Flora 209 (2014) 110–116

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Does disturbance affect bud bank size and belowground structures diversity in Brazilian subtropical grasslands?

Alessandra Fidelis[a,*], Beatriz Appezzato-da-Glória[b], Valério D. Pillar[c], Jörg Pfadenhauer[d]

[a] Chair of Vegetation Ecology, Technische Universität München, Emil-Ramann-Str. 6, 85354 Freising, Germany
[b] Laