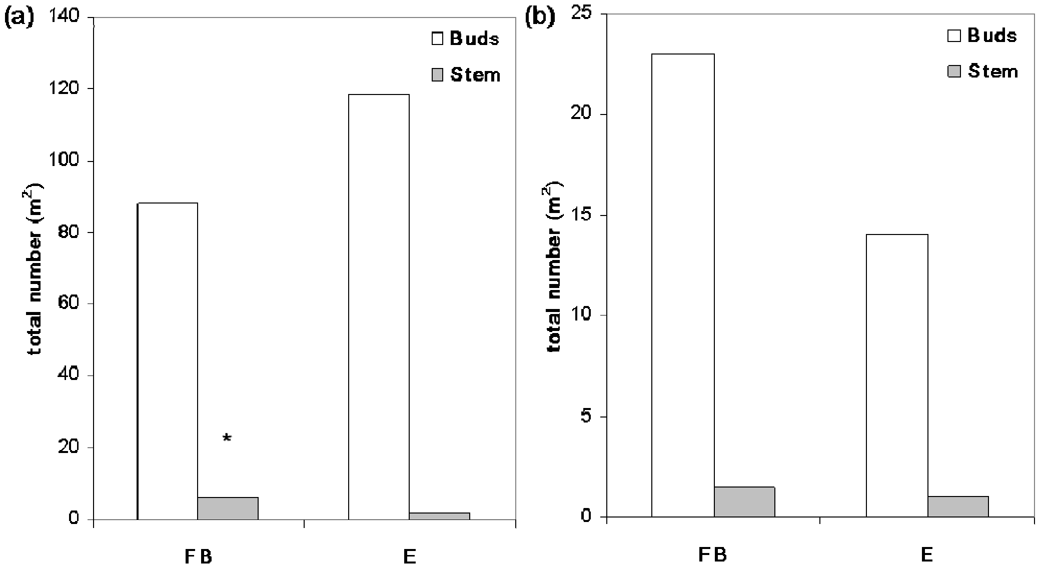

Fig 2. Total number of belowground buds (buds/m²) and stems (stem/m²) from (a) – *Eupatorium ligulaefolium* (shrub) and (b) - *Vernonia flexuosa* (forb). Asterisk means significant difference between study sites (FB – frequently burned, E – excluded since six years), based on randomization testing.

Discussion

Population structure and dynamics

Before fire experiments, all species showed more individuals in frequently burned sites (FB), except *Heterothalamus psiadioides*. This shrub species is an obligate seeder, which invades some grassland sites when fire is excluded. However, its populations are clumped, found only in patches and in some parts of the study area. The same tendency is found in other granitic hills (pers. obs.). Reasons for this patchiness of *H. psiadioides* are not clear. Its populations in site E could be considered as normal populations (Hegland *et al.* 2001; Oostermeijer *et al.* 1994). Populations still had juveniles (although in a small number) and adult individuals. Many flowering individuals could be observed only in these sites. By the time of fire experiments, flowering individuals had no mature seeds. In site FB, individuals of *H. psiadioides* were still small (14.87±7.28 cm) and not sexually mature. Less is known about its phenology and life cycle, but its individuals may not begin to flower before four years (pers. obs.).

Since fire is recurrent in site FB, individuals of *H. psiadioides* probably did not have enough time to develop flowers and seeds. Seeds are very small, with a probable transient seed bank that is not refilled due to the short period between fires. Lloret (1998) pointed out the importance of seed bank refill for seedling recruitment. Hence, in these sites, no new recruitments could be found, even after one year, as observed in site E. In the excluded site, a large number of flowering individuals could still be found near experimental plots and seeds might come from seed rain from neighbouring plants.

Seedling recruitment can be affected by several factors, such as microsite suitability (Keith 2002; Lloret 1998), fire frequency, regime and intensity (Hoffmann 1999; Knox and Clarke 2006; Lloret and Vilà 2003), timing of fire (Pausas 2001), competition, productivity (Bellingham and Sparrow 2000), post-fire soil temperatures (Christensen 1985; Knox and Clarke 2006), and rainy season (Heelemann *et al.* 2008). Germination experiments showed a high rate of germination and seeds emerging very fast. Therefore, the long time needed to seeds of *H. psiadioides* to germinate should be related to other factors, such as transient seed bank, unfavourable post-fire site conditions and mostly, spatial limited dispersion of propagules. If fire kills all *H. psiadioides* individuals in a site, seedling recruitment will seldom occur, since seeds coming from neighbouring plants are needed. Fruits of this species have no special structures (e.g. pappus), which could be a problem for long-distance dispersal. They are probably dispersed near the mother plant. Even though populations of *H. psiadioides* were considered to be stable, fire events seem to be required for seedling emergence, since no seedlings could be found before experiments in site FB and E.

Eupatorium ligulaefolium (resprouter) showed different patterns. 100% of all individuals were topkilled (death of aboveground stems, Hoffmann 1999). All new resprouters came from belowground buds located on the surface of the xylopodium. Fire might have destroyed epicormic buds and formation of new buds occurred only on the xylopodium surface (pers. obs). Topkilled individuals showed new resprouters after two months. There was a high stem recruitment of *E. ligulaefolium*, followed by high mortality rates, mostly in site FB. After two months, we found up to 45 stems coming from the same stem base (data not shown). Higher mortalities of stems in FB should be related to high fire frequency. With shorter intervals between fires, plants might not recover all storage necessary for allocation to stem resprouting (stem density was lower in FB than in E sites after two months). Knox & Clark (2006) demonstrated the ability of resprouters in creating and accumulating starch reserves, mostly in roots. The constant use of reserves might deplete starch concentration and two-year intervals might not be enough to replenish these reserves in order to achieve an optimal resprouting capacity. However, further studies about resource allocation and starch concentration should be carried out under different fire frequencies in order to confirm our hypothesis. Annual burns would lead populations to a decrease in number of individuals. Other studies also found different optimal fire intervals for populations of shrubs, but most of them agreed that, annual burns decrease populations of woody species (e.g. Heelemann *et al.* 2008; Quintana-Ascencio *et al.* 2002; Satterthwaite *et al.* 2002).

Despite the high mortality, FB site showed a higher number of individuals of *E. ligulaefolium* before fire experiments. Thus, six years of fire intervals showed most tall, non-flowering individuals, with few juveniles. Populations of *E. ligulaefolium* could be described as regressive (Oostermeijer et al. 1994) and if fire did not occur, there would be a decrease in number of individuals. No flowering individuals and seedlings of *E. ligulaefolium* could be found. Flowering time begins in February-March. During the second observation, plants were still very small and resource was mainly allocated for vegetative regeneration. Flowering individuals could only be observed in neighbouring sites. However, after one year, no seedlings could be observed. Small individuals in the site (single stemmed) might have been recruited from seeds, but we cannot assure it. Most of *E. ligulaefolium* individuals were multi-stemmed (pers. obs.).

Both forb species showed high recruitment after fire experiments. *Chaptalia runcinata* shows no evident belowground storage organ, but individuals were able to resprout immediately after fires. After one month, most individuals were flowering (Fidelis & Blanco, in preparation). Therefore, fire enhanced flowering, since flowering time for this species is during winter. Seeds have structures adapted to wind dispersion (pappus) and hence, seeds could be dispersed to neighbouring sites. Unfortunately, less is known about its dispersion biology and germination. New recruits of *C. runcinata* were usually solitary. After two months, few small seedlings (2%, less than 1 cm diameter) could be observed in both sites, showing that seeds can rapidly germinate after fire events. After fire, there is a higher opportunity for seedling establishment due to lower competition and higher availability of open spaces in vegetation. Many Asteraceae species in *Campos* grasslands showed no enhancement in germination after exposition to high temperatures (Overbeck *et al.* 2006b). Therefore, we do not believe that seeds from *C. runcinata* exhibit dormancy. Although this species show no belowground typical bud-bearing organ, dead individuals remain in the site and fire should stimulate the development of new stems.

Before fire, almost no individuals of *C. runcinata* could be found in excluded sites. This site shows a high cover of tussock grasses and shrubs, which might have hindered populations of *C. runcinata* due to competition to light. Since open sites were created, individuals of *C. runcinata* could establish and grow, facing less competition. Still after one year, populations showed a larger number of individuals than before experiments. By this time, both grass and shrub covers were still not high (Fidelis et al., Chapter 5). This species showed the lowest rates of mortality (20% in site FB and no mortality in site E). Populations showed no clumped patterns (pers. obs.). As a conclusion, individuals of *C. runcinata* take advantage of newly open sites in post fire environment due to the lack of competition with grasses and shrubs.

Finally, *Vernonia flexuosa* also showed great recruitment two months after fire experiments, mostly in site FB. Populations of *Vernonia flexuosa* decreased drastically after one year in frequently burned sites, probably due to the rapid depletion of reserves in belowground systems to stem growth. *V. flexuosa* individuals have rhizophores, which are underground cauline systems, originated from cotyledonary axillary buds, with resprouting and clonal propagation capacity (Hayashi and Appezzato-da-Glória 2005). Some *Vernonia* species have high concentrations of fructans (storage substance), such as *V. herbacea* (Carvalho and Dietrich 1993), *V. grandiflora*, *V. ferruginea,* and *V. oblongifolia*.

Flowering individuals *V. flexuosa* could be found in site E after two months of burns, as well as in neighbouring sites. Hence, fire did not hinder flowering in excluded sites. Carvalho and Dietrich (1993) verified oscillations in fructans content at different phases: there was a decrease in fructan during flowering and sprouting phase, whilst fructan accumulation occurred during summer, showing the relation of fructans and flowering.

Individuals of *V. flexuosa* in excluded sites might have higher contents of reserves in their belowground organs, since stem recruitment without stimulation is rare (pers. obs.), and thus, resource allocation is only for flowering. Therefore, individuals have more resources to allocate for resprouting and flowering after fire than individuals in site FB, as showed by our results.

As a conclusion, we believe that fire plays a major role on population structure and demography and is very important for plant recruitment, even for obligate seeder species. Other forb and shrub species might have populations highly influenced by fire events and further studies should be thus, carried out.

Sexual vs. vegetative regeneration

Fire neither enhanced nor hindered germination of studied species. Several studies show the influence of fire temperatures (González-Rabanal and Casal 1995; Hanley and Fenner 1998; Hanley and Lamont 2000; Martin *et al.* 1975; Roy and Sonié 1992; Tarrega *et al.* 1992) or smoke (Keeley and Bond 1997). In *Campos* grasslands, Overbeck et al. (2006b) could not find any relationship between higher temperatures and enhancement of germination for herbaceous, corroborating with our results.

On the other hand, regeneration from the bud bank seems to be more important for the study species (except for *H. psiadioides*, obliglate seeder). Fidelis et al. (Chapter 2) analyzed the bud bank in *Campos* grasslands in southern Brazil under different management (grazing, fire and exclusion) and found a relation between fire frequency and bud bank size. The larger the intervals of fire were, the smaller the bud bank was.

Both *Eupatorium ligulaefolium* and *Vernonia flexuosa* are not meristem-limited. *E. ligulaefolium* has a xylopodium, which is a structure with high gemmiferous potential (Appezzato-da-Glória and Estelita 2000; Rizzini 1965). One xylopodium showed to have up to 150 buds, whilst rhizophores from *V. flexuosa* had not more than 30 buds (data not shown).

Most species in the study site have the ability to resprout after fire events (ca. 90%, Fidelis et al., Chapter 4). Therefore, vegetative regeneration plays a major role in plant recruitment. Recurrent fires are needed in order to maintain plant populations, as showed by our study. Even *H. psiadioides*, which have no recruitment via vegetative regeneration, requires fires or other kind of disturbance for seedling recruitment. Longer intervals without fire would lead to a decrease in number of individuals and to the extinction of typical grassland species.

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References

Aguiar L. W., Martau L., Soares Z. F., Bueno O. L., Mariath J. E. & Klein R. M. (1986) Estudo preliminar da flora e vegetação de morros graníticos da Região da Grande Porto Alegre, Rio Grande do Sul, Brasil. *Iheringia* **34**, 3 - 38.

Appezzato-da-Glória B. & Estelita M. F. M. (2000) The development anatomy of the subterranean system in *Mandevilla ilustris* (Vell.) Woodson and *M. velutina* (Mart. ex Stadelm.) Woodson (Apocynaceae). *Revista Brasileira de Botânica* **23**, 27-35.

Barroso G., Morim M. P., Peixoto A. L. & Ichaso C. L. F. (1999) *Frutos e sementes: morfologia aplicada à sistemática de dicotiledôneas*. Editora Universidade Federal de Viçosa, Viçosa.

Behling H., Pillar V. D., Müller S. C. & Overbeck G. E. (2007) Late-Holocene fire history in a forest-grassland mosaic in southern Brazil: implications for conservation. *Applied Vegetation Science* **10**, 81-90.

Bell T. L. & Ojeda F. (1999) Underground starch storage in *Erica* species of the Cape Floristic Region - differences between seeders and resprouters. *New Phytologist* **144**, 143-52.

Bellingham P. J. & Sparrow A. D. (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* **89**, 409-16.

Boldrini I. I. (1997) Campos do Rio Grande do Sul: caracterização fisionômica e problemática ocupacional. *Boletim do Instituto de Biociências da Universidade Federal do Rio Grande do Sul* **56**, 1 - 39.

Bond W. J. & Keeley J. E. (2005) Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* **20**, 387-94.

Bond W. J. & van Wilgen B. W. (1996) *Fire and plants*. Chapman ¨Hall, London.

Bowen B. J. & Pate J. S. (2004) Effect of season of burn on shoot recovery and post-fire flowering performance in the resprouter *Stirlingia latifolia* R.Br. (Proteaceae). *Austral Ecology* **29**, 145 - 55.

Cabrera A. L. & Klein R. M. (1973) Compostas - Tribo Mutisae. In: *Flora Ilustrada Catarinense* (ed P. R. Reitz) p. 124, Itajaí.

Carvalho M. A. M. & Dietrich S. M. C. (1993) Variation in fructan content in the underground organs of *Vernonia herbacea* (Vell.) Rusby at different phenological phases. *New Phytologist* **123**, 735-40.

Christensen N. L. (1985) Shrubland fire regimes and their evolutionary consequences. In: *The ecology of natural disturbance and patch dynamics* (eds S. T. A. Pickett and P. S. White) pp. 85-100. Academic Press, San Diego.

Ferreira A. G., Cassol B., Rosa S. G. T., Silveira T. S., Stival A. L. & Silva A. A. (2001) Germinação de sementes de Asteraceae nativas no Rio Grande do Sul, Brasil. *Acta botanica Brasilica* **15**, 231-42.

Fidelis A., Overbeck G., Pillar V. D. & Pfadenhauer J. (2008) Effects of disturbance on population biology of a rosette species *Eryngium horridum* Malme in grasslands in southern Brazil. *Plant Ecology* **195**, 55-67.

García-Martinez P. (2005) Caracterización química y física de los suelos del Morro Santana (Porto Alegre, Rio Grande do Sul, Brasil). In: *Chair of Soil Sciences*. Technische Universität München, Freising-Weihenstephan, Germany.

González-Rabanal F. & Casal M. (1995) Effect of high temperatures and ash on germination of ten species from gorse shrubland. *Vegetatio* **116**, 123-31.

Hanley M. E. & Fenner M. (1998) Pre-germination temperature and the survivorship and onward growth of Mediterranean fire-following plant species. *Acta Oecologica* **19**, 181-7.

Hanley M. E. & Lamont B. B. (2000) Heat pre-treatment and the germination of soil- and canopy-stored seeds of south-western Australian species. *Acta Oecologica* **21**, 315-21.

Hayashi A. H. & Appezzato-da-Glória B. (2005) The origin and anatomy of rhizophores in *Vernonia herbacea* and *V. platensis* (Asteraceae) from the Brazilian Cerrado. *Australian Journal of Botany* **53**, 273-9.

Heelemann S., Proches S., Rebelo A. G., van Wilgen B. W., Porembski S. & Cowling R. M. (2008) Fire season effects on the recruitment of non-sprouting serotinous Proteaceae in the eastern (bimodal rainfall) fynbos biome, South Africa. *Austral Ecology* **33**, 119-27.

Hegland S. J., Oostermeijer J. G. B. & van Leeuwen M. (2001) Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. *Journal of Applied Ecology* **38**, 1277 - 89.

Hoffmann W. A. (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. *Journal of Ecology* **84**, 383 - 93.

Hoffmann W. A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* **80**, 1354 - 69.

Keeley J. E. & Bond W. J. (1997) Convergent seed germination in South African fynbos and Californian chaparral. *Plant Ecology* **133**, 153-67.

Keith D. A. (2002) Population dynamics of an endangered heathland shrub, *Epacris stuartii* (Epacridaceae): recruitment, establishment and survival. *Austral Ecology* **27**, 67 - 76.

Klimesová J. & Klimes L. (2007) Bud banks and their role in vegetative regeneration - a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* **8**, 115-29.

Knox K. J. E. & Clarke P. J. (2005) Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Functional Ecology* **19**, 690-8.

Knox K. J. E. & Clarke P. J. (2006) Fire season and intensity affect shrub recruitment in temperate slerophyllous woodlands. *Oecologia* **149**, 730-9.

Lamont B. B., Groom P. K., Richards M. B. & Witkowski E. T. F. (1999) Recovery of *Banksia* and *Hakea* communities after fire in mediterranean Australia - the role of species identity and functional attributes. *Diversity and Distrubutions* 5, 15 - 26.

Lavorel S., Canadell J., Rambal S. & Terradas J. (1998) Mediterranean terrestrial ecosystems: research priorities on global change effects. *Global Ecology & Biogeography* 7, 157 - 66.

Livi F. P. (1999) Elementos do clima: o contraste de tempos frios e quentes. In: *Atlas ambiental de Porto Alegre* (eds R. Menegat, M. L. Porto, C. C. Carraro and L. A. D. Fernandes) pp. 73 - 8. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre.

Lloret F. (1998) Fire, canopy cover and seedling dynamics in Mediterranean shrubland of northeastern Spain. *Journal of Vegetation Science* 9, 417-30.

Lloret F. & Vilà M. (2003) Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. *Journal of Vegetation Science* 14, 387-98.

Manly B. F. J. (2007) *Randomization, bootstrap, and Monte Carlo methods in biology*. Chapman & Hall/CRC, Boca Raron.

Martin R. E., Miller R. L. & Cushwa C. T. (1975) Germination response of legume seeds subjected to moist and dry heat. *Ecology* 56, 1441-5.

Matzenbacher N. I. (2003) Diversidade florística dos campos sul-brasileiros: asteraceae. In: *54o. Congresso Nacional de Botânica* pp. 124-7, Belém, Pará.

Menges E. S. & Dolan R. W. (1998) Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *Journal of Ecology* 96, 63 - 78.

Müller S. C., Overbeck G. E., Pfadenhauer J. & Pillar V. D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology* 189, 1-14.

Oliveira J. M. & Pillar V. D. (2004) Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. *Community Ecology* 5, 197-202.

Oostermeijer J. G. B., Van´t Veer R. & den Nijs J. C. M. (1994) Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology* 31, 428 - 38.

Overbeck G. E., Müller S. C., Fidelis A., Pfadenhauer J., Pillar V. D., Blanco C., Boldrini I. I., Both R. & Forneck E. D. (2007) Brazil´s neglected biome: the Southern Campos. *Perspectives in Plant Ecology and Systematics* 9, 101-16.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science* **16**, 655-64.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006a) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. *Brazilian Journal of Biology*.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006b) No heat-stimulated germination found in herbaceous species from burned subtropical grassland. *Plant Ecology* **184**, 237-43.

Pate J. S., Froend R. H., Bowen B. J., Hansen A. & Kuo J. (1990) Seedling growth and storage characteristics of seeder and resprouter species of Mediterranean-type ecosystems of S.W. Australia. *Annals of Botany* **65**, 585-601.

Pausas J. G. (2001) Resprouting vs. seeding - a Mediterranean perspective. *Oikos* **94**, 193-4.

Pfab M. F. & Witkowski E. T. F. (1999) Fire survival of the Critically Endangered succulent, *Euphorbia clivicola* R.A. Dyer - fire-avoider or fire-tolerant? *African Journal of Ecology* **37**, 249 - 57.

Pillar V. D. (2005) MULTIV: Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Pillar V. D. & Orlóci L. (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science* **7**, 585 - 92.

Quintana-Ascencio P. F., Menges E. S. & Weekley C. W. (2002) A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida Rosemay Scrub. *Conservation Biology* **17**, 433 - 49.

Rizzini C. T. (1965) Estudos experimentais sobre o xilopódio e outros órgãos tuberosos de plantas do cerrado. *Anais da Academia brasileira de Ciências* **37**, 87-113.

Roy J. & Sonié L. (1992) Germination and population dynamics of *Cistus* species in relation to fire. *Journal of Applied Ecology*.

Satterthwaite W. H., Menges E. S. & Quintana-Ascencio P. F. (2002) Assessing scrub buckwheat population viability in relation to fire using multiple modeling techniques. *Ecological Applications* **12**, 1672 - 87.

Statsoft INC. (2004) STATISTICA for Windows, Version 6. Tulsa.

Stokes K. E., Allchin A. E., Bullock J. M. & Watkinson A. R. (2004) Population responses of *Ulex* shrubs to fire in a lowland heath community. *Journal of Vegetation Science* **15**, 505-14.

Tarrega R., Calvo L. & Trabaud L. (1992) Effect of high temperatures on seed germination of two woody Leguminosae. *Vegetatio* **102**, 139-47.

Tertuliano M. F. & Figueiredo-Ribeiro R. C. L. (1993) Distribution of fructose polymers in herbaceous species of Asteraceae from the cerrado. *New Phytologist* **123**, 741-9.

Whelan R. J. (1995) *The ecology of fire*. Cambridge University Press, Cambridge.

Chapter 4

WHAT MATTERS FOR VEGETATION REGENERATION:
SEEDLINGS OR RESPROUTERS?
AN EXAMPLE FROM BRAZILIAN *CAMPOS* GRASSLANDS

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(Resprouter, Seedling)

Abstract: *Campos* grasslands are ecosystems under constant influence of disturbance (grazing and fire). After biomass removal, plants can establish by either seedling or resprouter. Therefore, in flammable ecosystems, plants are generally classified as obligate seeders and resprouters. In order to evaluate the different types of regeneration strategies in *Campos* grasslands, we analyzed two different sites on Morro Santana (Porto Alegre, sourthern Brazil): frequently burned (FB) and excluded from fire since six years (E) according to the number of seedlings and resprouters recruited after fire and mowing treatments. Seven plots were established in each site and for each treatment (total of 28). Before treatments, vegetation relevés were conducted and all plants were sampled, identified and had their cover estimated. Plants were later grouped in functional groups (graminoids, forbs and shrubs) for statistical analyses. Experimental burns and mowing were carried out in summer Observations were conducted after 30, 90 and 360 days. After treatments, less than 10% of established plants came from seedlings. The majority of species resprouted after biomass removal. Number of recruited seedlings and resprouters did not show significant differences between sites and treatments. However, a higher number of species with seedlings was observed in site FB, whilst the number of species with resprouters did not show any significant difference. Only three species showed to be obligate seeders in our study (two shrubs and one forb). More new species of seedlings established in burned plots in site FB, whilst most of species resprouting were the same before treatments. Seedlings of forbs recruited more in burned than in mowed plots. Resprouter was the most important strategy for all studied functional groups, mostly graminoids. Our results show the importance of vegetative regeneration in Campos grasslands and the importance of fire for the establishment of new species, maintaining thus, plant diversity.

Keywords: fire, mowing, regeneration strategies, vegetation responses, obligate seeders

Introduction

Campos grasslands in southern Brazil are unique ecosystems, rich in plant species (about 3000 to 4000 species, Boldrini 1997; Klein 1975). Plant diversity and vegetation physiognomy is maintained by disturbance (fire and grazing), since there are no climatic fluctuations (i.e. no predominant dry season, Overbeck et al. 2007). In the absence of disturbance, grassland and forest woody species invade the grassland matrix (Müller *et al.* 2007; Oliveira and Pillar 2004), leading to a loss of plant diversity and structure (Overbeck *et al.* 2005; 2006a).

Fire plays an important role in several ecosystems in the world. It is responsible for consumer control in many vegetation types (Bond and Keeley 2005). It influences plant community and population structures (Bond and van Wilgen 1996; Whelan 1995). Fire resistance of individuals involves a combination of traits (e.g. growth rate, bark properties, stem profile, protection structures), which can also influence competitive abilities and result in different patterns of recruitment and mortality in populations (Gignoux et al. 1997).

The most simple and used classification is according to plant regeneration ability: plants that resprout after fire (*Resprouters*) and plants with only seedling recruitment (*Obligate seeders*) (Whelan 1995). Differences in regeneration strategies can be found in flammable ecosystems. Fynbos are known to comprise a great number of obligate seeder species (more than 50%, Cowling et al. 2004), whilst in tallgrass prairie seedling recruitment is very rare (less than 1%, Benson and Hartnett 2006).

Several factors were pointed as affecting both seedling and resprout recruitment such as fire frequency and season (e.g. Bond and van Wilgen 1996; Bond *et al.* 1984a; Gibson 1988; Hodgkinson 1991; Hoffmann 1999; Knox and Clarke 2006; Naveh 1975; Whelan 1995) and post fire conditions such as increased light, nutrients (Rice 1993; Wrobleski and Kauffman 2003), and gap availability (Bond and van Wilgen 1996), soil temperatures (Auld and Denham 2006; Hoffmann 1996; Knox and Clarke 2006; Tyler 1995), and changes in competitive hierarchies (Laterra and Solbrig 2001; Marcos *et al.* 2004; Tyler 1995).

A better understanding of factors affecting post fire vegetation regeneration and strategies are of crucial importance for the maintenance of plant diversity and grassland dynamics. Few are the studies conducted in Brazilian *Campos* grasslands evaluating the effects of fire on vegetation dynamics. Overbeck et al. (2005) studied the effects of fire in *Campos* grasslands and observed the decrease in species number with longer intervals of fire. However, their study did not consider regeneration strategies, only plant species and functional types. Müller et al. (2007) classified shrubs and trees according to their ability to resprout or not. However, they considered only woody species.

Here, we aim to evaluate the importance of different regeneration strategies (obligate seeders vs. resprouters) for different functional groups (graminoids, forbs and shrubs) in *Campos* grasslands under different fire frequencies (frequently burned and excluded since six years) and comparing two treatments: fire and mowing.

We hypothesize that the most important regeneration strategy is resprouting for all functional groups, mostly for graminoids. Bond (2004) already emphasized the high resprouting ability of grasses in ecosystems under fire influence. Seedlings, therefore, might have a low contribution for vegetation regeneration, as already observed in other ecosystems (see Benson and Hartnett 2006; Coutinho 1982; Safford 2001). Moreover, recover by new species would occur mostly from the bud bank. Fidelis et al. (Chapter 2) showed the key role of the bud bank in subtropical grasslands. Several belowground structures showed no aboveground biomass, but organs with viable buds.

Furthermore, we also address the following questions: 1) does regeneration strategies differ between sites (frequently burned and excluded from fire since six years)?, 2) does recruitment differ between treatments (fire and mowing)?, and 3) is it continuous after experiments (until one year after experiments)?

Materials and Methods

Study area

The study was carried out in southern Brazil, in a granitic hill in Porto Alegre (Morro Santana hill, 30°03' S, 51°07' W; 311 m a.s.l.). The climate is subtropical humid (Köppen classification Cfa), with mean temperatures of 22°C and mean annual precipitation of 1350 mm (Livi 1999). Soils are dystrophic red-yellow argisols, corresponding to acrisols, alisols and umbrisols (according to FAO classification, García-Martinez 2005).

Most of grassland areas are located at the top and northern slope of Morro Santana (Aguiar et al. 1986). Fires, set mostly by local people every 2-5 years, maintain grasslands. According to Behling et al. (2007), fire has been present in these grasslands throughout the past 1200 years (palynological studies in the area). Atlantic forest is still present, manly at southern facing slope, forming a mosaic with the grasslands. Where fire has been excluded since many years, there is a tendency of diversity loss of grassland plant species, increase of shrub cover and expansion of forest species into the grassland (Müller and Forneck 2004; Müller *et al.* 2007).

Grasslands are very rich in species. Overbeck et al. (2006a) sampled 201 plant species from a estimated pool of 450-500 species. The most important families are Poaceae (mostly C_4

species) and small forbs of Asteraceae, Rubiaceae and Leguminosae (Overbeck *et al.* 2005; 2006a).

Two sites were chosen according to time since last fire for our experiments: FB – frequently burned grassland, last fire January 2005, and E – excluded from fire since six years. A continuous herbaceous layer, with less bare soil and litter, characterizes site FB. Graminoids are dominant, but one can still find several forb species and small shrubs establishing in the area. Site E has a higher cover of shrubs, with individuals reaching 50-70 cm, mostly belonging to three species: *Baccharis leucopappa, Eupatorium ligulaefolium* and *Heterothalamus psiadioides* (all Asteraceae). A grass layer is still present, but with a higher quantity of dead biomass. There is a decrease in forb species in this site.

Experiment design and methods

Seven experimental plots were established in each site for each treatment: fire and mowing. Plots were 5x5 m to avoid border effects. Inside each plot, six continuous sub-plots (0.2x0.2 m) were established in order to facilitate vegetation relevés.

Before experiments, vegetation relevés were conducted (T0). Plants were identified to species and latter grouped in functional groups: graminoids, forbs and shrubs. Moreover, species, bare soil and litter, as well as graminoid, forb and shrub covers were estimated. Stems (ramets) from forbs and shrubs were also counted.

Treatments were established in summer 2006-2007. Due to logistic problems, fire experiments were conducted with three weeks of difference between areas (for more details, see Fidelis et al., submitted). In the mowed plots, all aboveground vegetation was removed (but no litter). After fire, all plants were topkilled (combustion ca. 90%). Temperature at ground level varied between sites (48 – 537°C), as well as fire intensity (36 – 319 kW/m, Fidelis et al., submitted).

Observations were carried out 30 (T30) and 90 (T90) days after treatments. In each observation (T30 and T90), number of seedlings and resprouters were counted according to the number of species and ramets (only for forbs and shrubs). Each stem was considered to be a ramet. They were grouped in functional groups (graminoids, forbs, and shrubs) for statistical analysis. Bare soil and litter cover were also estimated. When it was not possible to differentiate between seedling and resprout, the plant was labelled as “not identified” and not used for statistical analyses. We also conducted observations after 360 days (T360) in order to verify if seedlings were still establishing.

The establishment of new species (which were not there before) and same species (which were already in the plots) was also observed. Before the last observation, an accidental fire occurred in the area and singed vegetation from two experimental burnt plots from area FB and destroyed 5 mowed plots in each area (FB and E, total of 10 plots), so they were not considered for statistical analysis of seedlings at T360.

Statistical analyses

Analyses of variance were performed, using treatment (fire and mowing) and site (FB and E) as factors, for total number of species for each strategy and total number of seedlings and resprouters and also for functional groups (graminoids, forbs and shrubs) for each time (T30, T90 and T360). We used analysis of variance with randomization tests (10000 iterations), with sum of squares computed based on Euclidean distance matrices of sampling units (Manly 2007; Pillar and Orlóci 1996). We chose randomization tests to avoid restricting distribution assumptions of conventional analysis of variance (for more details, see Manly 2007). In addition, Pearson's correlation was calculated between cover of functional groups, bare soil and litter, as well as fire variables (fire temperatures and fire intensity, data from Fidelis et al, submitted) and the total number of seedlings and resprouters. All statistical analyses were conducted with MULTIV (Pillar 2005).

Results

Seedlings

Less than 10% of all species showed seedlings after experiments (from a total of 146 taxa). After 30 days of fire and mowing treatments, there was a high recruitment of species with seedlings, which decreased with time. The highest recruitment of species occurred in burned plots after 30 days in area FB (Fig. 1a, p = 0.03). Less species were recruited after 90 and 360 days in this area. No significant differences could be found between treatments (fire and mowing) in area E. Mowed plots, on the other hand, showed an opposite tendency to increase species recruited with time in excluded sites.

The number of recruited seedlings (number of seedlings) did not show any significant differences (Fig. 1b) between sites (FB and E) and treatment (fire and mowing, p > 0.05). In the excluded area, there was a tendency of increasing recruitment after one year in both treatments.

A weak positive correlation was found between forb cover and total number of seedlings (r = 0.25, p = 0.03) and total number of species with seedlings and bare soil cover (r = 0.28, p =

0.02). No significant correlation could be found between number of species with seedlings and number of seedlings and fire variables (temperature at soil level and fire intensity).

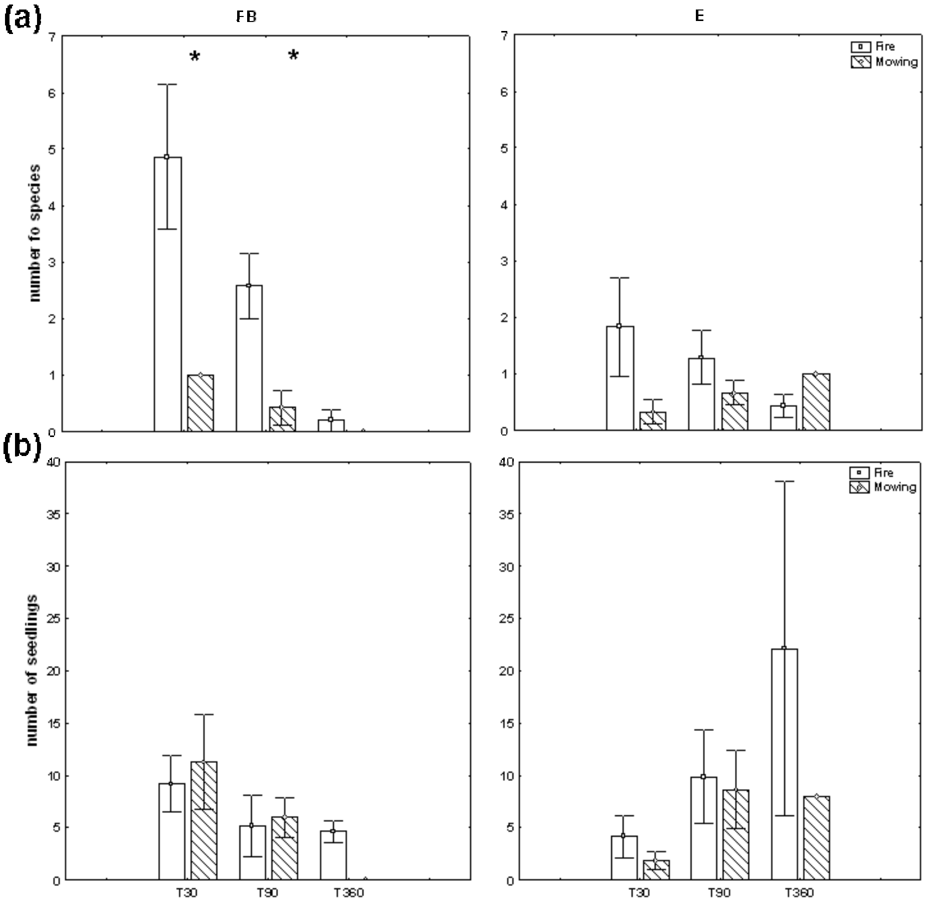

Fig 1. **(a)** – Number of species with seedlings and **(b)** – number of seedlings recruited in site FB (frequently burned) and E (excluded since six years) in plots under different treatments: fire (open bars) and mowing (dashed bars). Points illustrate means ± 1SE. Asterisks mean significant differences ($p \leq 0.05$) between treatments at each time of observation, based on randomization testing.

In both sites (FB and E), a higher percentage of new species (not present in experimental plots before treatments) could be observed in burned than in mowed plots (Fig. 2): 54.4% and 16.7% respectively in area FB, and 55.6% and 16.7% respectively in area E ($p = 0.02$ for area FB and $p = 0.02$ for area E). There were no significant differences between new and same species composition, except for mowed plots of the FB area (83.3% of same species, 16.7% of new species, $p = 0.04$). In excluded areas, mowed plots showed no seedling recruitment of new species.

Plants that were flowering (total of 33 species) before the treatments showed only two species with seedlings after 30 and 90 days: *Aspilia montevidensis* (Asteraceae, in a burned plot in area FB) and *Evolvulus sericeus* (Convolvulaceae, in a mowed plot in area E). Several seedlings of *Heterothalamus psiadioides* and *Baccharis leucopappa* (both Asteraceae) were found in excluded areas (both treatments), but only after 360 days.

Only three species were found to be obligate seeders in our experiments: *Baccharis leucopappa, Heterothalamus psiadioides* and *Gamochaeta americana* (all Asteraceae, only seedlings were observed). Other species showed to be facultative resprouters, such as *Aspilia montevidensis, Evolvulus sericeus, Cuphea glutinosa* and *Richardia grandiflora* (both seedlings and resprouters were found).

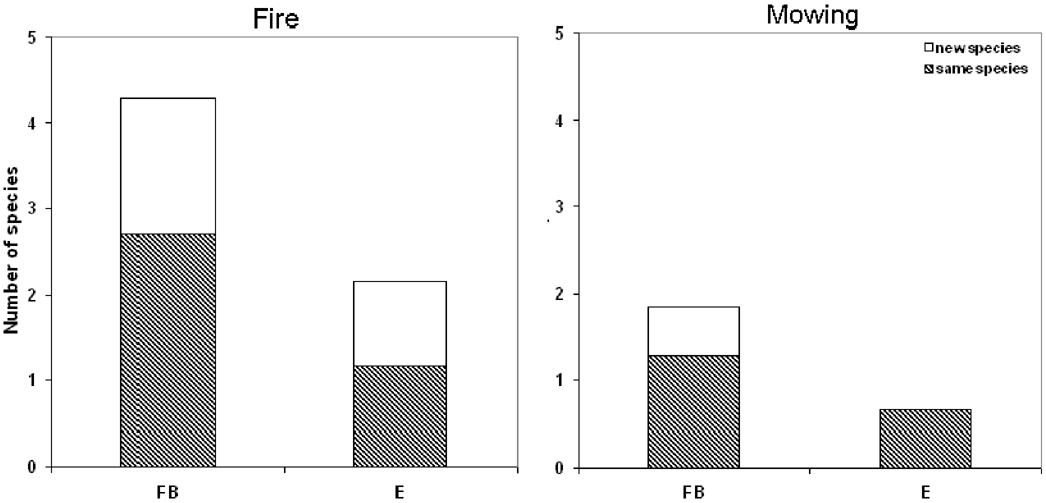

Fig 2. Number of new (open) and same species (dashed bars) of seedlings in sites FB (frequently burned) and E (excluded since six years) under different treatments: fire and mowing in Brazilian *Campos* grasslands.

Resprouters

The majority of species showed the ability to rapidly resprout after both fire and mowing treatments (ca. 90%). No significant differences regarding the number of species with resprouters could be found between sites and treatments (Fig. 3a), except in frequently burned areas at T30: mowed plots showed a higher recruitment of species resprouting than in burned ones ($p = 0.01$). The number of resprouters showed no significant differences between sites and treatments ($p > 0.05$, Fig. 1b). There was a tendency in excluded sites of increasing the number of resprouters with time in mowed plots. In burned plots, we found the opposite trend: number of resprouters tended to decrease with time. No interaction could be found between site and treatment ($p > 0.05$).

Number of species resprouting showed a weak negative correlation with bare soil ($r = -0.28$, $p = 0.04$). However, number of resprouters showed a strong negative correlation with temperature at soil level (Fig. 4., $r = -0.78$, $p = 0.0023$).

As showed by Fig. 5, most resprouters belonged to the same species that were present before fire experiments. In burned plots, 74.5% and 71.8% (sites FB and E, respectively) of recruited resprouters belonged to same species, whilst in mowed plots, 81.7% in frequently burned sites and 68.5% in excluded sites belonged to same species (no significant differences). However, significant differences could be found between the percentage of new and old species in all plots and areas ($p \leq 0.05$).

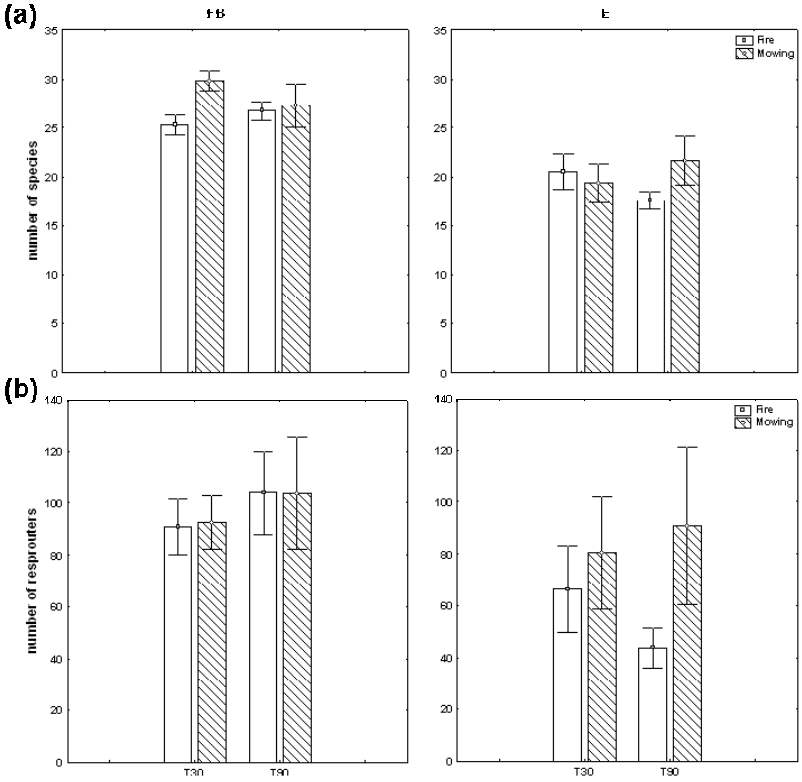

Fig 3. **(a)** – Number of species and **(b)** – number of resprouters (ramets) recruited in sites FB (frequently burned) and E (excluded since six years) in plots under different treatments: fire (open bars) and mowing (dashed bars). Points illustrate means ± 1SE. Asterisks mean significant differences ($p \leq 0.05$) between treatments (fire and mowing) at different times of observation, based on randomization testing.

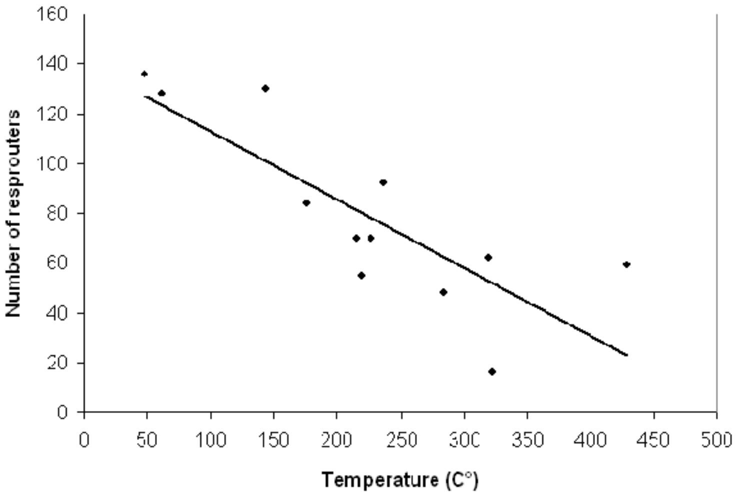

Fig 4. Relation between fire temperatures at soil level (°C) and number of recruited resprouters (ramets) after fire experiments (T30 and T90) in plots in *Campos* grasslands in southern Brazil. Pearson´s correlation $r = -0.78$, $p = 0.0023$, based on randomization testing.

In burned plots, nearly all plants flowering resprouted after experiments (98.5% in area FB and 100% and area E). In mowed plots, 90% of plants flowering resprouted after biomass removal in site E, whilst only 57.5% showed new stems in site FB.

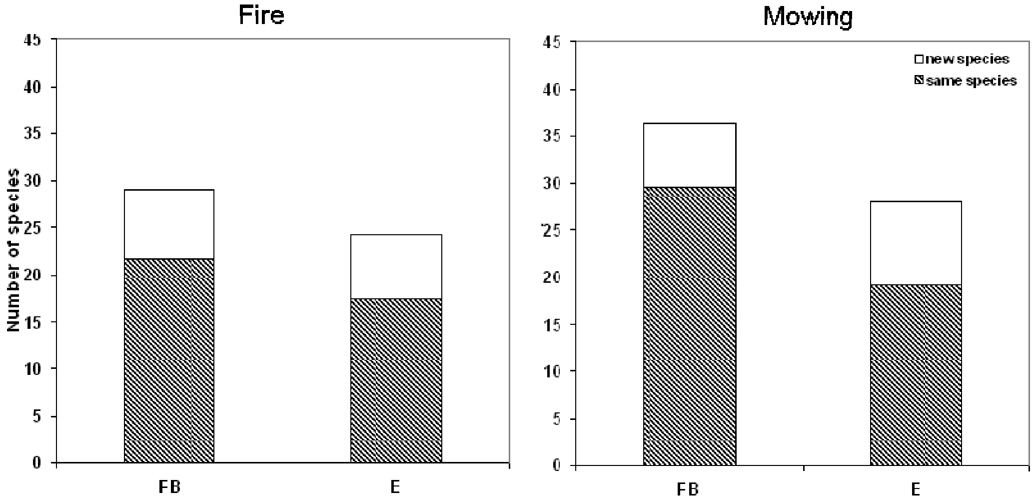

Fig 5. Number of new (open) and same species (dashed bars) of resprouters in sites FB (frequently burned) and E (excluded since six years) under different treatments: fire and mowing in Brazilian *Campos* grasslands.

Functional groups

Significant differences were observed for functional groups, both with seedlings and resprouters. More species of graminoids were recruited at T30 in burned plots in area FB than in mowed ones (p = 0.05, Table 1). At T90, more forb species were found in burned than in mowed plots in frequently burned areas (p = 0.02). More shrub species tended to be present at T360 in mowed plots. Interactions between area and treatment could be found only for graminoids (p = 0.04).

As showed in Table 1, significant differences could only be found for the number of forb and graminoid species with resprouters at T30. More forb and graminoid species with resprouters were observed in mowed plots in site FB than E (p = 0.003 and p = 0.01, respectively). No significant differences could be found at T90 (p > 0.05). Moreover, no interactions between site and treatment could be found for functional groups (p > 0.05), only for graminoid resprouters (site x treatment, p = 0.04). More species with seedlings were found in burned plots at T30 for both graminoids (p = 0.05). At T90, more forb seedling species were observed in burned than in mowed plots (p = 0.02). Moreover, interaction between site and treatment was found for forb seedling species (p = 0.02).

Table 1. Number of species of seedlings and resprouters (mean±SE) for the different functional groups (graminoids, forbs and shrubs) in different areas (FB – frequently burned and E – excluded since six years) under different treatments (fire and mowing) after 30 (T30), 90 (T90) and 360 days (T360) in Brazilian subtropical grasslands. An asterisk means significant differences between treatments (in columns, p ≤ 0.05) and small letters, between areas for each functional group and time (in rows, p ≤ 0.05), based on randomization testing.

Time	Site	Fire			Mowing		
		Graminoids	Forbs	Shrubs	Graminoids	Forbs	Shrubs
Seedling							
T30	FB	1.86±0.59	3.0±0.93	0±0	1.14±0.0.55*	1.57±0.57	0.28±0.18
	E	0.67±0.33	1.17±0.65	0±0	0.17±0.17	0.17±0.17	0±0
T90	FB	1.14±0.55	1.43±0.48	0±0	0.14±0.14	0.14±0.14*	0.14±0.14
	E	0.43±0.2	0.43±0.3	0.43±0.3	0.5±0.22	0.17±0.17	0±0
T360	FB	0±0	0.2±0.2	0±0	0±0	0±0	1.0±0
	E	0±0	0±0	0.43±0.2	0±0	0±0	0±0
Resprouter							
T30	FB	11.86±0.51	11.71±1.11	1.71±0.29	12.57±0.72 a	15.29±1.23 a	2.0±0.31
	E	10.5±0.76	8.5±1.36	1.5±0.43	8.83±0.95 b	8.0±0.89 b	2.5±0.5
T90	FB	12.57±0.75	12.43±1.17	1.71±0.29	10.14±1.42	14.14±1.83	3.0±0.58
	E	8.57±0.75	7.43±0.81	1.57±0.48	8.17±1.01	10.67±2.12	2.83±0.6

The number of recruited seedlings and resprouters (ramets) also differed among functional groups. Forb seedlings were more recruited in burned than in mowed plots in frequently burned grasslands at T30 ($p = 0.02$, Fig. 6a). Both forb and shrub seedling recruitment tended to decrease with time in this site, independently of treatment ($p > 0.05$).

However, in excluded sites, there was a drastic increase in number of recruited seedlings of shrubs after one year of experiments for both treatments (Fig. 6b). Resprouters showed an opposite tendency: there was an increase in number of resprouters after 90 days of experiments for forbs both in burned and mowed plots at site FB (no significant differences between treatments, Fig. 6c). In excluded sites, there was a light decrease in number of recruited resprouters for shrubs (both treatments) and forbs (burn treatment). Nevertheless, forb resprouters in mowed plots tended to increase in number after 90 days ($p > 0.05$, Fig. 6d).

Discussion

Seedling or resprouter?

Our results show a clear strategy of plants in *Campos* grasslands in Brazil: after biomass removal (both by fire and mowing), there is a pulse of plant recruitment, mostly by resprouting (ca. 90% of all species). Such strategy is of crucial importance for all functional groups: graminoids, forbs and shrubs. Even species that were flowering before fire experiments, successfully resprouted. Other species resprouted and showed flowers after less than three months (Fidelis & Blanco, in preparation).

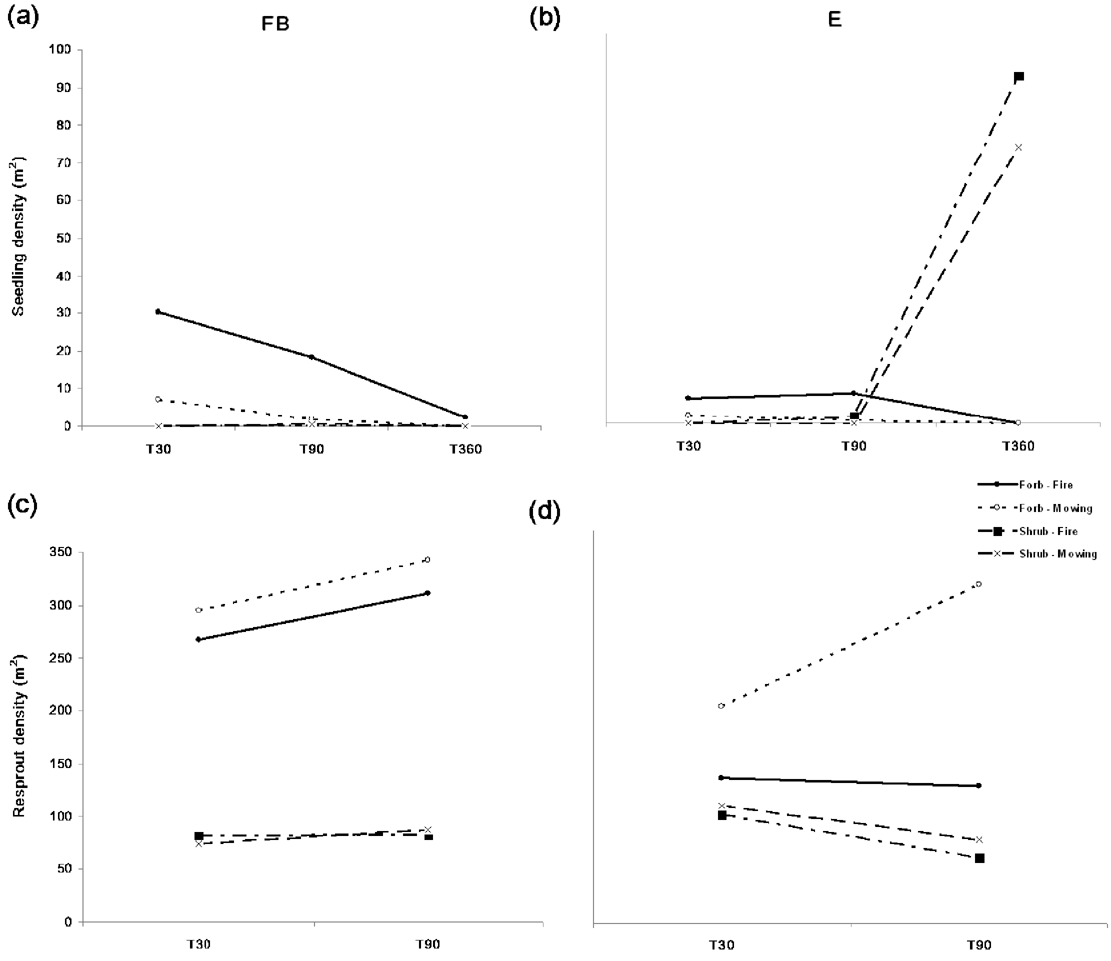

Fig 6. Density of seedlings (a,b) and resprouters (c,d) in frequently burned (FB) and excluded grasslands (E) under fire and mowing treatments after 30 (T30), 90 (T90) and 360 days (T360) after experiments in southern Brazil.

Three species showed to be obligate seeders in our study: two shrubs (*Heterothalamus psiadioides* and *Baccharis leucopappa*) and one forb (*Gamochaeta americana*). All graminoid species resprouted after biomass removal, some of them flowering after one month of experiments (*Leptocoryphium lanatum*, *Briza subaristata*, Fidelis & Blanco, in preparation). Müller (2005) studied the woody vegetation at the same study area and pointed four shrubs that could not resprout after fire events: *Baccharis dracunculifolia, Croton nitriariaefolium, Croton thermarum* and *Heterothalamus psiadioides* (from a total of 22 grassland woody species). Safford (2001) also found only two obligate seeder species (*Croton migrans* and *C. chloroleucus*, woody species) for highland grasslands under influence of fire in Brazil. Menges & Kohfeldt (1995) found in Florida scrub vegetation that 16% of woody and 11% of herbaceous species were obligate seeders.

Unfortunately, few studies were conducted with forbs in Brazilian grasslands and thus, almost no information about number of seeder and resprouter species is available. Overbeck and Pfadenhauer (2007) observed two forb species, which could not resprout after fire: *Evolvulus sericeus* and *Dichondra sericea*. However, in our study, we found both seedlings and resprouters of these species and therefore, they should not be classified as obligate seeders but as facultative resprouters.

According to Keeley and Zedler (1978), longer intervals of fire would favour seeder species. However, seedlings are only able to establish after long intervals of fire if there is a permanent dormant seed bank, as well as diaspore pools in neighbouring vegetation. And even if a soil seed bank is present, in general, few seedlings will be recruited after fire. Seedling recruitment would depend on the right depth (Auld and Denham 2006): they should be deep enough to avoid destruction and at the same time, not so deep in order to be able to emerge (Keeley 1992). There are no studies about seed bank dynamics in relation to fire frequency in southern Brazil. Nevertheless, studies about fire exclusion in *Campos* grasslands have demonstrated the colonization of grassland and forest woody species (shrubs and trees) into the grassland matrix (Müller *et al.* 2007; Oliveira and Pillar 2004). Most of these dominant shrubs are obligate seeders, such as *Baccharis uncinella*, *Heterothalamus psiadioides* and *Baccharis dracunculifolia*.

The high pulse of seedling recruitment in excluded areas after one year of experiments could be clearly observed in Fig. 5. All shrub seedlings at T360 in excluded sites belonged to obligate seeder species (*Heterothalamus psiadioides* and *Baccharis leucopappa*). Fidelis et al. (Chapter 3) hypothesized that seedlings of *H. psiadioides* were not recruited from the seed bank, but from diaspores coming from neighbouring plants. Carrington (1999) showed that post fire seedling establishment in sand pine scrub was more influenced by the location of adult plants than post fire microsite patterns, corroborating with observations of other authors about the importance of the presence of adult individuals from the same species for seedling recruitment (Bond *et al.* 1984a; Keeley 1992; Lloret 1998). *H. psiadioides* populations at grasslands of granitic hills are commonly found as gathered patches (Rambo 1954), so that patterns of seedling establishment may be more influenced by the location of adult plants than exclusively from site availability.

Besides the high seedling recruitment of obligate seeder shrubs after one year, most seedlings established just after experimental burning or mowing (T30), showing no significant differences of number of established seedlings between treatments (fire and mowing). In general, a decrease in recruited seedlings could be observed (except for shrubs in excluded areas) after initial post fire period. Recruitment of facultative and obligate seeder species occur principally during the first one or two years after fire (Moreno and Oechel 1991; Stokes *et al.*

2004). Several authors have already indicated factors influencing seedling recruitment in post fire conditions, such as increased availability of nutrients (Rice 1993; Wrobleski and Kauffman 2003), light (Wrobleski and Kauffman 2003), higher soil temperatures (Auld and Denham 2006; Hoffmann 1996; Knox and Clarke 2006; Tyler 1995), more availability of gaps (Bond and van Wilgen 1996), less herbivory (Bond and van Wilgen 1996; Tyler 1995) and changes in competitive hierarchies (Laterra and Solbrig 2001; Marcos *et al.* 2004; Tyler 1995).

Many species have dormant seeds and germination is triggered by exposition of high temperatures (González-Rabanal and Casal 1995; Hanley and Fenner 1998; Hanley and Lamont 2000; Martin *et al.* 1975; Roy and Sonié 1992; Tarrega *et al.* 1992). Both smoke and higher soil temperatures due to higher solar exposition would break seed dormancy of many species (Auld and Denham 2006; Hoffmann 1996; Knox and Clarke 2006; Tyler 1995), leading to a pulse of seedling recruitment. Nonetheless, germination experiments using heat shock treatment to break seed dormancy showed that several grassland species in southern Brazil show neither germination enhancement nor seed death after exposition to higher temperatures (Fidelis *et al.* 2007; Overbeck *et al.* 2006b). However, these studies were conducted mostly with grasses and Asteraceae species. Further experiments with other species (e.g. Leguminosae) should be carried out in order to verify the influence of fire on germination responses in *Campos* grasslands in southern Brazil.

The most interesting result of our study is the establishment of new species, mostly in burned plots. Fire removed more successfully dominant species, which may have prevented the establishment of new species before. In addition, burned plots had more gaps available and the input of nutrients after fire may have offered better conditions for seedling establishment than in mowed plots. Seedlings may have originated from both seed bank and seed rain from neighbouring plants, since many species show seeds with dispersal appendices (several graminoids and Asteraceae species), being able to reach newly open microsites. Bond and van Wilgen (1996) proposed the gap-availability hypothesis, which relates the increased seedling establishment with a higher availability of open sites. Indeed our results show a weak correlation between number of seedlings and bare soil cover ($r = 0.28$). Although other studies showed no relation of gaps and seedling establishment (Hoffmann 1996; Lloret 1998) or even the necessity of a nurse plant for seedling recruitment to occur (Keeley 1992), the recruitment of new species via seedling in *Campos* grasslands may be related to a higher availability of newly open microsites with better conditions for plant establishment and, in addition, better competition and nutrient conditions in post fire environment.

Resprouters have several advantages in post fire environments over seedlings, such as presence of protected and/or belowground buds, allowing them to resprout rapidly after biomass removal (Bond and van Wilgen 1996; James 1984), presence of storage organs which permit resource allocation for regrowth (Bellingham and Sparrow 2000; Bond and Midgley 2001; Verdú 2000), faster growth (Bond and Midgley 2001; Bond and van Wilgen 1996), competitive benefit (Vesk and Westoby 2004), rapidly recovery of reproductive capacity (Bond and van Wilgen 1996), buffering of disturbance effects (Bond and Midgley 2001), no dependence on seedling recruitment from a dormant seed bank or seed rain (Bond and Midgley 2001), a better water status (Clemente et al. 2005), guarantee plant persistence in disturbed environments (Ojeda *et al.* 2005; Vesk and Westoby 2004) and finally the maintenance of current generation (Bellingham and Sparrow 2000) and current niche. Although most studies associated resprouting events to disturbance (mostly to fire events), Keeley (1992) observed that resprouting in chaparral vegetation is a continuous process and populations of woody species restore their canopies with new resprouts in the absence of disturbance.

As already mentioned above, most species from *Campos* grasslands in southern Brazil have the ability to resprout after biomass removal, independently of functional groups or treatment (fire or mowing). Bond (2004) and Vesk et al (2004) mentioned grasses as the most fire-resistant component in plant communities, due to their high ability to resprout. In our study, all graminoid species (mainly caespitose species and some few with rhizomes) resprouted after fire and mowing. Some of them, such as *Aristida flaccida, Stipa filiculmis* and *Briza subaristata* were in reproductive phase by the time of experiments (the two last species already at the end of fruiting phase) and all of them resprouted already after one month of biomass removal (pers. obs.). Some individuals of *B. subaristata, Aristida laevis* and most of the individuals of *Leptocoryphium lanatum* and *Andropogon selloanus* showed inflorescences after 30 days of experiments, mostly in burned plots (Fidelis & Blanco, in preparation). All above cited species are caespitose grasses. Although these species do not have a storage organ (e.g. rhizome), caespitose grasses can accumulate nutrients in soil just beneath clones ("nutrient islands", Briske and Derner 1998; Derner and Briske 2001; Derner *et al.* 1997). Thus, caespitose species may have the ability to rapidly use nutrients accumulated in soil and available after fire to allocate for growth and fast reproductive recovery. This strategy gives caespitose graminoids an advantage in post fire colonization and explains the successful establishment of species with this strategy in *Campos* grasslands.

Forb and shrub resprouting is also associated to the presence of storage organs and resource allocation from these organs to plant growth and reproduction (Canadell and López-Soria 1998). Fidelis et al. (Chapter 2) found a high diversity of belowground organs in burned grasslands, which decreased the longer the interval of fire was. Such belowground organs bear numerous buds (as for example xylopodium), from where stems are recruited after biomass removal.

Fidelis et al. (Chapter 2) showed the crucial importance of the belowground bud bank for vegetation regeneration in *Campos* grasslands under different managements. The longer the interval of fire, the lower the density of belowground buds was. Most of buds found in the belowground bud bank belonged to forbs and shrubs, having the graminoid a low contribution. Shrubs resprouted exclusively from belowground buds (not from epicormic buds), forbs from both above- and belowground bud bank, whilst most graminoids resprouted from aboveground buds, protected by leaf sheaths in the crown, just above soil level. New graminoid species could also be observed resprouting in some plots. Since only live plants were identified, many of these “new” species were already there (mostly in site FB), but “dead” and fire may have stimulated resprouting.

As showed by our results, the number of resprouters was higher in mowed plots in excluded grasslands. Vesk et al (2004) found little effects of differences of clipping and burning treatments applied on species with weak and strong ability to resprout, only in intermediate. In excluded sites, fire intensity was the highest, as well as fire temperatures. Number of resprouts correlated negatively to fire temperature. Although fire temperatures above 60°C are known to be lethal for plants (Whelan 1995), fire intensity seems to be more relevant to tissue death (Bova and Dickinson 2005) found a relation between fire intensity and tissue death. The higher temperatures in excluded sites may have lead to meristematic tissue death, hindering the formation of new buds and/or the formation of new stems from these buds. Therefore, we suggest that fire temperature and subsequent death of meristematic tissue was the most important factor influencing recruitment of resprouters in excluded sites.

Other studies already showed the great importance of resprouters in vegetation regeneration after fire events. Benson & Hartnett (2006) found less than 1% of seedling recruitment in tallgrass prairie. The dominance of resprouters was also observed in other ecosystems, as for example short forests in South Africa (Kruger *et al.* 1997), Brazilian highland grasslands (Safford 2001), cerrado vegetation in Brazil (Coutinho 1982), grass páramos in Ecuador (Ramsay and Oxley 1996) and temperate grasslands in Australia (Morgan 1999).

What really matters for post fire plant community?

The absence of disturbance would lead to shrub encroachment and consequently, loss of grassland plant diversity and physiognomy. On the other hand, the use of management would imply biomass removal and changes in vegetation structure.

Overbeck et al. (2005; 2006a) showed that the absence of fire in *Campos* grasslands leads to a loss of grassland species. However, it is a very polemic issue in Brazil, being governmental authorities and even some scientists against the use of fire as a management tool. Therefore, mowing could be considered as an alternative.

Our results showed that fire has an important role on vegetation diversity and dynamics. It promoted not only resprouting from belowground bud bank, but also the recruitment of new species (mostly seedlings) colonizing newly open areas. Several factors may be involved in this process, such as a more successful removal of competitors and litter (Fidelis *et al.*, Chapter 5), stimulation of germination from seed bank, stimulation of new buds development and consequently, new stems, higher input of nutrients and thus, higher germination and resprouting rates.

Longer interval of fires in *Campos* grasslands leads to higher fire temperatures and fire intensities (Fidelis et al., submitted). Most studies about fire and vegetation regeneration already pointed out not only the direct influence of fire frequency, but also of fire season on plant ability to resprout and on seedling recruitment in different ecosystems (Bond and van Wilgen 1996; Bond *et al.* 1984b; Gibson 1988; Hodgkinson 1991; Hoffmann 1999; Knox and Clarke 2006; Naveh 1975; Whelan 1995). Unfortunately, less is known about the effects of fire season in Brazilian *Campos* grasslands and more studies are needed in order to provide better scientific subsidies for conservation biologists to elaborate management plans. Even though there are still several constraints about the use of fire as a management tool to maintain grasslands biodiversity, its use should be further investigated.

Due to their great ability of re-colonisation of post fire environment, mainly by resprouting, *Campos* grasslands in southern Brazil showed to be resilient to fire events. Several species showed to be well adapted to post fire environmental, with presence of storage and bud-bearing belowground structures, regenerating rapidly from above- (graminoids) and belowground buds (most forbs and shrubs). Seedling recruitment, despite its low contribution, occurred and showed to be important for the increase of plant diversity in post fire community and to maintain genetic variability in plant community.

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References

Aguiar L. W., Martau L., Soares Z. F., Bueno O. L., Mariath J. E. & Klein R. M. (1986) Estudo preliminar da flora e vegetação de morros graníticos da Região da Grande Porto Alegre, Rio Grande do Sul, Brasil. Iheringia 34, 3 - 38.

Auld T. D. & Denham A. J. (2006) How much seed remains in the soil after a fire? Plant Ecology 187, 15-24.

Behling H., Pillar V. D., Müller S. C. & Overbeck G. E. (2007) Late-Holocene fire history in a forest-grassland mosaic in southern Brazil: implications for conservation. Applied Vegetation Science 10, 81-90.

Bellingham P. J. & Sparrow A. D. (2000) Resprouting as a life history strategy in woody plant communities. Oikos 89, 409-16.

Benson E. J. & Hartnett D. C. (2006) The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. Plant Ecology 187, 163-77.

Boldrini I. I. (1997) Campos do Rio Grande do Sul: caracterização fisionômica e problemática ocupacional. Boletim do Instituto de Biociências da Universidade Federal do Rio Grande do Sul 56, 1 - 39.

Bond W. J. (2004) Fire. In: Vegetation of Southern Africa (eds R. M. Cowling, D. M. Richardson and S. M. Pierce) pp. 421-46. Cambridge University Press, Cambridge.

Bond W. J. & Keeley J. E. (2005) Fire as a global "herbivore": the ecology and evolution of flammable ecosystems. Trends in Ecology and Evolution 20, 387-94.

Bond W. J. & Midgley J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. Trends in Ecology and Evolution 16, 45-51.

Bond W. J. & van Wilgen B. W. (1996) Fire and plants. Chapman ¨Hall, London.

Bond W. J., Vlok J. & Viviers M. (1984a) Variation in seedling recruitment of Cape proteaceae after fire. Journal of Ecology 72, 209-21.

Bond W. J., Vlok J. & Viviers M. (1984b) Variation in seedling recruitment of Cape Proteaceae after fire. Journal of Ecology 72, 209-21.

Bova A. S. & Dickinson M. B. (2005) Linking surface-fire behavior, stem heating, and tissue necrosis. Canadian Journal of Forest Research 35, 814 - 22.

Briske D. D. & Derner J. D. (1998) Clonal biology of caespitose grasses. In: Population biology of grasses (ed G. P. Cheplick) pp. 107-35. Cambridge University Press, Cambridge.

Canadell J. & López-Soria L. (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Functional Ecology 12, 31-8.

Carrington M. E. (1999) Post-fire seedling establishment in Florida sand pine scrub. Journal of Vegetation Science 10, 403-12.

Clemente A. S., Rego F. C. & Correio O. A. (2005) Growth, water relations and photosynthesis of seedlings and resprouts after fire. Acta Oecologica 27, 233-43.

Coutinho L. M. (1982) Ecological effects of fire in Brazilian Cerrado. In: Ecology of tropical savannas (eds B. J. Huntley and B. H. Walker) pp. 273-91. Springer Verlag, Berlin.

Cowling R. M., Richardson D. M. & Mustart P. J. (2004) Fynbos. In: Vegetation of Southern Africa (eds R. M. Cowling, D. M. Richardson and S. M. Pierce) pp. 99-130. Cambridge University Press, Cambridge.

Derner J. D. & Briske D. D. (2001) Below-ground carbon and nitrogen accumulation in perennial grasses: a comparison of caespitose and rhizomatous growth forms. Plant and Soil 237, 117-27.

Derner J. D., Briske D. D. & Boutton T. W. (1997) Does grazing mediate soil carbon and nitrogen accumulation beneath C4, perennial grasses along an environmental gradient? Plant and Soil 191, 147-56.

Fidelis A., Müller S. C., Pillar V. D. & Pfadenhauer J. (2007) Efeito de altas temperaturas na germinação de espécies dos Campos Sulinos. Revista Brasileira de Biociências 5, 354-6.

García-Martinez P. (2005) Caracterización química y física de los suelos del Morro Santana (Porto Alegre, Rio Grande do Sul, Brasil). In: Chair of Soil Sciences. Technische Universität München, Freising-Weihenstephan, Germany.

Gibson D. J. (1988) Regeneration and fluctuation of tallgrass prairie vegetation in response to burning frequency. Bulletin of the Torrey Botanical Club 115, 1-12.

Gignoux J., Clobert J. & Menaut J.-C. (1997) Alternative fire resistance strategies in savanna trees. Oecologia 110, 576 - 83.

González-Rabanal F. & Casal M. (1995) Effect of high temperatures and ash on germination of ten species from gorse shrubland. Vegetatio 116, 123-31.

Hanley M. E. & Fenner M. (1998) Pre-germination temperature and the survivorship and onward growth of Mediterranean fire-following plant species. Acta Oecologica 19, 181-7.

Hanley M. E. & Lamont B. B. (2000) Heat pre-treatment and the germination of soil- and canopy-stored seeds of south-western Australian species. Acta Oecologica 21, 315-21.

Hodgkinson K. C. (1991) Shrub recruitment response to intensity and season of fire in a semi-arid woodland. Journal of Applied Ecology 28, 60-70.

Hoffmann W. A. (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. Journal of Ecology 84, 383 - 93.

Hoffmann W. A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. Ecology 80, 1354 - 69.

James S. (1984) Lignotubers and burls - their structure, function and ecological significance in Mediterranean ecosystems. The Botanical Review 50, 225-66.

Keeley J. E. (1992) Recruitment of seedlings and vegetative sprouts in unburned chaparral. Ecology 73, 1194-208.

Keeley J. E. & Zedler P. H. (1978) Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. The American Midland Naturalist 99, 142-61.

Klein R. M. (1975) Southern Brazilian phytogeographic features and the probable influence of upper Quaternary climatic changes in the floristic distribution. Boletim Paranaense de Geociências 33, 67 - 88.

Knox K. J. E. & Clarke P. J. (2006) Fire season and intensity affect shrub recruitment in temperate slerophyllous woodlands. Oecologia 149, 730-9.

Kruger L. M., Midgley J. J. & Cowling R. M. (1997) Resprouters vs reseeders in South African forest trees; a model based on forest canopy height. Functional Ecology 11, 101-5.

Laterra P. & Solbrig O. T. (2001) Dispersal strategies, spatial heterogeneity and colonization success in fire-managed grasslands. Ecological Modelling 139, 17-29.

Livi F. P. (1999) Elementos do clima: o contraste de tempos frios e quentes. In: Atlas ambiental de Porto Alegre (eds R. Menegat, M. L. Porto, C. C. Carraro and L. A. D. Fernandes) pp. 73 - 8. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre.

Lloret F. (1998) Fire, canopy cover and seedling dynamics in Mediterranean shrubland of northeastern Spain. Journal of Vegetation Science 9, 417-30.

Manly B. F. J. (2007) Randomization, bootstrap, and Monte Carlo methods in biology. Chapman & Hall/CRC, Boca Raron.

Marcos E., Tárrega R. & Luis-Calabuig E. (2004) Interactions between mediterranean shrub species eight years after experimental fire. Plant Ecology 170, 235 - 41.

Martin R. E., Miller R. L. & Cushwa C. T. (1975) Germination response of legume seeds subjected to moist and dry heat. Ecology 56, 1441-5.

Menges E. S. & Kohfeldt N. (1995) Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club 122, 282-97.

Moreno J. M. & Oechel W. C. (1991) Fire intensity effects on germination of shrubs and herbs in Southern California chaparral. Ecology 72, 1993-2004.

Morgan J. W. (1999) Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. Plant Ecology 144, 127-44.

Müller S. C. (2005) Padrões de espécies e tipos funcionais de plantas lenhosas em bordas de floresta e campo sob influência do fogo. In: Department of Ecology p. 135. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Müller S. C. & Forneck E. D. (2004) Forest-grassland mosaics in the hills of Porto Alegre: a study case of forest expansion patterns in Santana hill, Rio Grande do Sul, Brazil. In: Workshop Proteção e manejo da vegetação natural da região de Porto Alegre com base em pesquisas de padrões e dinâmica da vegetação (ed M. D. Porto) pp. 29-37. UFRGS, PPG Ecologia, Porto Alegre.

Müller S. C., Overbeck G. E., Pfadenhauer J. & Pillar V. D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. Plant Ecology 189, 1-14.

Naveh Z. (1975) The evolutionary significance of fire in the Mediterranean region. Vegetation 29, 199-208.

Ojeda F., Brun F. G. & Vergara J. J. (2005) Fire, rain and the selection of seeder and resprouter life-histories in fire-recruiting, woody plants. New Phytologist 169, 155-65.

Oliveira J. M. & Pillar V. D. (2004) Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. Community Ecology 5, 197-202.

Overbeck G. E., Müller S. C., Fidelis A., Pfadenhauer J., Pillar V. D., Blanco C., Boldrini I. I., Both R. & Forneck E. D. (2007) Brazil´s neglected biome: the Southern Campos. Perspectives in Plant Ecology and Systematics 9, 101-16.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. Journal of Vegetation Science 16, 655-64.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006a) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. Brazilian Journal of Biology.

Overbeck G. E., Müller S. C., Pillar V. D. & Pfadenhauer J. (2006b) No heat-stimulated germination found in herbaceous species from burned subtropical grassland. Plant Ecology 184, 237-43.

Pillar V. D. (2005) MULTIV: Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Pillar V. D. & Orlóci L. (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. Journal of Vegetation Science 7, 585 - 92.

Rambo B. (1954) Análise histórica da Flora de Porto Alegre. Sellowia 6, 9-169.

Ramsay P. M. & Oxley E. R. B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. Vegetatio 124, 129-44.

Rice S. K. (1993) Vegetation establishment in post-fire Adenostoma chaparral in reltion to fine-scale pattern in fire intensity and soil nutrients. Journal of Vegetation Science 4, 115-24.

Roy J. & Sonié L. (1992) Germination and population dynamics of Cistus species in relation to fire. Journal of Applied Ecology.

Safford H. D. (2001) Brazilian Páramos. III. Patterns and rates of postfire regeneration in the campos de altitude. Biotropica 33, 282 - 302.

Stokes K. E., Allchin A. E., Bullock J. M. & Watkinson A. R. (2004) Population responses of Ulex shrubs to fire in a lowland heath community. Journal of Vegetation Science 15, 505 - 14.

Tarrega R., Calvo L. & Trabaud L. (1992) Effect of high temperatures on seed germination of two woody Leguminosae. Vegetatio 102, 139-47.

Tyler C. M. (1995) Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. Journal of Ecology 83, 1009-20.

Verdú M. (2000) Ecological and evolutionary differences between Mediterranean seeders and resprouters. Journal of Vegetation Science 11, 265-8.

Vesk P. A., Warton D. I. & Westoby M. (2004) Sprouting by semi-arid plants: testing a dichotomy and predictive traits. Oikos 107, 72-89.

Vesk P. A. & Westoby M. (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. Journal of Ecology 92, 310-20.

Whelan R. J. (1995) The ecology of fire. Cambridge University Press, Cambridge.

Wrobleski D. W. & Kauffman J. B. (2003) Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. Restoration Ecology 11, 82-90.

Chapter 5

SHORT-TERM CHANGES CAUSED BY FIRE AND MOWING IN BRAZILIAN *CAMPOS* GRASSLANDS

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(T0, T30, T360)

Abstract: Disturbance is an important factor maintaining plant diversity and physiognomy of grasslands in southern Brazil. However, few are the studies about effects of fire and mowing on vegetation regeneration and dynamics in *Campos* grasslands. Therefore, we aim to evaluate short-term changes caused by fire and moing on grassland structure and dynamics, as well as to analyze changes in vegetation and functional groups cover and diversity in post disturbance communities. Seven plots were established in different sites on Morro Santana (Porto Alegre, southern Brazil): frequently burned (FB) and excluded from disturbance since six years (E) for each treatment: fire and mowing (total of 28 plots). Before treatments, bare soil and litter cover were visually estimated. Vegetation relevés were conducted and plants were identified and had as well their cover estimated. Later, plants were grouped according to their functional group (graminoids, forbs and shrubs) for statistical analyses. Moreover, stems of forbs and shrubs were counted. Treatments were performed in summer and observations were conducted after 30, 90 and 360 days. The most important effect of treatments was the removal of litter and consequently, increase in bare soil cover mostly by fire. Burned plots always showed a higher percentage of bare soil, whilst mowed plots had higher litter cover. Fire enhanced graminoids and forbs, but did not affect shrubs. There was an abrupt change in species cover and compomsition in burned plots in site FB, whilst in mowed plots the greatest changes occurred in sites E. Species turnover was very high, mainly in mowed plots in site E. After one year, species diversity in burned plots was still lower in sites FB, but the same in sites E. In mowed plots, number of species was still lower after one year of treatmens in both sites. As a conclusion, the most important short-term effect after biomass removal, principally from fire, was the removal of litter and consequently opening of gaps. It stimulated vegetation regeneration and provided microsites for the establishment of new species.

Keywords: disturbance, vegetation regeneration, functional groups, subtropical grasslands, fire intensity

Introduction

Campos are subtropical grasslands located in the southernmost State of Brazil. It is an extension of the Uruguayan and Paraguayan grasslands and Argentinean Pampa (Cabrera and Willink 1973; Pallarés *et al.* 2005). It is a very species rich ecosystem, with about 3000 plant species (Boldrini 1997). These grasslands are composed by an association of C_4 (e.g. *Andropogon* spp., *Aristida* spp., *Axonopus* spp.) and C_3 grasses (e.g. *Briza* spp., *Piptochaetium* spp., *Stipa* spp.) and a species rich forb component combined with dwarf shrubs (Asteraceae, Leguminosae, Rubiaceae, Boldrini 1997; Overbeck *et al.* 2007; Pallarés *et al.* 2005).

The Brazilian *Campos* grasslands dynamics and ecology is closely associated with management. The maintenance of plant diversity and physiognomy are dependent on disturbance events (e.g. fire and grazing), since there are no markedly seasonal climate fluctuations (Overbeck *et al.* 2007). Exclusion can lead to shrub encroachment (Müller *et al.* 2007; Oliveira and Pillar 2004) and consequent changes in vegetation composition.

Fire has been present in *Campos* grasslands since ca. 7000 BP (Behling and Pillar 2007; Behling *et al.* 2004) and can also be considered as an important factor driving vegetation dynamics and diversity. Currently, fire is normally set by farmers at least every two years in order to stimulate resprouting of forage species and thus, improve pasture quality.

Plant responses to fire will depend on how and when they regenerate (Bond 2004). Vegetation responses are usually affected by fire season, frequency and intensity (Bond and van Wilgen 1996; Gibson 1988; Hodgkinson 1991; Hoffmann 1999; Knox and Clarke 2006; Naveh 1975; Slocum *et al.* 2003; Trollope 1982; Whelan 1995). One of the most important effects of fire in post-fire communities is the removal of litter, following the opening of gaps within the vegetation (Beckage and Stout 2000; Bond 2004; Bond and van Wilgen 1996; Hulbert 1969; 1988; Lloyd 1968), changes in dominance of species, decreasing thus competition (De Luis *et al.* 2006; Morgan and Lunt 1999; Noble and Slatyer 1980) and input of nutrients (Coutinho 1982; Debano and Conrad 1978; Rice 1993; Wilson and Shay 1990). The increase in temperature and solar radiation in newly open gaps (Hulbert 1988; Knapp 1984; Lloyd 1968) enhances seedling establishment and propagation of vegetative ramets.

Less than 1% of *Campos* grasslands are under legal protection (Overbeck *et al.* 2007). Moreover, following governmental policy, areas in national parks should be completely excluded from disturbance. As a consequence, several areas under protection, which were previous grassland ecosystems, have already lost their physiognomy and diversity. Management of these grasslands is urgently needed in order to maintain plant diversity and vegetation dynamics. Unfortunately, few are the ecological studies conducted to evaluate vegetation responses to disturbance in *Campos* grasslands. Studies were usually carried out to analyze the effects of grazing on plant diversity and dynamics (e.g. Boldrini and Eggers 1996; Sosinski and Pillar 2004), but few are the studies about fire and mowing effects on vegetation dynamics (but see Eggers and Porto 1994; Müller *et al.* 2007; Overbeck *et al.* 2005).

Therefore, we aim to 1) evaluate short-term changes caused by fire and mowing on grassland vegetation structure, and 2) analyze changes in vegetation and functional groups (graminoids, forbs and shrubs) cover and diversity in post-fire community.

Material and Methods

Study area

This study was carried out in the southernmost state in Brazil (Rio Grande do Sul), where grassland physiognomies (*Campos* grasslands) occupies nearly 23 % of the total area (Overbeck *et al.* 2007). The study area is located on the top of Morro Santana Hill, which belongs to a chain of granitic hills in Porto Alegre (30°03' S, 51°07' W; 311 m a.s.l.). Soils are dystrophic red-yellow argisols, corresponding to acrisols, alisols and umbrisols (according to FAO classification, García-Martinez 2005) and the climate is subtropical humid (Köppen classification Cfa), with mean temperatures of 22°C and precipitation of 1350 mm/year (Livi 1999). Grasslands are situated at the top and northern slopes of the hill (Aguiar *et al.* 1986), forming a mosaic with Atlantic forest. Local flora of grasslands is very rich. Overbeck et al. (2006a) listed 201 plant species, mostly Poaceae, Asteraceae, Leguminosae and Rubiaceae. Fire has been present in these grasslands at least since 1200 years according to paleaopalynological studies (Behling *et al.* 2007). They are at present mostly set by local people living in illegal settlements around the area, with return intervals of 2-5 years.

Two sites with different fire histories were chosen for the study: FB – frequently burned grasslands (last fire: two years before experiments) and E – exclusion of fire since six years. A continuous vegetation matrix, with several caespitose grasses, but still a high contribution of different forb species, characterizes the site FB. Shrubs are present at the site, but are short (not taller than 1 m). Site E, on the other hand, shows a high percentage of shrub cover, with individuals taller than 1 m. Caespitose grasses are still present with high percentage of dead biomass. There is an evident decrease in forb species and cover.

Vegetation survey

Seven pairs of plots (25 m^2 each, in both sites, FB and E) were established for each treatment: fire and mowing (total of 28 plots). Treatments were applied in summer (head fire, for more details about fire experiments and results, see Fidelis et al., submitted). In mowed plots, all aboveground vegetation was cut and removed as much as possible.

Within each plot, six continuous subplots (0.04 m^2 each) were established in the centre of each plot to avoid border effects. All species inside each subplot were identified and had their percentage cover visually estimated (in classes of 5 %, beginning with 1%). For shrubs and forbs, we also sampled the number of basal stems for each species. Species were later grouped according to their functional groups: graminoids, forbs and shrubs for further statistical analyses. In addition to species cover, bare soil and litter cover were also estimated. Due to an accidental fire, part of burned (two in FB site) and mowed plots (total of 10 plots) was destroyed before the end of observations, being not considered for statistical analyses. Since the aim of this study was to evaluate vegetation recover after disturbance, vegetation composition and structure at T0 were considered “control”. Evaluations were performed before treatments (T0), after 30 (T30), 90 (T90) and 360 days (T360).

Statistical analyses

Univariate and multivariate analysis of variance were performed in order to test statistical significance of differences in cover, number of stems, and species richness (total and for functional groups) according to sites (FB; E), treatments (fire or mowed) at the different times of observation (T0, T30, T90 and T360). Evenness was additionally calculated for each site and treatment (according to Smith and Wilson 1996). The test statistics was the sum of squares between groups computed from Euclidean distances (Pillar and Orlóci 1996). We used randomization testing in order to avoid the restricting distribution assumptions of conventional analysis of variance (for more details, see Manly 2007). Analyses were performed for each observation time, since our objective was to compare vegetation changes at each specific time between factors (site and treatment). Repeated measures are serially correlated, increasing rates for wrongly rejection of the null hypothesis (Gotelli and Ellison 2004). Exceptionally, to compare changes in vegetation structure before and after one year of treatments, we used repeated measures analysis (program Statistica 6.0).

To verify relationship between descriptors of plant community (cover, species richness, number of stems) of post-fire environmental conditions (at T30) and fire parameters (fire intensity, temperature at soil level, temperature at 50 cm and residence time of fire, data from Fidelis et al, submitted), we performed Pearson’s correlation and tested significance with randomization tests (10000 iterations).

Changes in vegetation through time was evaluated with trajectories, using ordination methods (Principal Coordinates Analysis, PCoA, for more details, see Podani 2000), with sampling units described by species cover at each time of observation. Resemblance measure used was Chord distance between sampling units.

All statistical analyses (except for repeated measures ANOVA) were performed by the software MULTIV 2.53 beta (Pillar 2008).

Results

Effects of fire and mowing on vegetation structure and diversity

Differences in bare soil and litter cover between burned and mowed plots were significant ($p \leq 0.05$). In excluded sites (E), bare soil cover showed no significant differences between treatments at any time of observation (Fig 1a). However, in frequently burned sites (FB), bare soil cover was significantly higher at T30 ($p = 0.0003$) and T90 ($p = 0.05$) in burned than in mowed plots. Litter showed an opposite tendency (Fig 1b): mowed plots had higher litter cover than burned ones. After one year, bare soil cover at site FB was the same as before treatments. In excluded sites, on the other hand, bare soil cover increased after fire ($F = 59.55$, $p = 0.0001$) and mowing experiments ($F = 20.48$, $p = 0.003$). Litter cover, however, was still lower after one year of treatments. No interaction between site and treatment could be found for soil and litter

Number of species showed a significant interaction between site and treatment ($p = 0.04$). In general, species richness was higher in frequently burned sites than in excluded ones ($p = 0.0001$, Fig 2a). However, in both sites, one can observe a decrease in number of species 30 days after experiments. Treatment did not show significant differences in site FB for any time of observation. Nevertheless, in site E, there was a larger number of species in burned plots at T30 and at T90 more species were observed in mowed ($p = 0.01$ and $p = 0.02$, respectively). In burned plots at site E, species richness increased with time, reaching nearly the same value after one year in excluded sites, but was still lower in frequently burned sites ($F = 6.36$, $p = 0.04$). In mowed plots after one year, the number of species was not the same, being lower in both sites ($F = 24.08$, $p = 0.002$ in site FB and $F = 26.07$, $p = 0.001$ in site E). Evenness differed between sites ($p = 0.02$, Fig 2b), but treatment did not affect it.

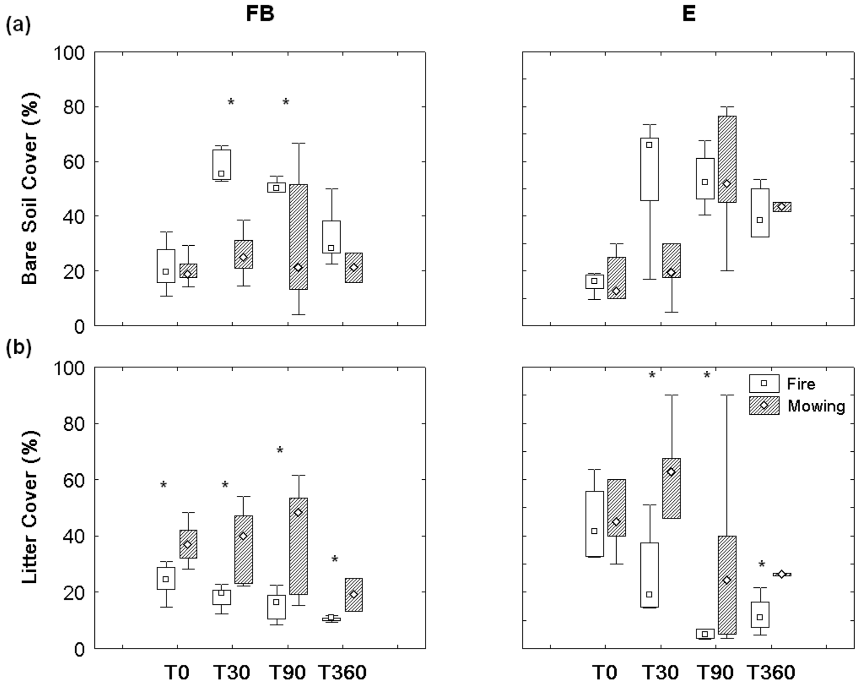

Fig 1. (a) - Bare soil and (b) - litter cover from frequently burned (FB) and grasslands excluded since six years (E) for two treatments (fire and mowing) and at different times: before experiments (T0), after 30 (T30), 90 (T90) and 360 days (T360). Asterisks mean significant differences ($p \leq 0.05$) between treatments, based on randomization testing. The squares between boxes represent the median, boxes 25%-interquartils, and the t-shaped lines the maximum and minimum values.

Vegetation dynamics after fire

After fire experiments, plots in frequently burned sites had more abrupt changes in species cover and composition, though returning to a similar condition after one year of experiments (Fig 3a). Plots in excluded sites, on the other hand, did not show such changes. *Waltheria douradinha* (r = -0.92), *Stipa melanosperma* (r = -0.89), *Eryngium horridum* (r = -0.88), and *Baccharis ochracea* (r = -0.88) showed the highest correlations to ordination Axis 1 and were more related to excluded sites (E). *Chamaechrista repens* (r = 0.9), *Eragrostis polythrica* (r = 0.87), *Paspalum plicatulum* (r = 0.86), and *Trachypogon montufari* (r = 0.85) were more related to frequently burned sites (FB). In mowed plots (Fig 3b), species pool was different in both sites even at T0, and thus also trajectories of vegetation change. The frequently burned site illustrated a different tendency showing a more gradual change in species composition when compared to the trajectory of burned plots of FB in Figure 3a. Plots in excluded sites also had a gradual change after mowing but an abrupt one after 90 days. Species with the highest correlation to Axis 1 were: *Eragrostis polythrica* (r = 0.97), *Polygala linoides* (r = 0.95), *Crotalaria tweediana* (r = 0.93), *Aspilia montevidensis* (r = 0.93) and *Richardia grandiflora* (r = 0.92).

Eupatorium ascendens (r = -0.73) correlated negatively to Axis 1, being more related to plots in excluded areas.

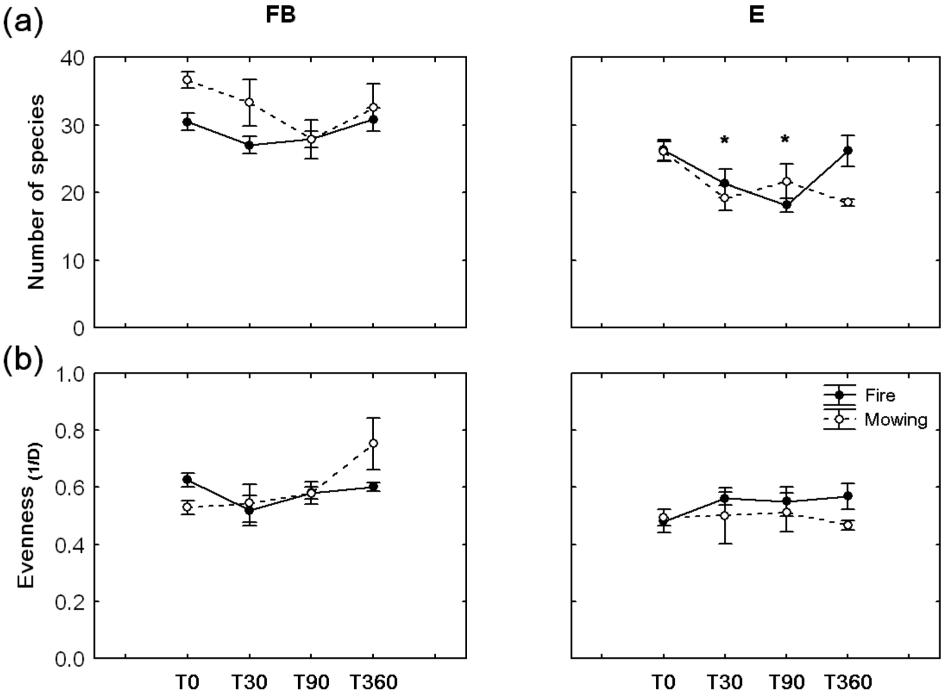

Fig 2. (a) - Species richness (number of species), and **(b)** - Evenness (1/D), in frequently burned (FB) and grasslands excluded since six years (E) for different treatments (fire and mowing) before treatment (T0), after 30 (T30), 90 (T90) and 360 days (T360). Asterisks mean significant differences ($p \leq 0.05$) between treatments, based on randomization testing. Markers are means ± 1SE.

These changes can be more clearly viewed in terms of species composition by comparing species turnover between sites under different treatments. Species turnover was high, mainly in excluded areas (Table 1). There was a lost of 33.28% of species in burned plots in site FB just after the treatment. The lost in mowed plots in the same site was nearly the same (29.95%). Same tendency could be observed in excluded sites (lost of 40.49% and 35.8 % in burned and mowed plots respectively). More new species were recruited in burned plots in both sites just after fire experiments (see Table 1). After one year, there was a lost of 27.7% and 34.8% in burned and mowed plots respectively in frequently burned sites. Excluded sites showed higher values of species lost: 32.68% (fire) and 55.77% (mowing). More new species established in burned plots in site FB (27.48% and 16.88%, burned and mowed plots respectively), whilst in excluded areas, more species recruited in mowed plots (44.44%) than in burned ones (29.16%). *Relbunium richardianum* disappeared from all plots, independently of treatment and site. *Gamochaeta americana* and *Hydrocotyle exigua* disappeared just after experiments and established again after one year. In frequently burned areas, *Baccharis* *leucopappa* did not establish after fire and mowing experiments and *Stylosanthes montevidensis* disappeared in mowed plots. In excluded areas, *Waltheria douradinha* could not re-establish after mowing experiments, as well as *Stevia aristata* after fire experiments.

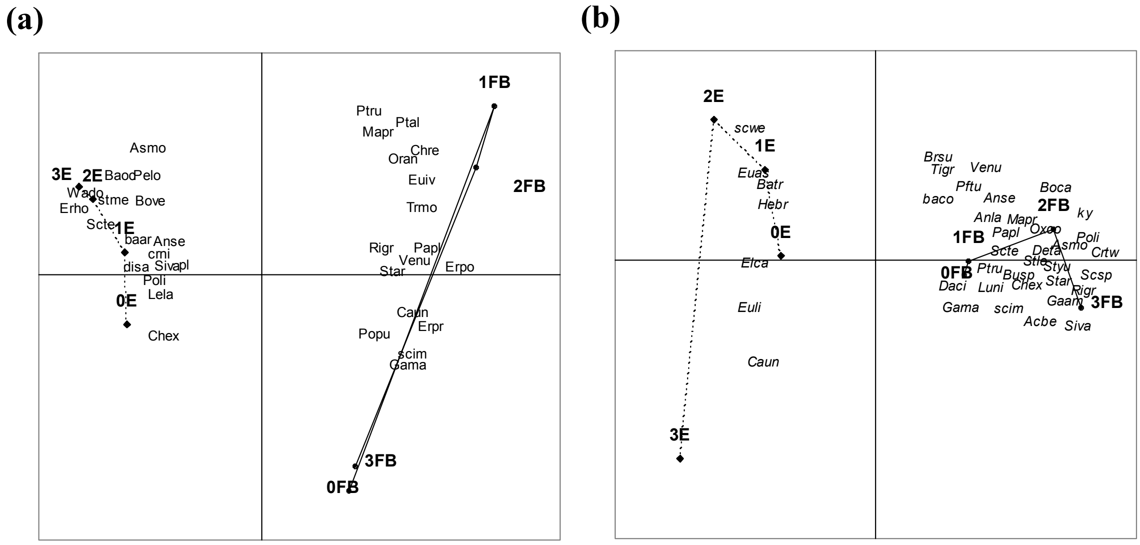

Fig 3. Ordination diagrams (PCoA) as trajectory types of sampling units at the different study sites: frequently burned (FB) and excluded since six years (E) before treatment (0), after 30 (1), 90 (2) and 360 days (3) in burned (a) and mowed plots (b). Resemblance measure used was chord distance between sampling units. Only species that correlated with some of the axes are showed (r ≥ 0.5): *Acbe – Acmella bellidioides, Anla – Andropogon lateralis, Anse – Andropogon selloanus, Asmo – Aspilia montevidensis, Baar – Baccharis articulata, Baco – Baccharis cognata, Baoc – Baccharis ochracea, Batr – Baccharis trimera, Boca – Borreria capitata, Bove – Borreria verticillata, Brsu – Briza subaristata, Busp - Bulbostylis sphaerocephala , Caun – Calea uniflora, Chex – Chaptalia exscapa, Chre – Chamaechrista repens, Crtw – Crotalaria tweediana, Daci – Danthonia cirrata, Deta – Desmanthus tatuhyensis, Disa – Dichanthelium sabulorum Elca – Elyonurus candidus, Erho – Eryngium horridum, Erpo – Eragrostis polythrica, Erpr – Eryngium pristis, Euas – Eupatorium ascendens, Euiv – Eupatorium ivaefolium, Euli – Eupatorium ligualefolium, Gaam – Gamochaeta americana, Gama – Galactia marginalis, Hebr – Helianthemum brasiliensis, ky – Kyllinga odorata, Lela – Leptocoriphyium lanatum, Luni – Lucilia nitens, Mapr – Macroptilium prostratum, Oran – Orthopappus angustifolius, Oxco – Oxalis conorrhiza, Papl – Paspalum plicatulum, Pelo – Peltodon longipes, Pftu – Pfaffia tuberosa, Poli – Polygala linoides, Popu – Polygala pumila, Ptal – Pterocaulon alocuperioideum, Rigr – Richardia grandiflora, Scim – Schizachyrium imberbe, Scsp – Schizachyium spicatum, Scte – Schizachyrium tenerum, Scwe – Schinus weinmanniaefolius, Siva – Sisyrinchium vaginatum, Star – Stevia aristata, Stle – Stylosanthes leiocarpa, Stme – Stipa melanosperma, Styu – Stipa yurgensis, Tigr – Tibouchina gracilis, Venu – Veronia nudiflora, Wado – Waltheria douradinha*

Galianthe fastigiata and *Pterocaulon rugosum* established after fire experiments in both study sites. These species were not present in these plots before experiments. In site FB, *Schizachyrium spicatum* and *Cliococca selaginoides* appeared after fire treatments, whilst *Borreria verticillata, Hypoxis decumbens* and *Peltodon longipes* recruited in plots in excluded sites. In mowed plots, *Baccharis articulata, Borreria capitata, Clitoria nana* and *Helianthemum brasiliensis* established in plots in excluded site (E).

Table 1. Species turnover (%) at the different sites (FB – frequently burned, and E – excluded since six years) at different treatments (fire and mowing) from T0 (before experiments), to T30 (30), T90 (90) and T360 (360 days after experiments).

		Fire		*Mowing*	
Plot	Site	new	lost	new	lost
T0-T30	FB	19.64	33.28	15.08	29.95
	E	24.19	40.49	12.33	35.80
T0-T90	FB	25.20	31.23	11.33	35.77
	E	20.35	46.31	27.48	45.42
T0-T360	FB	27.48	27.77	16.88	34.78
	E	29.16	32.68	44.44	55.77

Analysis of post disturbance changes in functional groups

Responses of the different functional groups varied. Graminoid covers were higher in frequently burned grasslands (p = 0.005, Fig 4a) and also showed significant difference between treatments (p = 0.001). After 30 days, graminoid cover was higher in site FB in burned plots than in excluded grasslands. At T90, mowed plots showed a significant higher cover than burned ones in site FB (p = 0.006). After one year, site FB showed higher covers, independently of treatment. Burned plots in excluded areas had higher cover of graminoids than mowed ones (p ≤ 0.05). After 90 days, forb cover was higher in site FB than in E. After one year of treatments, no significant differences could be observed between sites and treatments. Moreover, fire intensity and graminoids cover correlated negatively (r = -0.65, p = 0.02). Site and treatment showed a significant interaction for forb cover (p = 0.005). Shrub cover only differed significantly before fire experiments between sites. At 360, cover of graminoids was only higher than at T0 for burned plots (F = 119.97, p = 0.00001 and F = 38.85, p = 0.004 for sites FB and E respectively). Forb cover, on the other hand, was higher in site FB (F = 62.74, p = 0.0001 for burned and F = 21.62, p = 0.002 for mowed plots). Shrub cover showed no significant differences between observations before and after one year of experiments. There was a negative correlation of forbs cover and temperatures at soil level (r = - 0.58, p = 0.04) and residence time of fire (r = -0.71, p = 0.001).

Number of species from functional groups varied (see Fig 4b). Before experiments, no significant differences could be found (between sites and treatments) for graminoids. Already after 30 days, more species were observed in burned plots in site E than in mowed ones (p = 0.05). At T90, plots in site FB had more species than excluded grasslands, regardless of treatment. Forb species number also showed significant differences only after 30 and 90 days: in burned plots, more species were found in site FB than E ($p \leq 0.05$). Moreover, in site E, more species were sampled in mowed than in burned plots. In general, the number of shrub species was higher in mowed than in burned plots (p = 0.001). After one year, the number of species was lower for graminoids, except in burned plots in excluded sites. Number of species of forbs and shrubs did not differ before and at T360. Temperature at soil level and number of graminoid species correlated negatively (r = -0.62, p = 0.02).

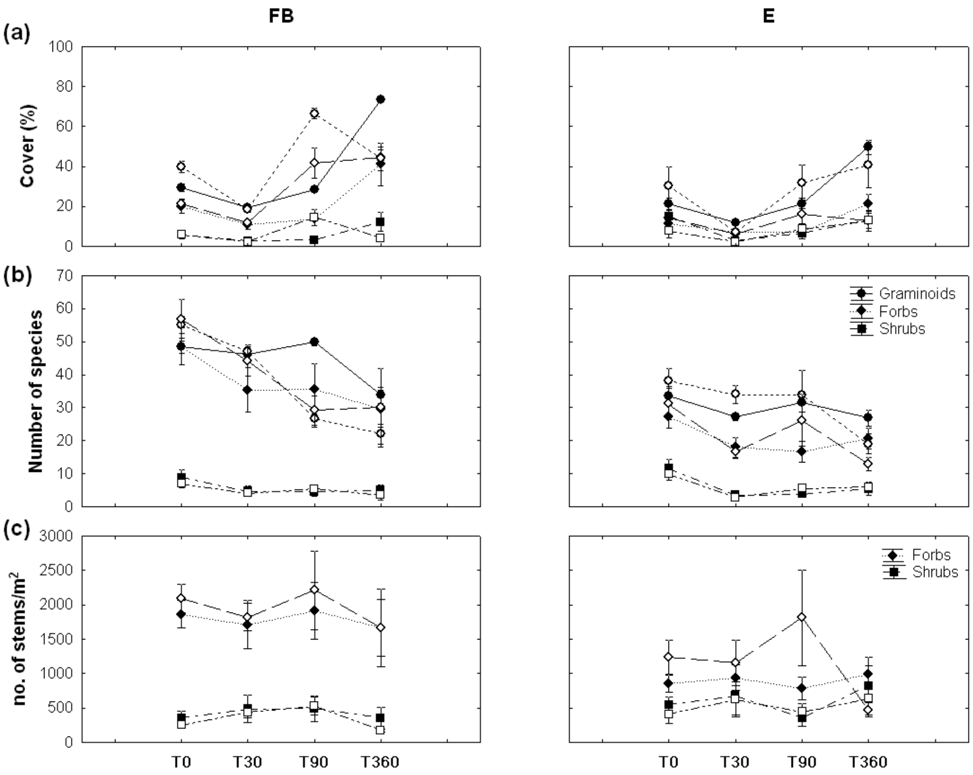

Fig 4. **(a)** – Cover (%), **(b)** - species richness (number of species) and **(c)** – number of stems (stems/m^2) of functional groups (graminoids, forbs and shrubs) in frequently burned (FB) and grasslands excluded since six years (E) for different treatments (fire – filled and mowing – blanked markers) before treatments (T0), after 30 (T30), 90 (T90) and 360 days (T360). Significant differences between treatments are described in the text. Markers are means ± 1SE.

Number of stems was only measured for forbs and shrubs. Forbs always showed more stems in frequently burned sites than in excluded ones before experiments ($p \leq 0.05$, Fig 4c). At T90, significant differences could be observed in burned plots between sites FB and E (p = 0.03). No significant differences could be observed for number of shrub stems neither between sites nor treatments. For both forbs and shrubs, the number of stems before and after one year of experiments was the same, independently of site and treatment. Number of stems of forbs and temperatures at soil level correlated negatively (r = - 0.62, p = 0.03) and number of stems of shrubs correlated positively to temperatures at 50 cm (r = 0.58, p = 0.04).

Discussion

Post-fire vegetation structure

Fire and mowing affected vegetation structure in several ways. In frequently burned sites, there was an increase in bare soil cover, but after one year of experiments, values were the same as before experiments. In excluded sites, on the other hand, percentage of bare soil was still higher. The higher cover of shrubs in excluded sites would have led to the formation of larger gaps after fire experiments (Keeley and Zedler 1978).

Litter was more efficiently removed by fire than mowing. After fire, only graminoid crowns, dead stems from shrubs and rosette bases could be observed (Fidelis et al, submitted). The effects of litter removal and the consequently opening of gaps are well discussed in the literature. The most important benefits are reduction in competition intensity, mostly for light (Beckage and Stout 2000; Wilson and Shay 1990) and increase in soil temperature (Hulbert 1988; Knapp 1984; Lloyd 1968). Indeed, after 30 days, the measured PAR in burned plots was in average 128% higher than in control sites (Fidelis, unpublished data).

As a consequence, seedling establishment may be enhanced due to an increase in free space (Bond and van Wilgen 1996), break of seed dormancy by higher soil temperatures (Auld and Denham 2006; Hoffmann 1996; Knox and Clarke 2006; Tyler 1995) and decrease in competition with dominant species (Laterra and Solbrig 2001; Marcos *et al.* 2004; Tyler 1995). Actually, a weak positive correlation between number of established seedlings and bare soil cover was found (r = 0.28, Fidelis et al., Chapter 4). Additionally, new gaps can ben colonized by vegetative ramets from both bud bank and neighbouring vegetation.

Disturbance causes the removal of aboveground biomass (Grime 1979). Decrease in vegetation cover due to fire and mowing treatments lead to distinct responses of functional groups. An increase in graminoids cover in burned plots (42%) was observed. A common trend observed for graminoids was the more rapid recover in mowed plots in frequently burned sites until T90. After that, the cover drastically decreases, probably due to tillering competition. Grasses are known to be the most fire-resistant group in grasslands (Bond 2004; Frost 1984), with a high capacity of rapid biomass recover (Naveh 1975). Buds are insulated from direct damage caused by fire by the protection of leaf sheaths at the crown, resprouting thus, vigoursly after fire. Despite the lack of organ reserves, caespitose grasses have the ability to accumulate nutrients underneath their clones (Briske and Derner 1998; Derner and Briske 2001; Derner *et* *al.* 1997), assuring their fast recovery. Caespitose grasses, therefore, have a great advantage in post fire environments due to its prompt recover and ability to rapidly use nutrients released.

Several studies showed the importance of fire season on vegetation regeneration and dynamics. Spring burns usually favour C_4 over C_3 species (Collins and Gibson 1990; Ewing and Engle 1988; Gibson and Hulbert 1987) and increase the number of forb species (Brockway *et al.* 2002). In Australian grasslands, repeated spring burning may help to control annual exotic species (Lunt and Morgan 2001). In *Campos* grasslands, the highest accumulation of dead biomass occurs in autumn and winter, decreasing in spring and summer (Heringer and Jacques 2002a). Therefore, fire intensities are probable different from burns during spring-summer, leading thus, to different vegetation responses. Unfortunately, no further studies about effects of fire season on vegetation dynamics are available, showing the necessity of more data for a better understanding of fire effects on *Campos* grasslands.

Forb species showed a rapid recover of cover, mostly in burned plots. After one year in frequently burned sites, an increase in forbs cover could be observed. The same was not true for excluded areas. Most of forb species rapidly resprouted after fire and mowing and new species established in site FB such as *Galianthe fastigiata* (Rubiaceae) and *Pterocaulon rugosom* (Asteraceae). Both species have bud-bearing belowground reserve organs, where most buds are insulated from fire damage. Fidelis et al (Chapter 2) observed that forbs belowground bud bank was more sensitive to longer intervals of fire. They found a significant decrease in bud bank size with already six years of fire exclusion, what undoubtedly reflects on the functional group capacity to regenerate after disturbance.

Forbs are very important in *Campos* grassland ecosystems. In this study, they represented about 50% of all plant species found in frequently burned plots and ca. 43% found in excluded sites. Nevertheless, exclusion of fire leads to a replacement of forb species by larger tussocks and shrub species. If fire intervals are too long, regeneration of forb species may not be as successful as in areas under recurrent disturbance. In short-term, fire enhances the establishment of herbaceous species, which may be mostly exotic and annuals, such as in Australian grasslands (Lunt and Morgan 2001), limestone grasslands (Lloyd 1968), chaparral (Franklin *et al.* 2004; Guo 2001; Hanes 1971; Keeley *et al.* 1981; Safford and Harrison 2004), and páramos (Ramsay and Oxley 1996). In our study, annual and exotic species were completely absent, as already reported by previous studies (Overbeck and Pfadenhauer 2007).

Shrubs suffered almost no changes caused by both fire and mowing. Number of species, cover and number of stems did not vary among times of observation, treatments and sites. However, there was an important change of dominance: in excluded areas, *Heterothalamus psiadioides* and *Baccharis leucopappa*, dominant shrubs before fire experiments, decreased drastically after one year of experiments in both treatments. Both species are obligate seeders and seedlings began to establish only one year after experiments. Fidelis *et al.* (Chapter 3) hypothesized that seedling establishment occurred mostly from seeds from neighbouring individuals and not from the seed bank. Therefore, fire frequency would be an important factor for the maintenance of obligate seeder species populations. If fire frequency is too high, individuals will not reach mature phase and therefore, will not be able to produce seeds, leading to a lower capacity of regeneration after disturbance events and even a subsequently replacement by shrub and herbaceous species with resprouting ability.

Post-fire diversity

Fire may alter plant species richness (Bond and van Wilgen 1996; Christensen 1985; Whelan 1995). Several studies found a short-term increase in species diversity after fire events (Guo 2001; Morgan 1999; Safford and Harrison 2004). Nevertheless, a great part of new species establishing in these areas were annuals and exotic ones and as already cited above, our study showed neither annuals nor exotic species.

In short-term, fire and mowing did not enhance plant diversity, which contradicts results found by Overbeck et al. (2005). Such differences could be related to the size of sampling units used in both studies (0.24 m^2 in this study and 0.75 m^2 in Overbeck's study) or the short period of observation (only one year). However, species turnover was high. After one year, the highest establishment of new and loss of plant species was in mowed plots in excluded sites (44.44% and 55.77%, respectively). In frequently burned sites, the establishment of new species was higher in burned plots. After fire, 54.4% of all established seedlings in site FB were new species, whilst new species of resprouters corresponded to 25.5% (Fidelis et al, Chapter 4). Except for *Hypoxis decumbens*, the new species established after experiments were present in other plots before. New species were recruited from both seed bank, seed rain from neighbouring plants and from the bud bank. However, most of the species were already there before experiments.

Temperature at soil level correlated negatively to number of graminoid species (this study) and stems in these sites (Fidelis et al., Chapter 4). High temperatures reached in excluded areas (until ca. 500°C) might have killed viable seeds and destroyed buds, hindering the establishment of new species. The high establishment of new species in mowed plots could demonstrate the potential of excluded area in increasing plant diversity.

Fire highly changed communities in frequently burned areas. Nevertheless, after one year, species composition was nearly the same as before fire, showing a high resilience of these grasslands. Excluded areas, on the other hand, did not show the same tendency, which might be related to the higher fire temperatures and intensities. Mowing plots in excluded sites, in opposite, exhibited higher changes in vegetation community than frequently burned areas, showing the regeneration potential of excluded areas.

Conclusions

Probably the most important short-term effect after fire and mowing was the removal of litter and consequently opening of gaps within the vegetation. Fire removed the litter layer more efficiently than mowing and in addition, the input of nutrients provided by fire might have contributed to the rapid recover of vegetation, mostly of caespitose grasses.

The removal of aboveground biomass stimulated vegetation regeneration and provided microsites for the establishment of new species. The removal of dominant competitors, such as large tussock grasses, enhanced the establishment of forbs (from both seed bank, seed rain and mostly from the seed bank), showing their dependence on disturbance.

Our study reinforces the urgent necessity for further short- and long-term studies about fire effects on *Campos* grasslands. Future studies considering fire frequencies and mostly fire seasons should be carried out in order to provide scientific data for future management plans. It is already known that the total exclusion of these grasslands will lead to drastic losses of plant diversity and physiognomy. Mowing can be an alternative to fire, since it is such a polemic tool among Brazilian environmental policy and scientists. However, as showed by our study, fire has important effects on plant community and should not be neglected in future studies about *Campos* grasslands dynamics.

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References

Aguiar, L. W., Martau, L., Soares, Z. F., Bueno, O. L., Mariath, J. E. & Klein, R. M. (1986) Estudo preliminar da flora e vegetação de morros graníticos da Região da Grande Porto Alegre, Rio Grande do Sul, Brasil. *Iheringia,* **34,** 3 - 38.

Auld, T. D. & Denham, A. J. (2006) How much seed remains in the soil after a fire? *Plant Ecology,* **187,** 15-24.

Beckage, B. & Stout, I. J. (2000) Effects of repeated burning on species richness in a Florida pine savanna: a test of the intermediate disturbance hypothesis. *Journal of Vegetation Science,* **11,** 113-122.

Behling, H. & Pillar, V. D. (2007) Late quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. *Philosophical Transactions of the Royal Society B,* **362,** 243-251.

Behling, H., Pillar, V. D., Müller, S. C. & Overbeck, G. E. (2007) Late-Holocene fire history in a forest-grassland mosaic in southern Brazil: implications for conservation. *Applied Vegetation Science,* **10,** 81-90.

Behling, H., Pillar, V. D., Orlóci, L. & Bauermann, S. G. (2004) Late Quaternary *Araucaria* forest, grassland (campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogegraphy, Palaeoclimatology, Palaeoecology,* **203,** 277 - 297.

Boldrini, I. I. (1997) Campos do Rio Grande do Sul: caracterização fisionômica e problemática ocupacional. *Boletim do Instituto de Biociências da Universidade Federal do Rio Grande do Sul,* **56,** 1 - 39.

Boldrini, I. I. & Eggers, L. (1996) Vegetação campestre do sul do Brasil: dinâmica de espécies à exclusão do gado. *Acta botanica Brasilica,* **10,** 37 - 50.

Bond, W. J. (2004) Fire. *Vegetation of Southern Africa* (ed^(eds R. M. Cowling, D. M. Richardson & S. M. Pierce), pp. 421-446. Cambridge University Press, Cambridge.

Bond, W. J. & van Wilgen, B. W. (1996) *Fire and plants*. Chapman ¨Hall, London.

Briske, D. D. & Derner, J. D. (1998) Clonal biology of caespitose grasses. *Population biology of grasses* (ed^(eds G. P. Cheplick), pp. 107-135. Cambridge University Press, Cambridge.

Brockway, D. G., Gatewood, R. G. & Paris, R. B. (2002) Restoring fire as an ecological process in shortgrass prairie ecosystems: initial effects of prescribed burning during the dormant and growing seasons. *Journal of Environmental Management,* **65,** 135-152.

Cabrera, A. L. & Willink, A. (1973) *Biogeografia de America Latina*. Secretaria General de la Oganización de los Estados Americanos, Washington, D.C.

Christensen, N. L. (1985) Shrubland fire regimes and their evolutionary consequences. *The ecology of natural disturbance and patch dynamics* (ed^(eds S. T. A. Pickett & P. S. White), pp. 85-100. Academic Press, San Diego.

Collins, S. L. & Gibson, D. J. (1990) Effects of fire on community structure in tallgrass and mixed-grass prairie. *Fire in North American Tallgrass prairie* (ed^(eds S. L. Collins & L. L. Wallace), pp. 81-98. University of Oklahoma Press, Norman.

Coutinho, L. M. (1982) Ecological effects of fire in Brazilian Cerrado. *Ecology of tropical savannas* (ed^(eds B. J. Huntley & B. H. Walker), pp. 273-291. Springer Verlag, Berlin.

De Luis, M., Raventós, J. & González-Hidalgo, J. C. (2006) Post-fire vegetation succession in Mediterranean gorse shrublands. *Acta Oecologica,* **30,** 54-61.

Debano, L. F. & Conrad, C. E. (1978) The effect of fire on nutrients in a chaparral ecosystem. *Ecology,* **59,** 489-497.

Derner, J. D. & Briske, D. D. (2001) Below-ground carbon and nitrogen accumulation in perennial grasses: a comparison of caespitose and rhizomatous growth forms. *Plant and Soil,* **237,** 117-127.

Derner, J. D., Briske, D. D. & Boutton, T. W. (1997) Does grazing mediate soil carbon and nitrogen accumulation beneath C4, perennial grasses along an environmental gradient? *Plant and Soil,* **191,** 147-156.

Eggers, L. & Porto, M. L. (1994) Ação do fogo em uma comunidade campestre secundária, analisada em bases fitossociológicas. *Boletim do Instituto de Biociências,* **53,** 1 - 88.

Ewing, A. L. & Engle, D. M. (1988) Effects of late summer fire on tallgrass prairie microclimate and community composition. *The American Midland Naturalist,* **120,** 212-222.

Franklin, J., Coulter, C. L. & Rey, S. J. (2004) Change over 70 years in a southern California chaparral community related to fire history. *Journal of Vegetation Science,* **15,** 701-710.

Frost, P. H. G. (1984) The responses and survival of organisms in fire-prone environments. *Ecological effects of fire in South African ecosystems* (ed^(eds P. d. V. Booysen & N. M. Tainton), pp. 274-325. Springer Verlag, Berlin.

García-Martinez, P. (2005) Caracterización química y física de los suelos del Morro Santana (Porto Alegre, Rio Grande do Sul, Brasil). Master thesis, Technische Universität München.

Gibson, D. J. (1988) Regeneration and fluctuation of tallgrass prairie vegetation in response to burning frequency. *Bulletin of the Torrey Botanical Club,* **115,** 1-12.

Gibson, D. J. & Hulbert, L. C. (1987) Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio,* **72,** 175-185.

Gotelli, N. J. & Ellison, A. M. (2004) *A primer of ecological statistics*. Sinauer Associates, Inc., Massachusetts.

Grime, J. P. (1979) *Plant Strategies and vegetation processes*. John Wiley and Sons, Chichester, UK.

Guo, Q. (2001) Early post-fire succession in California chaparral: Changes in diversity, density, cover and biomass. *Ecological Research,* **16,** 471-485.

Hanes, T. L. (1971) Succession after fire in the chaparral of Southern California. *Ecological Monographs,* **41,** 27-52.

Heringer, I. & Jacques, A. V. A. (2002) Acumulação de forragem e material morto em pastagem nativa sob distintas alternativas de manejo em relação às queimadas. *Revista brasileira de Zootecnia,* **31,** 599-604.

Hodgkinson, K. C. (1991) Shrub recruitment response to intensity and season of fire in a semi-arid woodland. *Journal of Applied Ecology,* **28,** 60-70.

Hoffmann, W. A. (1996) The effects of fire and cover on seedling establishment in a neotropical savanna. *Journal of Ecology,* **84,** 383 - 393.

Hoffmann, W. A. (1999) Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology,* **80,** 1354 - 1369.

Hulbert, L. C. (1969) Fire and litter effects in undisturbed bluestem prairie in Kansas. *Ecology,* **50,** 874-877.

Hulbert, L. C. (1988) Causes of fire effects in tallgrass prairie. *Ecology,* **69,** 46-58.

Keeley, J. E. & Zedler, P. H. (1978) Reproduction of chaparral shrubs after fire: a comparison of sprouting and seeding strategies. *The American Midland Naturalist,* **99,** 142-161.

Keeley, S. C., Keeley, J. E. & Hutchings, S. M. (1981) Postfire succession of the herbaceous flora in Southern California chaparral. *Ecology,* **62,** 1608-1621.

Knapp, A. K. (1984) Post-burn differenes in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. *American Journal of Botany,* **71,** 220-227.

Knox, K. J. E. & Clarke, P. J. (2006) Fire season and intensity affect shrub recruitment in temperate slerophyllous woodlands. *Oecologia,* **149,** 730-739.

Laterra, P. & Solbrig, O. T. (2001) Dispersal strategies, spatial heterogeneity and colonization success in fire-managed grasslands. *Ecological Modelling,* **139,** 17-29.

Livi, F. P. (1999) Elementos do clima: o contraste de tempos frios e quentes. *Atlas ambiental de Porto Alegre* (ed^(eds R. Menegat, M. L. Porto, C. C. Carraro & L. A. D. Fernandes), pp. 73 - 78. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre.

Lloyd, P. S. (1968) The ecological significance of fire in limestone grassland communities of the Derbyshire Dales. *Journal of Ecology,* **56,** 811-826.

Lunt, I. D. & Morgan, J. W. (2001) The role of fire regimes in temperate lowland grasslands of southeastern Australia. *Flammable Australia: the fire regimes and biodiversity of a continent* (ed^(eds R. A. Bradstock, J. E. Williams & A. M. Gill), pp. 177-197. Cambridge University Press, Cambridge.

Manly, B. F. J. (2007) *Randomization, bootstrap, and Monte Carlo methods in biology,* 3rd. edn. Chapman & Hall/CRC, Boca Raron.

Marcos, E., Tárrega, R. & Luis-Calabuig, E. (2004) Interactions between mediterranean shrub species eight years after experimental fire. *Plant Ecology,* **170,** 235 - 241.

Morgan, J. W. (1999) Defining grassland fire events and the response of perennial plants to annual fire in temperate grasslands of south-eastern Australia. *Plant Ecology,* **144,** 127-144.

Morgan, J. W. & Lunt, I. D. (1999) Effects of time-since-fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. *Biological Conservation,* **88,** 379-386.

Müller, S. C., Overbeck, G. E., Pfadenhauer, J. & Pillar, V. D. (2007) Plant functional types of woody species related to fire disturbance in forest-grassland ecotones. *Plant Ecology,* **189,** 1-14.

Naveh, Z. (1975) The evolutionary significance of fire in the Mediterranean region. *Vegetation,* **29,** 199-208.

Noble, I. R. & Slatyer, R. O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio,* **43,** 5-21.

Oliveira, J. M. & Pillar, V. D. (2004) Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. *Community Ecology,* **5,** 197-202.

Overbeck, G. E., Müller, S. C., Fidelis, A., Pfadenhauer, J., Pillar, V. D., Blanco, C., Boldrini, I. I., Both, R. & Forneck, E. D. (2007) Brazil´s neglected biome: the Southern Campos. *Perspectives in Plant Ecology and Systematics,* **9,** 101-116.

Overbeck, G. E., Müller, S. C., Pillar, V. D. & Pfadenhauer, J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science,* **16,** 655-664.

Overbeck, G. E., Müller, S. C., Pillar, V. D. & Pfadenhauer, J. (2006) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. *Brazilian Journal of Biology*.

Overbeck, G. E. & Pfadenhauer, J. (2007) Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora,* **202,** 27-49.

Pallarés, O. R., Berretta, E. J. & Maraschin, G. E. (2005) The south American campos ecosystem. *Grasslands of the world* (ed^(eds J. M. Suttie, S. G. Reynolds & C. Batello), pp. 171-219. FAO, Rome.

Pillar, V. D. (2008) Multiv: Multivariate exploratory analysis, randomization testing and bootstrap resampling. . (ed^(eds. Universidade Federal do Rio Grande do Sul, Porto Alegre.

Pillar, V. D. & Orlóci, L. (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science,* **7,** 585 - 592.

Podani, J. (2000) *Introduction to the exploration of multivariate biological data*. Backhuys Publishers, Leiden.

Ramsay, P. M. & Oxley, E. R. B. (1996) Fire temperatures and postfire plant community dynamics in Ecuadorian grass páramo. *Vegetatio,* **124,** 129-144.

Rice, S. K. (1993) Vegetation establishment in post-fire *Adenostoma* chaparral in reltion to fine-scale pattern in fire intensity and soil nutrients. *Journal of Vegetation Science,* **4,** 115-124.

Safford, H. D. & Harrison, S. (2004) Fire effects on plant diversity in serpentine vs. sandstone chaparral. *Ecology,* **85,** 539-548.

Slocum, M. G., Platt, W. J. & Cooley, H. C. (2003) Effects of differences in prescribed fire regimes on patchiness and intensity of fires in subtropical savannas of Everglades National Park, Florida. *Restoration Ecology,* **11,** 91-102.

Smith, B. & Wilson, J. B. (1996) A consumer's guide to evenness. *Oikos,* **76,** 72-82.

Sosinski, E. E. & Pillar, V. D. (2004) Respostas de tipos funcionais de plantas à intensidade de pastejo em vegetação campestre. *Pesquisa agropecuária brasileira,* **39,** 1 - 9.

Statsoft INC. (2004) STATISTICA for Windows, Version 6. Tulsa.

Trollope, W. S. W. (1982) Ecological effects of fire in South African Savannas. *Ecology of tropical savannas* (ed^(eds B. J. Huntley & B. H. Walker), pp. 293-306. Springer-Verlag, Berlin.

Tyler, C. M. (1995) Factors contributing to postfire seedling establishment in chaparral: direct and indirect effects of fire. *Journal of Ecology,* **83,** 1009-1020.

Whelan, R. J. (1995) *The ecology of fire*. Cambridge University Press, Cambridge.

Wilson, S. D. & Shay, J. M. (1990) Competition, fire, and nutrients in a mixed-grass prairie. *Ecology,* **71,** 1959 - 1967.

Appendix 1. Species recorded in burned and mowed plots in frequently burned (FB) and grasslands excluded from fire since six years (E) at different times of observation: T0 (before treatments), T30 (30 days), T90 (90 days) and T360 (360 days after treatments) on Morro Santana, Porto Alegre. Species cover and bare soil and litter cover are given (%). No information is given for species that had less than 1% of cover.

	T0				T30				T90				T360			
	Fire		Mowing		Fire		Mowing		Fire		Mowing		Fire		Mowing	
Species	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E
Bare soil	21.39	15.26	20.14	26.64	57.86	57.72	26.37	47.23	50.24	53.51	28.89	43.32	33.17	40.95	43.33	19.44
Litter	24.32	47.50	37.66	42.26	18.33	25.05	37.56	37.63	15.15	4.69	36.47	25.47	10.50	11.60	26.25	21.11
Acmella bellidioides (Sm.) R.K.Jansen	23.21	23.47	11.94	3.67	8.71	24.64	6.16	1.00	9.77	3.17	11.00	0.00	13.40	6.20	5.00	8.57
Andropogon lateralis Nees	17.79	23.50	18.18	0.00	13.54	13.00	12.00	0.00	20.00	25.00	15.00	1.00	15.00	10.00	0.00	0.00
Andropogon selloanus Hack.	14.43	11.91	23.29	23.57	6.67	8.14	7.36	3.67	10.00	26.88	20.17	17.86	7.50	12.86	1.00	15.00
Angelonia integerrima Spreng.	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00
Aristida filifolia (Arechav.) Herter	5.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00
Aristida flaccida Trin. & Rupr.	19.36	22.76	21.41	23.69	15.15	11.00	9.20	12.68	18.76	21.22	20.48	20.29	18.17	16.24	8.44	10.00
Aristida jubata (Arechav.) Herter	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.67	0.00	0.00
Aristida laevis Kunth.	14.47	16.33	22.22	26.88	10.54	8.75	7.33	10.00	13.44	25.00	12.00	12.43	11.88	12.58	10.00	7.50
Aspilia montevidensis Kuntze	5.25	14.00	10.33	7.50	11.67	18.33	10.00	2.33	13.33	40.00	16.36	0.00	8.33	20.00	1.00	6.50
Asteraceae sp1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Axonopus affinis Chase	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Axonopus siccus Kuhlm.	0.00	0.00	7.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Axonopus suffultus (Mikan ex Trin.) Parodi	17.62	9.75	10.91	20.00	13.90	7.75	16.38	18.20	21.19	22.83	20.00	17.00	18.84	13.00	5.00	6.67
Baccharis articulata Pers.	0.00	60.00	5.29	16.50	0.00	5.50	4.25	0.00	0.00	33.33	12.67	3.67	0.00	20.00	0.00	0.00
Baccharis cognata DC.	18.06	14.09	28.25	16.67	14.47	10.14	12.08	5.00	16.37	34.00	17.08	15.00	17.50	18.10	1.00	5.25
Baccharis leucopappa DC.	3.40	40.00	8.33	29.17	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	8.30	0.00	0.00
Baccharis ochracea Spreng.	0.00	30.00	10.00	15.00	0.00	30.00	5.00	5.00	0.00	72.50	5.00	10.00	0.00	70.00	0.00	0.00
Baccharis trimera DC.	0.00	0.00	0.00	10.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00
Borreria capitata DC.	3.00	3.00	6.67	0.00	3.00	1.00	5.00	0.00	3.83	0.00	12.75	6.00	0.00	2.33	0.00	10.00
Borreria verticillata G.Mey	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Briza rufa Steud.	10.00	10.00	6.67	20.00	0.00	0.00	5.00	3.00	0.00	0.00	1.00	0.00	0.00	5.00	0.00	5.00
Briza subaristata Lam.	13.10	6.83	8.35	7.82	2.00	3.00	5.00	2.71	2.71	4.00	8.57	8.67	4.57	5.67	0.00	4.00
Briza uniolae Nees ex Steud.	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

(continued)	T0				T30				T90				T360			
	Fire		Mowing		Fire		Mowing		Fire		Mowing		Fire		Mowing	
Species	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E
Bulbostylis juncoides (Vahl) Kük.	0.00	0.00	5.00	7.56	0.00	0.00	5.50	2.70	0.00	0.00	0.00	10.00	0.00	0.00	7.29	7.50
Bulbostylis sphaerocephala C.B. Clarke	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	5.00
Calamagrostis viridiflavescens Steud.	0.00	5.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	1.00	5.00	0.00	0.00
Calea uniflora Less.	7.17	5.00	6.07	7.83	5.19	0.00	3.75	4.40	8.36	0.00	0.00	0.00	4.40	0.00	10.00	0.00
Carex phalaroides Kunth.	0.00	0.00	50.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chamaecrista repens (Vogel) H.S.Irwin & Barneby	10.00	0.00	8.14	12.50	60.00	0.00	14.00	5.00	60.00	0.00	11.57	20.00	10.00	0.00	0.00	0.00
Chaptalia exscapa Poepp. ex DC.	5.80	13.57	5.38	3.40	1.00	3.83	2.50	0.00	2.60	6.20	5.00	2.33	4.20	4.00	1.00	5.00
Chaptalia integerrima (Vell.) Burkart	30.00	5.00	0.00	70.00	6.25	0.00	20.00	0.00	10.00	5.00	10.00	1.00	13.33	1.00	0.00	10.00
Chaptalia runcinata Kunth.	10.33	8.60	14.74	12.67	4.13	4.13	8.91	4.22	4.90	6.26	5.42	4.55	10.58	6.64	10.00	6.17
Chevreulia acuminata Less.	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Cliococca selaginoides (Lam.)C.M.Rogers & Mildner	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00
Clitoria nana Benth.	5.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	10.00	5.00	0.00	10.00	0.00
Crotalaria tweediana Benth.	14.17	5.00	13.00	0.00	10.00	5.00	7.00	0.00	10.00	50.00	10.00	0.00	8.33	1.00	0.00	10.00
Croton cf. nitrariaefolius	0.00	15.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	5.00	0.00	0.00	4.00	0.00	0.00
Cuphea glutinosa Cham. & Schltdl.	1.00	5.00	3.00	5.00	3.00	5.00	5.00	1.00	3.00	20.00	1.00	3.67	1.00	1.00	0.00	0.00
Cyperaceae sp1	13.32	7.28	8.33	5.60	7.41	7.63	3.35	2.50	13.11	11.10	10.25	7.53	12.68	7.92	0.00	0.00
Cyperaceae sp2	7.46	8.57	9.27	5.53	7.67	5.57	5.44	5.38	10.62	8.94	10.83	0.00	9.17	8.08	0.00	6.25
Cyperus reflexus Vahl ex Kunth.	10.00	5.00	0.00	10.00	10.00	8.75	0.00	5.33	11.67	13.00	0.00	0.00	10.00	7.00	5.00	12.50
Danthonia cirrata Hackel & Arechav.	35.00	38.33	16.25	0.00	12.00	13.67	3.00	0.00	11.25	0.00	0.00	0.00	8.75	18.33	0.00	5.00
Desmanthus tatuhyensis Hoehne	15.00	12.50	4.60	5.00	5.20	5.00	8.00	0.00	7.50	0.00	5.75	1.00	7.50	7.50	0.00	5.00
Desmodium incanum DC.	5.00	0.00	5.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00
Dichanthelium sabulorum (Lam.) Gould & C.A.Clark	10.50	5.25	12.91	4.80	3.00	11.67	3.00	5.20	1.00	20.00	4.25	10.00	5.00	6.50	0.00	5.00
Dichondra sericea Sw.	0.00	0.00	8.40	3.00	0.00	0.00	3.15	0.00	0.00	0.00	7.13	0.00	1.00	0.00	1.00	0.00
Elyonurus candidus (Trin.) Hack.	15.21	13.33	22.45	22.03	9.55	8.25	15.50	9.12	16.67	32.14	18.67	35.56	9.10	17.91	29.10	8.75
Eragrostis polytricha Nees	5.00	0.00	10.00	0.00	10.00	0.00	5.00	0.00	10.00	0.00	7.50	0.00	10.00	0.00	0.00	5.00
Eryngium horridum Malme	5.43	17.20	14.40	22.24	5.00	12.50	20.50	16.69	5.00	15.20	15.00	35.42	5.00	20.33	0.00	5.00
Eryngium pristis Cham. & Schltdl.	22.50	0.00	55.00	70.00	22.50	0.00	35.00	50.00	23.33	0.00	10.00	20.00	30.00	0.00	20.00	7.50
Eryngium sanguisorba Cham. & Schltdl.	12.07	16.43	14.67	14.11	15.05	11.57	10.73	2.00	17.90	13.67	13.92	9.00	14.67	14.00	20.00	3.00
Eupatorium ascendens Mart. ex Baker	20.00	5.00	0.00	8.75	5.00	5.00	3.00	5.00	10.00	12.50	5.00	8.71	3.00	5.00	3.00	0.00

(continued)	T0				T30				T90				T360			
	Fire		Mowing		Fire		Mowing		Fire		Mowing		Fire		Mowing	
Species	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E
Eupatorium intermedium DC.	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	80.00	0.00	0.00	0.00	0.00
Eupatorium ivifolium L.	0.00	0.00	0.00	0.00	7.50	0.00	0.00	0.00	10.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00
Eupatorium ligulaefolium Hook. et Arn.	15.41	45.00	26.43	40.50	14.00	10.43	11.67	7.00	14.29	10.33	10.88	22.78	16.25	5.50	33.33	1.00
Eupatorium subhastatum Hook. et Arn.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Eupatorium tanacetifolium Gill. ex Hook. & Arn.	8.33	0.00	50.00	5.00	0.00	0.00	0.00	20.00	0.00	0.00	9.67	0.00	0.00	0.00	0.00	10.00
Eupatorium tweendianum Hook. et Arn.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00
Euphorbia selloi Boiss.	1.00	16.14	2.00	1.00	1.00	1.00	2.00	3.00	1.00	1.00	0.00	0.00	2.33	3.40	1.00	0.00
Evolvolus sericeus Benth.	1.91	3.66	4.61	4.47	4.57	8.43	4.00	3.25	6.58	3.60	2.61	5.43	6.23	5.53	4.57	4.00
Poaceae sp1	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp2	5.00	6.29	0.00	0.00	5.00	11.50	0.00	0.00	5.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp3	18.00	5.00	0.00	0.00	8.67	0.00	0.00	0.00	8.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp4	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp5	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp6	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp7	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp8	0.00	0.00	0.00	0.00	20.00	5.00	0.00	0.00	15.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp9	0.00	5.00	11.63	21.57	0.00	0.00	4.30	6.67	0.00	0.00	23.33	0.00	0.00	0.00	0.00	0.00
Poaceae sp10	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp11	8.33	0.00	0.00	0.00	5.00	0.00	0.00	0.00	7.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp12	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Poaceae sp14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Galactia marginalis Benth.	4.75	3.00	4.62	5.00	3.00	1.00	1.00	0.00	5.00	0.00	1.00	0.00	5.00	1.00	1.00	5.00
Galianthe fastigiata Griseb.	0.00	0.00	0.00	6.67	4.46	1.00	6.25	1.00	7.29	0.00	0.00	7.50	3.00	6.20	0.00	0.00
Gamochaeta americana Wedd.	9.00	1.00	5.17	2.33	0.00	0.00	5.00	0.00	0.00	1.00	3.00	0.00	2.33	1.00	0.00	10.00
Glechon squarrosa Benth.	8.00	7.89	10.56	10.53	4.80	5.00	4.67	5.43	6.30	0.00	5.50	10.77	10.00	2.33	0.00	0.00
Helianthemum brasiliense Pers.	5.50	5.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	3.67	3.00	2.60	1.00	0.00
Heterothalamus psiadioides Less.	7.00	38.19	5.00	40.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	2.00	5.88	0.00
Hydrocotyle exigua Malme	4.00	1.00	4.50	2.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	1.00	1.00	2.60	0.00	1.00

(continued)	T0				T30				T90				T360			
	Fire		Mowing		Fire		Mowing		Fire		Mowing		Fire		Mowing	
Species	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E
Hyphochaeris sp	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00
Hypoxis decumbens L.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
Indet 1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 2	0.00	5.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 3	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 4	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.50	0.00	0.00	0.00
Indet 5	0.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 6	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 7	5.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 9	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 10	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 11	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Indet 12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.87	0.00	1.00	0.00	5.33	0.00	0.00
Indet 13	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Iridaceae sp1	30.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00
Iridaceae sp2	0.00	8.33	7.00	7.50	10.00	4.25	3.50	3.00	10.00	10.50	1.00	3.00	0.00	3.40	1.00	0.00
Kyllinga vaginata Lam.	5.69	8.42	9.25	5.07	5.17	4.50	8.22	5.25	6.94	6.58	8.96	6.82	10.08	7.14	5.00	12.50
Leptocoryphium lanatum Nees	15.83	43.85	21.43	27.13	7.50	20.92	20.92	7.36	11.21	28.67	15.42	17.86	16.67	14.50	0.00	0.00
Lucilia nitens Less.	4.40	10.25	6.89	8.33	5.33	1.00	3.00	0.00	6.67	4.40	2.60	2.33	12.75	5.25	0.00	10.00
Macroptilium prostratum Urb.	5.00	5.00	9.80	5.00	20.00	5.00	7.89	10.00	20.00	5.00	10.88	0.00	0.00	3.00	0.00	7.20
Mecardonia tenella (Cham. & Schlechtend.) Pennell.	0.00	0.00	0.00	1.00	0.00	10.00	5.00	0.00	0.00	0.00	0.00	12.50	0.00	0.00	0.00	0.00
Monnina oblongifolia Arechav.	0.00	0.00	30.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Noticastrum gnaphalioides (Baker) Cuatrec.	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Orthopappus angustifolius Gleason	5.00	0.00	0.00	0.00	80.00	0.00	0.00	0.00	50.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00
Oxalis conorrhiza Jacq.	3.33	2.33	5.33	1.80	2.00	5.00	3.00	0.00	2.00	1.00	8.00	3.10	5.25	5.00	0.00	5.00
Paspalum notatum Flüggé	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Paspalum plicatulum Michx.	10.45	5.25	21.36	0.00	13.25	4.00	21.38	0.00	24.17	3.40	22.00	1.00	14.00	3.00	0.00	0.00
Pavonia hastata Cav.	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.00	0.00	0.00	0.00	0.00	0.00

(continued)	T0				T30				T90				T360			
	Fire		Mowing		Fire		Mowing		Fire		Mowing		Fire		Mowing	
Species	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E
Peltodon longipes A.St.-Hil. ex Benth.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	10.00	0.00	0.00
Petunia sp	7.00	5.00	4.25	0.00	5.00	1.00	0.00	0.00	0.00	5.00	1.00	0.00	1.00	5.00	0.00	0.00
Pfaffia tuberosa (Moq. ex DC.) Hicken	8.00	7.00	6.82	4.58	3.78	6.73	4.77	2.33	3.40	6.44	2.78	5.00	10.00	5.20	0.00	5.00
Piptochaetium montevidensis (Spreng.) Parodi	13.53	15.00	20.00	9.47	8.73	11.00	4.67	5.57	11.18	9.50	8.00	18.00	16.43	7.20	5.00	0.00
Polygala linoides Poir.	1.00	2.14	1.67	1.00	0.00	0.00	1.00	0.00	0.00	3.67	2.33	0.00	1.00	1.00	0.00	1.00
Polygala pumila Norlind.	1.80	0.00	1.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00
Porophyllum lanceolatum DC.	0.00	0.00	5.00	5.00	0.00	0.00	20.00	0.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00	0.00
Pterocaulon alopecuroideum Chodat	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pterocaulon rugosum Malme	0.00	0.00	57.50	0.00	10.33	5.00	6.67	0.00	18.00	0.00	15.25	1.00	0.00	5.00	0.00	5.00
Relbunium richardianum Hicken	1.00	1.00	3.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Richardia grandiflora Steud.	6.85	0.00	11.89	5.00	6.00	5.00	5.78	1.00	8.00	0.00	10.33	1.00	5.00	5.00	0.00	10.00
Schinus weinmanniaefolius Engl.	0.00	0.00	0.00	10.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	13.33	0.00	0.00	0.00	0.00
Schizachyrium imberbe (Hack.) A. Camus	10.00	0.00	5.00	0.00	10.00	1.00	12.60	1.00	6.67	0.00	5.00	0.00	15.00	0.00	0.00	12.50
Schizachyrium spicatum (Sprenger) Herter	0.00	0.00	15.17	0.00	0.00	0.00	13.67	0.00	0.00	0.00	20.00	0.00	5.00	0.00	0.00	20.00
Schizachyrium tenerum Nees.	0.00	6.08	16.62	0.00	0.00	10.00	5.00	0.00	0.00	8.25	18.33	0.00	0.00	3.67	0.00	0.00
Senecio heterotrichus DC.	12.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Setaria parviflora (Poir.) Kerguélen	5.00	1.00	3.00	0.00	10.00	6.78	7.29	0.00	6.67	1.80	6.25	10.00	4.00	6.20	0.00	0.00
Setaria vaginata Spreng.	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00
Sisyrinchium vaginatum Spreng.	1.00	7.50	5.14	0.00	0.00	0.00	5.50	0.00	0.00	0.00	4.25	0.00	0.00	5.00	0.00	5.50
Stevia aristata D.Don ex Hook. & Arn.	3.22	5.00	5.20	0.00	3.38	0.00	1.00	0.00	10.00	0.00	5.00	0.00	5.00	0.00	0.00	5.00
Stevia cinerascens Sch.Bip. ex Baker	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stipa filiculmis Delile	16.36	10.56	27.11	14.29	5.29	5.00	12.32	5.20	6.43	10.00	14.06	15.14	8.70	7.20	7.50	0.00
Stipa melanosperma J. Presl.	0.00	10.20	0.00	0.00	0.00	6.50	0.00	0.00	0.00	18.33	0.00	0.00	0.00	6.67	0.00	0.00
Stipa juergensii Hack.	0.00	0.00	5.00	0.00	0.00	0.00	5.25	0.00	0.00	0.00	3.00	0.00	0.00	5.00	0.00	5.00
Stylosanthes leiocarpa Vog.	0.00	0.00	3.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	1.00
Stylosanthes montevidensis Vog.	1.00	0.00	14.00	0.00	0.00	4.00	5.00	0.00	0.00	2.33	1.00	0.00	5.00	3.00	0.00	0.00
Tibouchina gracilis Cogn.	26.36	5.00	10.08	12.27	4.58	3.00	5.29	4.00	8.07	4.25	16.75	11.14	12.50	5.33	0.00	5.00
Trachypogon montufari Nees	11.50	0.00	0.00	17.10	15.00	0.00	0.00	0.00	13.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trixis stricta Less.	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	T0				T30				T90				T360			
	Fire		Mowing		Fire		Mowing		Fire		Mowing		Fire		Mowing	
Species	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E	FB	E
Verbena ephedroides Cham.	3.67	0.00	7.50	3.67	0.00	0.00	10.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Verbena pseudojuncea Gay	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Verbesina sordescens DC.	0.00	20.00	12.50	33.75	0.00	5.00	0.00	37.50	0.00	0.00	5.00	30.67	0.00	0.00	0.00	0.00
Vernonia flexuosa Sims	11.20	5.25	11.00	20.00	16.00	17.50	3.93	10.00	12.33	12.50	11.25	20.00	10.00	5.11	3.67	9.00
Vernonia megapotamica Spreng.	0.00	0.00	5.00	0.00	0.00	5.00	0.00	5.00	0.00	0.00	10.00	6.67	0.00	0.00	0.00	0.00
Vernonia nudiflora Less.	15.92	0.00	15.75	21.25	12.44	0.00	18.33	13.67	20.00	5.00	40.00	15.00	10.56	7.50	0.00	10.00
Waltheria douradinha A.St.-Hil.	0.00	27.50	0.00	10.00	0.00	25.00	0.00	0.00	0.00	32.27	0.00	0.00	0.00	30.00	0.00	0.00

CONCLUSIONS

"… fire differs from other disturbances, such as cyclones or floods, in that it feeds on complex organic molecules (as do herbivores) and converts them to organic and mineral products. Fire differs from herbivory in that it regularly consumes dead and living material and, with no protein needed for its growth, has broad dietary preferences. Plants that are inedible for herbivores commonly fuel fires." (William J. Bond and Jon E. Keeley, 2005, TREE 20:387)

Fire and plant strategies

Several efforts in the last decades were made to group plants according to their different strategies (e.g. Raunkiaer, 1934; Grime, 1979; Noble and Slatyer, 1980). They were grouped regarding the position of buds (Raunkiaer, 1934), their phenology (Sarmiento, 1984), persistence (Pausas and Lavorel, 2003), and their resistance to disturbance events, as for example fire (see Whelan, 1995; Bond and van Wilgen, 1996).

In flammable ecosystems, plants were grouped according to their regeneration and colonization traits (see Noble and Slatyer, 1980), their responses to fire, such as fire-persisters (resilients to fire) and fire-recruiters (increase after fire events, Keeley, 1992), or more generally, as obligate seeder (recruitment exclusively by seedlings) and resprouters (no seedling establishment, regeneration via resprouting). Overbeck and Pfadenhauer (2007) tried to classify plants according to fire life forms, using Raunkiaer's life form systems. However, a better classification was reached using the regeneration strategies (non-sprouting vs sprouting species) for the different functional groups (graminoids, forbs and shrubs). It is still difficult to propose a classification system for *Campos* grasslands species based on their responses to fire, due to the lack of information about plant life forms, dispersion syndromes, population biology and description of belowground organs. In this study, the more general approach was used (obligate seeders vs. resprouters) and some strategies could be analyzed more in detail, considering location of buds and type of belowground systems for the different functional groups.

Different types of regeneration could be observed in *Campos* grasslands after disturbance. Most of them related to the position and protection of buds and with the type of belowground organ. Obligate seeder strategy is not so common in these grasslands, being represented in the study area by only 3 species (*Heterothalamus psiadioides, Baccharis leucopappa* and *Gamochaeta americana,* Chapter 4). As showed by Chapter 4, seedling establishment corresponded to less than 10% of species recover after disturbance. Resprouter is thus, the most important regeneration strategy in *Campos* grasslands. Nevertheless, although seedling establishment is low, it is of crucial importance for plant diversity, since a higher number of new species colonized post-fire environments by germinating from seeds than being recruited from the bud bank. Moreover, it maintains the genetic diversity of plant communities.

In a general way, graminoids showed three principal strategies of regeneration after biomass losses (see Table 1): from aboveground buds protected by leaves at the crown basis, resprouting from rhizomes and from seed (but no obligate seeder species was observed). Graminoid seedlings could be found in both areas, under different treatments (fire and mowing, Chapter 4). However, in comparison to resprouters, seedling establishment was not significant for graminoid recover.

Few graminoid species on Morro Santana have rhizomes and therefore, the number of graminoid belowground buds is very low in comparison to other functional groups (Chapter 2). Some species with rhizomes, e.g. *Cyperus reflexus*, resprouted from the belowground bud bank, but the majority resprouted from buds located at the bases of crowns. After fire, nearly all plants were consumed and residuals were composed by graminoid crowns, rest from rosette species and burned shrub stems (Fig 1a, Chapter 1). After already two weeks, new resprouters could be observed emerging from the burned crowns (Fig 1b).

Table 1. Summary of principal regeneration strategies from graminoids, forbs and shrubs.

funtional groups	obligate seeder	resprouter		
		aboveground buds	*belowground buds*	*presence of belowground organs*
graminoids	no	yes	few species (e.g. *Cyperus reflexus)*	few species (rhizome)
forbs	yes *(Gamochaeta americana)*	yes (e.g. *Chaptalia runcinata)*	yes (e.g. *Vernonia flexuosa)*	yes (bulbs, corms, rhizophores, rhizome, xylopodium)
shrubs	yes *(Heterothalamus psiadioides, Baccharis leucopappa)*	no	yes (e.g. *Eupatorium ligulaefolium*)	yes (xylopodium)

Forbs showed to be the most sensitive functional group to exclusion of fire (Chapter 2, 4, and 5), with different strategies of regeneration in *Campos* grasslands after biomass removal: seedling establishment, resprouting from above- and belowground bud bank. As already cited for graminoids, seedling establishment was low in comparison to resprouter recruitment (Chapter 4).

Some forb species did not have belowground organs, resprouting thus from aboveground bud bank (e.g. *Chaptalia runcinata*, see Chapter 3). Recover after biomass removal was rapid but, if fire intensity is very high, buds may be killed by fire and plants will not be able to regenerate in these areas. In *Campos* grasslands, fire intensities were not so high in comparison to other ecosystems (see Chapter 1). Moreover, fire spread very fast. Most hemicryptophytes were completely consumed by fire, remaining only plant basis with viable buds from which new stems and leaves could regenerate. Other species, which were apparently dead before experiments, had their dead biomass removed and stem and leaf formation were thus stimulated. *Schlechtendalia luzulaefolia* (Asteraceae) showed an interesting strategy: although leaves were almost completely consumed by fire, after experiments they continued to grow and at the same time, new leaves could be observed resprouting from basal buds protected by the leaf crown (pers. obs., Fig 2a).

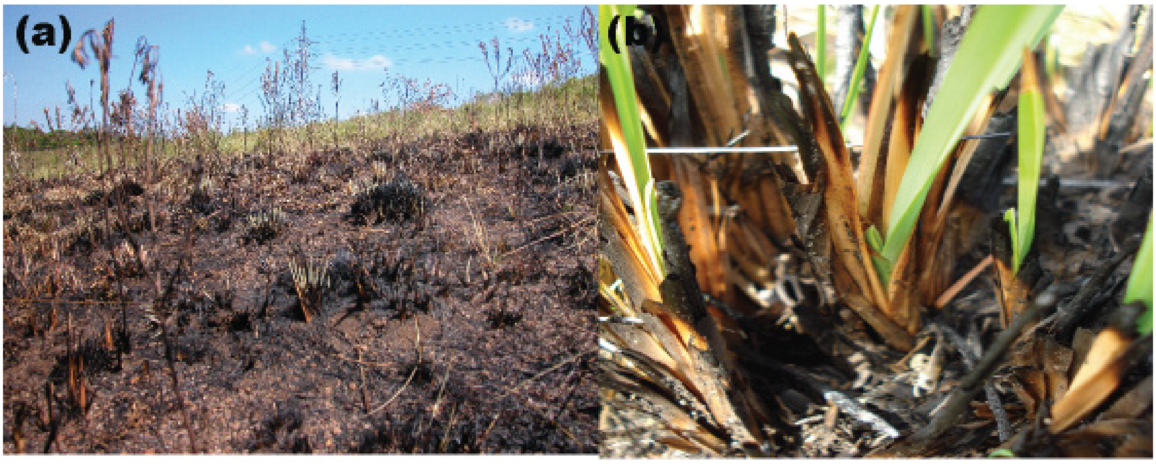

Fig 1. (a) - Plot in frequently burned area two days after fire experiments on Morro Santana. **(b)** – Detail of a new tiller resprouting from aboveground buds protected in crown bases of a grass species (Picture 2b: Carolina Blanco).

Resprouting from the belowground bud bank can be subdivided in three types:

- from bulbs and corms: *Habranthus gracilifolius* (bulb, Amaryllidaceae) and *Hypoxis decumbens* (corm, Hypoxidaceae) could only be observed after fire (Chapter 5). An accidental fire at the end of this study stimulated these species growth, as showed in Fig 2b, followed by flowering. Other species with bulbs, as for example *Oxalis conorrhiza* (Oxalidaceae), rapidly recover its aboveground biomass, flowering within the first weeks after fire (Fig 2c, Fidelis & Blanco, in preparation).

- from rhizophores, rhizomes and tuberous roots: these are storage structures with vegetative reproduction potential (Fig 2d, for more details about terminology see Chapter 2). As showed in Chapter 3, *Vernonia flexuosa*, a forb species with rhizophore could promptly recover its aboveground biomass and flower after fire events. *Eryngium horridum* (with rhizome) has a great capacity of resprouting after biomass removal from both above- and belowground buds (Fig 2e, Fidelis *et al.* 2008). These species can persist recurrent fires due to their reserve organs. However, if fire intervals are too short, stem recruitment can be hindered or decreased due to the depletion of reserve organs. Besides the high production of seeds of some species (as for example *Vernonia flexuosa* or *Eupatorium* *tanacetifolium*), clonal growth guarantee their persistence if there are no good opportunities for seedling establishment.

- from xylopodium: species with xylopodia showed the highest recruitment of new stems after removal (unpublished data). As already mentioned in Chapter 2, xylopodia are not typical storage structures, but have a great gemmiferous potential, which could be confirmed with this study (see the bud bank of *Eupatorium ligulaefolium*, Chapter 3). *Stylosanthes montevidensis* (Fig 2f) and *Desmanthus tatuhyensis* (both Leguminosae) resprouted and quickly flowered after fire events (Fidelis & Blanco, in preparation). Seedlings from both species could be found after fire on Morro Santana (data not shown). Xylopodium has no vegetative spread potential and nutrients are probably stored in tuberous roots usually present in species with this structure. Therefore, reproduction of species with this structure is dependent on seed production and seedling establishment. Furthermore, the relation of this structure with fire is clear, since burned sites showed a higher density of xylopodia. The longer the exclusion of fire, the lower xylopodium density (Chapter 2).

Most of the shrubs have a kind of burl on their bases, from where stems resprouted. Besides the presence of buds in the stems (epicormic buds) before experiments, no resprouting from aboveground bud bank could be observed, only from buds located in belowground organs (Chapter 4). Xylopodia is present in several species, such as *Eupatorium ligulaefolium*. After fire, stems recruitment was very high, declining after one year, probably due to stem competition (Chapter 3, Fig 3a). Other shrub species, *Baccharis cognata* also showed high stem recruitment after biomass removal, mostly in burned plots (data not shown, Fig 3b).

Two obligate seeder shrub species were observed in this study: *Baccharis leucopappa* and *Heterothalamus psiadioides*. Both species (mainly *H. psiadioides*) dominated the excluded area before experiments. Seedling recruitment occurred only after one year after experiments and it was hypothesized that seeds might come from the seed rain of neighboring individuals than from the seed bank (Chapter 3).

Obligate seeder shrub species appear to be very important for *Campos* grasslands dynamics. In excluded areas on Morro Santana, both shrubs were dominant. At the highland grasslands (*Campos de Cima da Serra*, northern from Rio Grande do Sul), *Campos* grasslands form a mosaic with Araucaria forest. In these areas, the exclusion of disturbance leads to shrub encroachment (Oliveira and Pillar 2004), where *Baccharis uncinella* (another obligate seeder shrub species) dominates. The longer the time of exclusion is, the higher the number of individuals and cover of *B. uncinella.* Individuals of *B. uncinella* shade grass matrix, decreasing the flammable biomass.

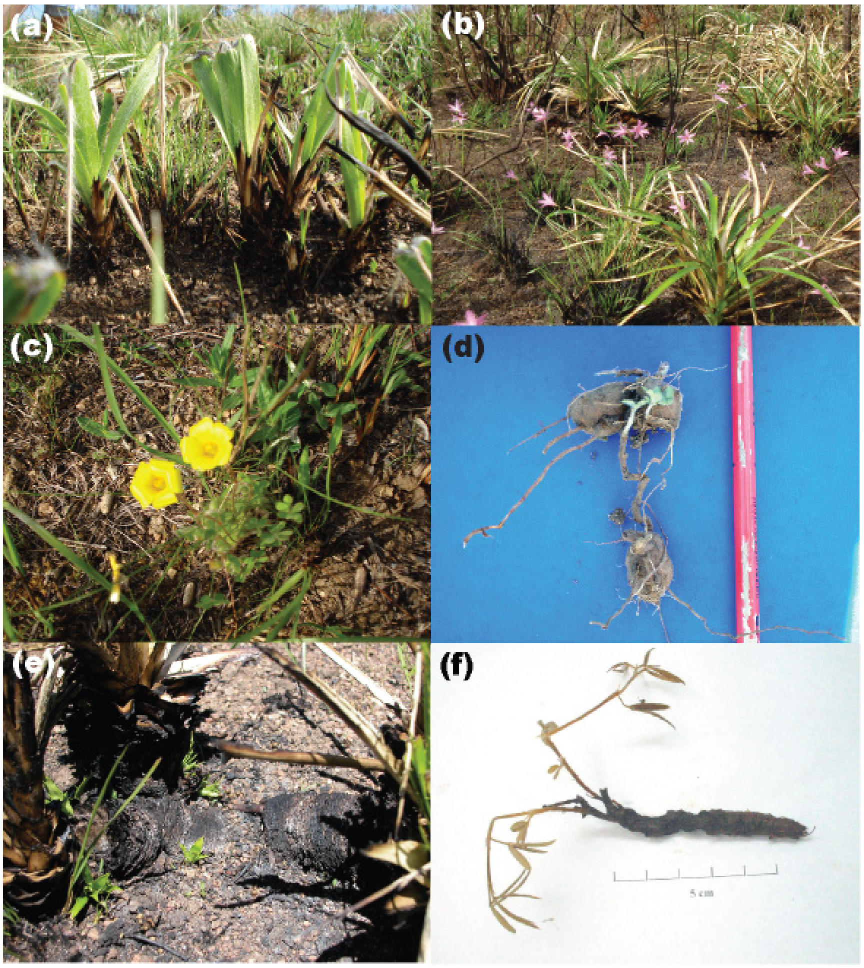

Fig 2. **(a)** – Individuals of *Schlechtendalia luzulaefolia,* **(b)** – Flowering individuals of *Habranthus gracilifolius* and **(c)** – Flowering individuals of *Oxalis conorrhiza* after two weeks of fire, **(d)** – Clonal growth of *Vernonia flexuosa*, **(e)** – *Eryngium horridum* after three weeks of fire, with new rosettes resprouting from exposed rhizomes, and **(f)** – Xylopodium structure of *Stylosanthes montevidensis* (Pictures 2a and b – Carolina Blanco, Picture 2d – Bruno Fonseca).

Fig 3: **(a)** – Xylopodium structure of *Eupatorium ligulaefolium*, showing new and old stems. **(b)** – Resprouters of *Baccharis cognata* after one month of fire experiments.

Obligate seeder species guarantee genetical diversity in Campos grasslands, but resprouters assure plant persistence after fire events. Obligate seeder species are dependent on seed bank and seed rain from neighbouring plants, whilst resprouters need a viable bud bank. Plants with belowground organs have an extra source of resource to allocate for building up of aboveground biomass after fire. Plants resprouting from aboveground bud banks, such as caespitose grasses, have to rapidly use nutrients released after fire in order to resprout. Additionally, species with rhizomes and rhizophores for example, also have clonal growth and can thus, reproduce vegetatively. Xylopodium structures from other species have no vegetative clonal growth, but a high gemminferous potential, guaranting hence, regeneration and persistence of these species.

It is difficult to group species according to strategies related to fire in *Campos* grasslands, even using a general classification (obligate seeder vs. resprouters). Information about plants is still missing for these grasslands and thus, analyses using data from literature are difficult to be performed. This study shows the importance of recording data on the field about plant traits and strategies, in order to evaluate vegetation responses to fire events.

Fire and vegetation dynamics

Fire is a natural element in vegetation since ca 7400 cal yr BP (Behling and Pillar 2007; Behling *et al.* 2004). Currently, fire is usually set by humans, with different purposes: “clean” the area, kill animals or only for entertainment reasons. In large areas of the northern part of the state, grasslands are burned every two years in order to enhance resprouting of forage species for cattle grazing, improving thus pasture quality (Nabinger *et al.* 2000).

Not only fire intensity, but also fire frequency and season are important aspects affecting vegetation dynamics. In tallgrass prairies for example, spring burns often enhance C_4 grasses and forbs (Collins and Gibson 1990; Ewing and Engle 1988; Gibson and Hulbert 1987). Fire season and frequency are also used in order to control annual exotic species in Australian grasslands (Lunt and Morgan 2001). Winter burns, on the other hand, decrease the number of C_3 species (Llorens and Frank 2004), leading to the increase of caespitose grasses (Jacques 2003). The results of this thesis are restricted to summer burns and generalizations about fire effects on vegetation dynamics should be carefully considered. During winter, accumulation of dead biomass is higher (Heringer and Jacques 2002) and therefore, fire intensities and temperatures might be higher than during summer burns. Moreover, plants are not producing flowers (except for C_3 grasses and some forb species) and thus, effects of fire on vegetation regeneration can be expected to be different from summer burns.

Probable the most important effect of fire on vegetation dynamics is the removal of litter and consequent open of new microsites for plant establishment. Such effect was also accomplished with mowing, however less intense, since there is no complete removal of litter.

Additionally, the input of nutrients provided after fire might enhance resprouting and germination of several species.

The results of this thesis leave several open questions for further studies, such as: a) how is the impact of winter fires on vegetation?, b) will functional groups responses be the same as in summer fires?, c) areas with longer times of exclusion will have the same pattern of regeneration?, d) will the importance of resprouting decrease the longer the intervals of fire are? and e) what are the effect of nutrient input in vegetation dynamics in post-fire environments?

Can fire be considered an efficient management tool for Campos grasslands?

Generalizations of this unique study for *Campos* grasslands should be cautiously considered. Experiments were performed during one season and only in frequently burned and sites excluded since six years. There are not enough data to provide a consistent affirmation about the optimal interval of fire and when fire should be carried out..

In October 2007 (after 10 months of experiments), an accidental fire occurred in the area. All control and most of the mowed plots were destroyed or singed by fire. However, burned plots were not affected (except for two plots). Fuel load was not enough to burn. Mowed plots still had a higher cover of litter left by experiments. Therefore, in these areas, fires can be conducted at least after two years due to the biomass accumulation.

Fire showed to be an efficient tool in enhancing graminoid and forb cover and the establishment of new species from both seed and bud bank. Environmental authorities and government should review its use at least for scientific purposes. National parks exclude grassland areas in southern Brazil. Actually, they are protecting the area from external disturbances, which leads to losses of biodiversity and grassland physiognomy. There is no effective management plan for vegetation in these parks. As an example, in Aparados da Serra National Park, some areas are excluded more than 10 years. In 2004, summer was very dry and as a consequence, different areas of the park burned. Wildfires are common in National Parks in Brazil, burning vast areas and killing many animals and affecting vegetation regeneration. They are hardly controlled by fire fighters and sometimes escape into residential and rural neighboring areas.

If National Parks manage vegetation correctly, such events could be avoided. Mowing also showed to be an efficient tool for management, although its costs might be higher and implementation might be more complicate than fire, due to the need of machines. Probably the best solution would be the creation of a mosaic of different managements, as for example with grazed, mowed and burned areas, at different times. With a mosaic, even if a wildfire occurs, its effect would be minimized.

Campos grasslands are not a priority for both local government and environmental authorities. Several people consider grasslands a result of deforestation and thus, grassland areas should be reforested. Brazil is a “dendromaniac” country, where forests are more valuable ecosystems than others such as Caatinga or even the grasslands. As an example, Brazilian law to protect native vegetation is called “Código Florestal” (“Florestal Code”). Therefore, efforts should be directed to environmental education of local people in order to valorize the ecosystem where they are living. Government should support initiatives that seek the conservation of *Campos* grasslands, as for example, cattle grazing in southern Brazil instead of encourage changes in land use, such as afforestation of vast areas of Campos grasslands with exotic tress (*Pinus* spp. and *Eucalyptus* spp).

References

Behling, H. & Pillar, V. D. (2007) Late quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. *Philosophical Transactions of the Royal Society B,* **362,** 243-251.

Behling, H., Pillar, V. D., Orlóci, L. & Bauermann, S. G. (2004) Late Quaternary *Araucaria* forest, grassland (campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogegraphy, Palaeoclimatology, Palaeoecology,* **203,** 277 - 297.

Bond, W. J. (2004) Fire. *Vegetation of Southern Africa* (ed^(eds R. M. Cowling, D. M. Richardson & S. M. Pierce), pp. 421-446. Cambridge University Press, Cambridge.

Bond, W. J. & van Wilgen, B. W. (1996) *Fire and plants*. Chapman ¨Hall, London.

Collins, S. L. & Gibson, D. J. (1990) Effects of fire on community structure in tallgrass and mixed-grass prairie. *Fire in North American Tallgrass prairie* (ed^(eds S. L. Collins & L. L. Wallace), pp. 81-98. University of Oklahoma Press, Norman.

Ewing, A. L. & Engle, D. M. (1988) Effects of late summer fire on tallgrass prairie microclimate and community composition. *The American Midland Naturalist,* **120,** 212-222.

Fidelis, A., Overbeck, G., Pillar, V. D. & Pfadenhauer, J. (2008) Effects of disturbance on population biology of a rosette species *Eryngium horridum* Malme in grasslands in southern Brazil. *Plant Ecology,* **195,** 55-67.

Frost, P. H. G. (1984) The responses and survival of organisms in fire-prone environments. *Ecological effects of fire in South African ecosystems* (ed^(eds P. d. V. Booysen & N. M. Tainton), pp. 274-325. Springer Verlag, Berlin.

Gibson, D. J. & Hulbert, L. C. (1987) Effects of fire, topography and year-to-year climatic variation on species composition in tallgrass prairie. *Vegetatio,* **72**, 175-185.

Grime, J. P. (1979) *Plant Strategies and vegetation processes*. John Wiley and Sons, Chichester, UK.

Heringer, I. & Jacques, A. V. A. (2002) Acumulação de forragem e material morto em pastagem nativa sob distintas alternativas de manejo em relação às queimadas. *Revista brasileira de Zootecnia,* **31**, 599-604.

Jacques A. V. A. (2003) A queima das pastagens naturais - efeitos sobre o solo e a vegetação. *Ciência Rural* **33**, 177 - 81.

Keeley, J. E. (1992) Recruitment of seedlings and vegetative sprouts in unburned chaparral. *Ecology,* **73**, 1194-1208.

Llorens E. M. & Frank E. O. (2004) El fuego en la provincia de La Pampa. In: *Fuego en los ecosistemas argentinos* (eds C. Kunst, S. Bravo and J. L. Panigatti). Instituto Nacional de Tecnología Agropecuaria, Santiago del Estero.

Lunt, I. D. & Morgan, J. W. (2001) The role of fire regimes in temperate lowland grasslands of southeastern Australia. *Flammable Australia: the fire regimes and biodiversity of a continent* (ed^(eds R. A. Bradstock, J. E. Williams & A. M. Gill), pp. 177-197. Cambridge University Press, Cambridge.

Nabinger, C., Moraes, A. d. & Maraschin, G. E. (2000) Campos in Southern Brazil. *Grassland Ecophysiology and Grazing Ecology* (ed^(eds G. Lemaire, J. Hodgson, A. d. Moraes, C. Nabinger & P. C. F. Carvalho), pp. 355-376. CAB International.

Noble, I. R. & Slatyer, R. O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio,* **43**, 5-21.

Oliveira, J. M. & Pillar, V. D. (2004) Vegetation dynamics on mosaics of Campos and Araucaria forest between 1974 and 1999 in Southern Brazil. *Community Ecology,* **5**, 197-202.

Overbeck, G. E., Müller, S. C., Pillar, V. D. & Pfadenhauer, J. (2005) Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. *Journal of Vegetation Science,* **16**, 655-664.

Overbeck, G. E., Müller, S. C., Pillar, V. D. & Pfadenhauer, J. (2006) Floristic composition, environmental variation and species distribution patterns in a burned grassland in southern Brazil. *Brazilian Journal of Biology*.

Overbeck, G. E. & Pfadenhauer, J. (2007) Adaptive strategies in burned subtropical grassland in southern Brazil. *Flora,* **202**, 27-49.

Pausas, J. G. & Lavorel, S. (2003) A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science,* **14**, 409 - 416.

Raunkiaer, C. (1934) *The life forms of plants and statistical plant geography*. Claredon Press, Oxford.

Sarmiento, G. (1984) *The ecology of neotropical savannas*. Harvard University Press, Cambridge.

Whelan, R. J. (1995) *The ecology of fire*. Cambridge University Press, Cambridge.

Subtropical grasslands (*Campos*) are unique ecosystems located in southernmost part of Brazil. They are relict from a drier and colder period. Besides the propitious climate for forest, grassland physiognomies can be found throughout the entire state of Rio Grande do Sul, corresponding to 23% of total cover area. Grasslands are very high in species richness (about 3000 – 4000 plant species), which are maintened mostly by disturbance (mainly grazing and fire). Although *Campos* grasslands are important ecosystems (also economically due to cattle grazing), they have been neglected by both government and scientists. Less than 1% of its total area is under legal protection and more than 30% of its original area has already been changed into another land use, as for example soja beans plantations. The greatest threat nowadays for the conservation of *Campos* grasslands is the afforestation of exotic trees (*Pinus* spp. and *Eucalyptus* spp.). Several studies have been conducted in *Campos* grasslands, mainly analyzing the effects of grazing on vegetation dynamics and plant diversity. However, few studies evaluated the effects of fire on vegetation. Exclusion of disturbance leads to shrub enchroachment and consequently, to the loss of plant diversity and vegetation physiognomy. Therefore, disturbance events are required in order to maintain *Campos* grasslands in southern Brazil. Because of this, this thesis aims to evaluate the effects of fire on *Campos* grasslands, mainly on plant strategies (regeneration strategies) and vegetation dynamics.

Since there is no data about fire behaviour for these grasslands, **Chapter 1** describes the most important fire parameters: fire temperatures (at soil level and at 50 cm), spread of fire, fuel load (fine and coarse), combustion, residence time of fire, residuals and fire intensity. Seven experimental plots were established in two sites on Morro Santana (Porto Alegre, southern Brazil): frequently burned (FB) and excluded since six years. Experimental burns were performed in summer. Results showed a variation of fuel load between 0.39 to 1.44 kg/m^2 in both sites. Fire temperatures varied from 47°C (50 cm above soil surface) to 537.5°C(at soil level), being higher in excluded sites. Fire intensity was low in comparison to grasslands elsewhere (36.5 to 319.5 kW/m^2), differing significantly between sites. Fine fuel was the best variable to explain fire intensity. The results showed that, the longer grasslands are excluded, the hotter and more intense fires are. Such differences in fire temperature and mainly, in fire intensity lead to different responses of vegetation and should be considered for future management plans.

After fire experiments, most of species resprouted. Therefore, bud bank may play an important role on vegetation regeneration in *Campos* grasslands. As a result, the bud bank was analyzed in order to verify the potential of vegetation to regenerate after disturbance events (**Chapter 2**). Five areas were chosen with different managements and fire histories: grazing (EEAGr), frequently burned grassland (MSFb), exclusion from fire since six (MSe), 15 (APN15) and 30 years (ESA30). Since several species have storage organs, the belowground system of plant in these areas were also analyzed. The number of buds decreased the longer the intervals of disturbance

were. Grazed areas showed the largest bud bank (mainly composed by graminoids), whilst excluded areas since 30 years showed the smallest one. Forbs showed to be the most sensitive group to exclusion of disturbance. The variety and number of belowground organs also decreased the longer the intervals of fire were. Xylopodium, a belowground organ with no storage tissue, but with a high gemmiferous potential, was clearly associated with fire. Therefore, the results of **Chapter 2** show the importance of disturbance in maintaining *Campos* grasslands and as a consequence, the crucial role of bud bank on vegetation regeneration after disturbance events.

Effects of fire were also analyzed at population level in **Chapter 3**. Four species (all Asteraceae) were chosen for the study of population biology according to their functional group (forbs and shrubs) and regeneration strategy (obligate seeder and resprouter). Experimental burns were conducted in summer and populations were sampled before and after 90 and 360 days after fire experiments. The obligate seeder species (*Heterothalamus psiadioides*) had all their individuals killed by fire and first seedling establishment could only be observed after one year. It was hypothesized that seeds might have come from neighbouring plants. The other shrub species (*Eupatorium ligulaefolium*) showed only resprouters after fire experiments, with a high mortality rate of stems after 90 days. This species have a xylopodium and up to 150 buds could be observed on the surface of its belowground organ, showing its high capacity to resprout after biomass removal. *Vernonia flexuosa* (forb, presence of rhizophore) showed only resprouters as well and flowered after two months of experiments. Rhizophores have storage parenchyma and can show clonal growth and is a bud-bering organ. A higher number of stems could be observed after fire experiments. *Chaptalia runcinata* individuals took advantage of new microsites after fire and could establish in excluded areas, where tussock grasses dominated before and hindered its persistence. Both seedlings and resprouters were observed for this species, however seedlings corresponded to only 2% of all individuals. Fire affected plant population structure and demography of all species, being important for population dynamics of *Campos* grassland species.

The importance of the regeneration strategies in *Campos* grasslands were described in **Chapter 4**. Fire and mowing treatments were compared in frequently burned and excluded grasslands. Results showed the high importance of resprouters for these grasslands: 90% of all species showed resprouters and only 10% seedlings. Only three obligate seeder species could be found in these areas: *Heterothalamus psiadioides*, *Baccharis leucopappa* (both shrubs) and *Gamochaeta americana* (forb). The most interesting result in this chapter is the high establishment of new species of seedlings in burned plots in site FB. Resprouters were usually the same species present before treatments, but new species could also be observed. New species might have come from both seed bank, seed rain and bud bank. Results of chapter 4 corroborate the importance of resprouters in *Campos* grasslands.

Finally, effects of fire and mowing were analyzed for vegetation dynamics and functional groups in **Chapter 5**. Fire enhanced graminoids and forbs and did not affect shrub species. The most important short-term effect after biomass removal, mostly by fire, was the removal of litter and consequently, the opening of new gaps. It stimulated vegetation regeneration and provided microsites for the establishment of species. Abrubpt changes in species cover and composition could be observed in burned plots in site FB, wilst in mowed plots the greates changes occurred in sites E. Species turnover was very high, mainly in mowed plots in site E. After one year of treatments, species diversity was still lower in burned plots in site FB, but the same in site E. In mowed plots, species diversity was still lower than before treatments in both sites.

Fire plays an important role in *Campos* grasslands in southern Brazil. **Conclusions** summarize the results from the preceding chapters and describes the most important plant strategies for these grasslands: regeneration via sexual reproduction (with obligate seeder and facultative resprouter species) and vegetative regeneration. The last one was subdivided in regeneration from aboveground and belowground buds or even from both. Plants in *Campos* grasslands show a high diversity of belowground organs, which can serve as storage (e.g. rhizomes, rhizophores, tuberour roots) or only as bud-bearing organs (e.g. xylopodium). Since vegetative regeneration is the most important strategy in these grasslands, the bud bank has a more important role for vegetation regeneration and dynamics after disturbance than the seed bank. Therefore, future studies about the bud bank in other areas of these grasslands are of crucial importance. Finally, fire could be an alternative for management of *Campos* grasslands, since it removes more efficiently litter and enhances graminoids and forbs.

Subtropische Grasländer (*Campos*) sind einzigartige Ökosysteme im südlichsten Teil von Brasilien. In Rio Grande do Sul, dem südlichsten Bundesstaat Brasiliens, bedecken Grasländer 23 % des Gesamtgebietes und beherbergen eine sehr artenreiche Flora mit insgesamt 3000 bis 4000 Pflanzenarten. Feuer stabilisiert die *Campos* in Südbrasilien seit ihrer Entstehung in früh- und postglazialen Trockenperioden und verhindert unter den derzeitigen humiden Klimabedingungen die Entwicklung zum Wald. Obwohl Campos sehr wichtige Ökosysteme sind, wurden sie von Politik und Wissenschaft in den letzten Jahren vernachlässigt. Weniger als 1% der Gesamtfläche steht unter Schutz und mehr als 30% ihrer ursprünglichen Fläche wurde bereits in Soja- and Maisplantagen verwandelt. Heutzutage stellt die Aufforstung mit exotischen Bäumen (*Pinus* spp. und *Eukalyptus* spp.) eine Bedrohung für die Erhaltung der Campos dar. Mehrere Studien wurden in den Campos durchgeführt, vor allem über die Auswirkungen von Beweidung auf die Vegetationsdynamik und die Pflanzenvielfalt. Nur wenige Studien bewerten aber die Auswirkungen von Feuer auf die Vegetation. Das Klima im Untersuchungsgebiet unterliegt keinerlei Schwankungen, so dass die hohe Diversität mit anderen Faktoren, wie Störungen durch Feuer oder Beweidung, zusammenhängen muss. Ziel der vorliegenden Arbeit war es, die Wirkung von Feuer auf die Vegetation zu untersuchen, wobei die einzelne Art mit ihrem Verhalten gegen regelmäßige Brände im Vordergrund stand. Nach künstlich erzeugten Bränden und Mahdexperimenten wurden die Regenerationsfähigkeit und -geschwindigkeit repräsentativer Arten gemessen.

Kapitel 1 beschreibt die wichtigsten Parameter des Feuerverhaltens: Feuertemperaturen, Feuerausbreitung, Brennmaterial (fein und grob), Verbrennung, Verweilzeit von Feuer, Feueresiduen und Feuerintensität. Sieben experimentelle Flächen wurden an zwei Standorten in Morro Santana (Porto Alegre, Südbrasilien) angelegt: einem häufig abgebrannten (FB) und einem seit sechs Jahren nicht mehr abgebrannten Bereich (E). Künstlich erzeugte Brände wurden im Sommer gelegt. Die Ergebnisse zeigten eine Schwankungsbreite von Brennmaterial zwischen 0,39 bis 1,44 kg/m^2 an beiden Standorten. Die Feuertemperaturen schwankten zwischen 47 ° C und 537,5°C. Die Feuerintensität war im Vergleich zu anderen Grasländer relativ schwach (36,5 bis 319,5 kW/m), der Unterschied zwischen den Standorten war aber signifikant. Die Feinbiomasse zeigte die beste Variable, um die Feuerintensität zu erklären. Die Ergebnisse der Untersuchung machte deutlich, dass die Intensivität der Brände besonders bei Grassland nachzuweisen war, dass länger nicht gebrannt hatte. Solche Unterschiede bei der Feuertemperatur und vor allem bei der Feuerintensität führen zu unterschiedlichen Auswirkungen auf die Vegetation und sollten für die zukünftige Entwicklung von Landnutzungsstrategien in Betracht gezogen werden.

Nach den Brandexperimenten konnten die meisten Arten wieder austreiben. Deshalb spielt die Knospenbank eine wichtige Rolle für die Regenerationsfähigkeit der Campos Südbrasiliens. Als Folge wurde die Knospenbank untersucht, um die potenzielle Regenerationsfähigkeit der Vegetation nach Störung festzustellen (**Kapitel 2**). Fünf Gebiete mit verschiedenem Management wurden

ausgewählt: Beweidung (EEAGr), häufig gebrannt (MSFb), Abwesenheit von Feuer seit sechs (MSE), 15 (APN15) und 30 Jahren (ESA30). Da mehrere Arten Speicherorgane aufwiesen, wurden die unterirdischen Teile ebenfalls untersucht. Die Anzahl der Knospen sank, mit der Länge der Störungsintervalle. Auf den beweideten Flächen zeigte sich die größte Knospenbank (hauptsächlich bestehend aus Gräser), während ESA30 die kleinste aufwies. Kräuter reagierten am empfindlichsten auf die Abwesenheit von Störungen. Die Vielfalt und Anzahl der unterirdischen Organe sank, je länger die Intervalle zwischen den Feuern stiegen. Xylopodien (keine Speicherorgane) sind unterirdische Systeme mit einem hohen Potenzial an Knospenbildung. Außerdem sind Xylopodien eng an Gebiete gebunden, in denen Feuer häufig auftritt. Die in **Kapitel 2** dargestellten Ergebnisse zeigen die Bedeutung von Störungen für das Wiederaustreiben der Campos und als Folge davon die entscheidende Rolle der Knospenbank auf die Regenerationsfähigkeit der Vegetation.

In **Kapitel 3** wurden die Auswirkungen von Feuer auch auf der Ebene der Populationsbiologie analysiert. Vier Arten (alle Asteraceae) wurden für die populationsbiologischen Untersuchungen nach ihren Pflanzenfunktionstypen (Kräuter und Sträucher) und Regenerationsstrategien (nur durch Samen vermehrenden Arten und nur durch vegetativen Wiederaustrieb) ausgesucht. Die Populationen der Arten auf den im Sommer künstlich gelegten Brandexperimenten wurden nach 90 und 360 Tagen erneut aufgenommen. Alle Individuen der sich nur durch Samen vermehrenden Art (*Heterothalamus psiadioides*) starben nach dem Feuer; hier konnten erst nach einem Jahr Keimlinge beobachtet werden. Es wird vermutet, dass Samen aus den benachbarten Standorten übertragen wurden. Eine andere Strauchart *(Eupatorium ligulaefolium*) zeigte nach dem Brandexperiment nur vegetative Neuaustrieb, mit einer hohen Mortalitätsrate der Sprösse nach 90 Tagen. Diese Arten haben ein Xylopodium, und bis zu 150 Knospen konnte auf der Oberfläche der Organe beobachtet werden. *Vernonia flexuosa* (krautige Art) zeigte nur vegetative Neuaustrieb, und Blüten konnten schon zwei Monaten nach der Behandlung beobachtet werden. Rosetten von *Chaptalia runcinata* nutzten nach dem Feuer neue Micro-habitat, wo vorher Horstgräser dominiert hatten. Sowohl Keimlinge als auch vegetative Neuaustrieb konnten gefunden werden, obwohl nur 2% aller Individuen Keimlinge waren. Feuer hat die Populationsstruktur und –dynamik in den Campos-Grasländern beeinflusst.

Die Bedeutung der Regenerationsstrategien in den Campos wurde in **Kapitel 4** beschrieben. Hierzu wurden Brand- und Mahdexperimente durchgeführt und die Ergebnisse verglichen. Die Ergebnisse zeigten die hohe Bedeutung der vegetative Neuaustrieb für Vegetationsdynamik und Regeneration: 90% aller Arten zeigten vegetative Neuaustrieb und nur 10% Keimlinge. Nur drei Arten, beides Sträucher *Heterothalamus psiadioides, Baccharis leucopappa* wurden gefunden, die sich nur über Samen vermehren; und das Kraut *Gamochaeta americana*. Das interessanteste Ergebnis dieses Kapitels war die hohe Etablierungsrate von Keimlingen neuer Arten auf den gebrannten Flächen von site FB. Bei den Neuaustrieben zeigten sich in der Regel keine

Unterschiede zu den Behandlungen vorher. Die beobachteten neuen Arten können sowohl aus Samen- und Knospenbank als auch durch den Samenregen an die Standorte gelangt sein. Die Ergebnisse des **Kapitels 4** bekräftigen die Bedeutung der vegetativen Regeneration für die Campos in Südbrasilien.

Schließlich wurden in **Kapitel 5** die Auswirkungen von Feuer und Mahd auf Vegetationsdynamik und Pflanzenfunktionstypen analysiert. Feuer wirkte sich positiv auf Gräser und krautige Arten aus und hatte keinen Einfluss auf Strauchartigen. Die wichtigste kurzfristige Wirkung einer Störung (meist durch Feuer) war die Beseitigung von Streu und somit die Öffnung neuer Lücken in der Vegetation. Es stimuliert die Regeneration der Vegetation, meistens durch Wiederaustreiben. Deutlich wird die aprupte Veränderung in der Artzusammensetzung und Deckung der gebrannten Fläche in FB beobachtet, während in gemähten Flächen nur Veränderungen am Standort E zu sehen waren. Das Artturnover war sehr hoch, vor allem in gemähten Flächen des Standorts E. Nach einem Jahr Untersuchungszeit ist die Artenvielfalt auf den gebrannten Flächen (FB) niedriger als vor den Eingriffen, auf dem Standort E zeigen sich keine Veränderungen wie zu Beginn der Untersuchungsreihen. Die Artenvielfalt der gemähten Flächen an beiden Standorten ist niedriger als vor den Behandlungen.

Feuer spielt eine sehr wichtige Rolle in den *Campos*-Grasländern Südbrasiliens. Die **Schlussfolgerung** fasst die Ergebnisse aus den vorangegangenen Kapiteln zusammen und beschreibt die wichtigsten Pflanzenstrategien: generative und vegetative Regeneration. Letztere war unterteilt in Regeneration aus oberirdischen und unterirdischen Knospen oder sogar aus beiden. Da vegetative Regeneration die wichtigste Strategie in diesen Grasländern darstellt, spielt die Knospenbank für die Regeneration der Vegetation und die Dynamik nach Störungen eine größere Rolle als die Samenbank. Die Ergebnisse erwiesen sich als bedeutsam für die Entwicklung von Landnutzungsstrategien auf dem südbrasilianischen Campo.

A vegetação campestre, também conhecida como Campos, é um ecossistema único, localizado no sul do Brasil. Apesar do clima propício para floresta, as fisionomias campestres do sul do Brasil podem ser encontradas por todo o estado do Rio Grande do Sul, correspondendo a aproximadamente 23% de todo território do estado. Os campos são ricos em espécies (3000 a 4000 espécies vegetais), que são mantidas principalmente pelo distúrbio (pastejo e fogo). Apesar da importância dos Campos (também do ponto de vista econômico por causa da criação de gado), eles vêm sendo negligenciados tanto pelo governo como pela comunidade científica. Menos de 1% das áreas de campos já foram convertidas em plantação de soja ou milho. Atualmente, a maior ameaça para a proteção deste ecossistema é o rápido avanço de monoculturas de árvores exóticas, principalmente *Pinus* spp. e *Eucalyptus* spp. Vários estudos já foram realizados nos Campos, porém com um enfoque mais voltado para o efeito do pastejo na dinâmica da vegetação e diversidade de espécies. Entretanto, poucos estudos tiveram como objetivo avaliar os efeitos do fogo na vegetação. A exclusão de qualquer tipo de distúrbio pode levar a um aumento da camada arbustiva e consequentemente, a uma perda da diversidade de espécies típicas dos Campos. Por isso, distúrbios são necessários para a manutenção dos Campos no sul do Brasil. Desta forma, este tese tem como objetivo avaliar os efeitos do fogo nos Campos, principalmente nas estratégias das plantas (estratégias de regeneração) e na dinâmica da vegetação.

Uma vez que não há dados sobre o comportamento do fogo para os Campos, o **Capítulo 1** desta tese descreve os parâmetros de fogo mais importantes: temperatura do fogo (no solo e a 50 cm de altura), material combustível (fino e grosso), combustão, tempo de residência do fogo, resíduos e a intensidade do fogo. Sete parcelas experimentais foram estabelecidas no Morro Santana (Porto Alegre, Rio Grande do Sul) em duas áras diferentes: frequentemente queimada (FB) e excluída do fogo há seis anos (E). Os experimentos de queima foram conduzidos no verão. Os resultados mostram uma variação do material combustível entre 0,39 e 1,44 kg/m^2 em ambas as áreas. Temperatura do fogo variou de 47 a 537,5ºC, sendo maior nas áreas excluídas. A intensidade do fogo foi baixa em comparação com outras áreas campestres do mundo (36,5 a 319,5 kW/m), diferindo significativamente entre áreas. Material combustível fino foi a variável que melhor explicou a intensidade do fogo. Os resultados mostraram que, quanto maior o tempo de exclusão do fogo das áreas campestres, mais quente e mais intenso serão os incêndios. Tais diferenças em temperatura e principalmente, em intensidade do fogo levam a diferentes respostas da vegetação e devem, portanto, ser levadas em consideração para futuros planos de manejo destes campos.

Após os experimentos de fogo, a vegetação rapidamente rebrotou. Desta forma, o banco de gemas deve exercer um importante papel na regenração da vegetação dos Campos após eventos de distúrbio. Por isso, o banco de gemas de cinco áreas diferentes foi estudado **(Capítulo 2)** no Rio Grande do Sul: pastejada (EEAGr), frequentemente queimada (MSFb), excluída há seis (MSe), 15 (APN15) e 30 anos (ESA30). Várias espécies dos Campos possuem órgãos de reserva. Por isso,

além do banco de gemas, os órgãos subterrâneos também foram quantificados e identificados. O número de gemas diminui quanto maior o tempo de exclusão. Áreas pastejadas apresentaram os maiores banco de gemas (principalmente formado por graminóides), enquanto as áreas excluídas há 15 e 30 anos apresentaram os menores bancos de gemas. Herbáceas mostraram ser o grupo mais sensível à exclusão do distúrbio. A variedade e o número de órgãos subterrâneos diminuíram quanto maior o tempo de exclusão. Xilopódio, uma estrutura subterrâneo sem função de reserva, mas com um grande potencial gemífero se mostrou claramente associado com o fogo. Por isso, os resultados do **Capítulo 2** mostram a importância do distúrbio na manutenção dos Campos e consequentemente, a relevância dos estudos com banco de gemas.

Os efeitos do fogo também foram analisados em populações de plantas **(Capítulo 3)**. Quatro espécies (todas da família Asteraceae) foram selecionadas de acordo com seu grupo funcional (herbácea e arbustos) e sua estratégia de regeneração ("obligate seeder" ou "resprouter"). Queimas experimentais foram conduzidas no verão e populações foram amostradas antes, depois de 90 e 360 dias dos experimentos. A única espécie que só regenera através de sementes (*Heterothalamus psiadioides*) teve todos seus indivíduos mortos pelo fogo e as primeiras plântulas só foram observadas após um ano de experimentos. Tem-se como hipótese que as sementes devem ter vindo principalmente da vegetação vizinha às parcelas estudadas. A outra espécie de arbusto (*Eupatorium ligulaefolium*) mostrou apenas rebrotes após a queima, com uma alta taxa de mortalidade após 90 dias. Esta espécie possui xilopódio e até 150 gemas viáveis foram encontradas na superfície de um xilopódio analisado, mostrando sua grande capacidade de regeneração após a remoção de biomassa aérea. *Vernonia flexuosa* (herbácea, presença de rizóforos) também apresentou apenas rebrotes após as queimas e depois de dois meses seus indivíduos já tinham flores. Os indivíduos da outra espécie herbácea, *Chaptalia runcinata*, se estabeleceram nos novos microsites abertos pelo fogo, aproveitando a baixa competição causada pela remoção das dominantes touceiras de gramíneas que ali se encontravam antes do fogo. Esta espécie apresentou ambas as estratégias, tanto regeneração por sementes como por rebrotes. Fogo afetou tanto a estrutura como a demografia das populações das espécies estudadas, sendo um fator chave na dinâmica destas espécies.

A importância das estratégias de rengeração nos Campos do sul do Brasil foi descrita no **Capítulo 4**. Tratamentos com fogo e roçada foram aplicadas em duas áreas no Morro Santana (Porto Alegre, Rio Grande do Sul): frequentemente queimada (FB) e excluída do fogo há seis anos (E). Resultados mostraram a grande importância do rebrote para a regeneração da vegetação: 90% de todas as espécies mostraram rebrotes, enquanto apenas 10% apresentaram plântulas após os tratamentos. Apenas três espécies tiveram como estratégias a regeneração exclusiva por sementes: *Heterothalamus psidioides, Baccharis leucopappa* e *Gamochaeta americana*. O resultado mais interessante deste capítulo foi o recrutamente de novas espécies, principalmente em parcelas queimadas na área FB através de plântulas. Rebrotes eram geralmente as mesmas espécies ali presentes antes da aplicação dos tratamentos. Desta forma, os resultados do **Capítulo 4** corroboram a importância da regeneração via rebrotes nos Campos do Rio Grande do Sul.

Finalmente, o **Capítulo 5** trata dos efeitos do fogo e da roçada na dinâmica da vegetação e dos grupos funcionais dos Campos no sul do Brasil. Fogo teve efeitos positivos tanto nas graminóides quanto nas herbáceas. Arbustos não foram afetados pelo fogo. O resultado em curto prazo mais importante foi a remoção da serrapilheira e consequente abertura da vegetação, principalmente pelo fogo. Tais aberturas possibilitaram o estabelecimento de espécies que antes não conseguiam persistir frente à competição com as dominantes touceiras de gramíneas. A remoção da vegetação estimulou a sua regeneração. Mudanças abruptas na cobertura e composição de espécies foram observadas em parcelas queimadas na área FB, enquanto tais mudanças foram observadas em parcelas roçadas na área E. Turnover de espécies foi muito alto, principalmente em parcelas roçadas na área E. Após um ano da aplicação dos tratamentos, a diversidade de espécies nas parcelas queimadas da área FB ainda era menor, mas já a mesma na área excluída. Nas parcelas queimadas, já não havia mais diferença significativa em relação à diversidade de espécies em ambas as áreas.

Fogo tem um papel importante nos Campos do sul do Brasil e deve ser considerado em estudos futuros sobre esta vegetação. As conclusões recapitulam os resultados dos capítulos anteriores e descreve as estratégias mais importantes encontradas neste ecossistema: regeneração via sementes (com obligate seeder e resprouters facultativos) e a regeneração vegetativa, através dos rebrotes. Esta última foi subdividida em rebrote do banco de gemas aéreo e subterrâneo e de ambos. Regeneração através de rebrotes mostrou ser a estratégia mais importante das plantas nos Campos do sul do Brasil, tendo desta maneira, o banco de gemas um papel mais importante do que o banco de sementes. Por isso, estudos futuros sobre os efeitos do fogo na vegetação campestre devem considerar a dinâmica do banco de gemas e a regeneração da vegetação. Finalmente, o fogo poderia ser considerado como uma ferramenta alternativa para o manejo de áreas campestres no sul do Brasil.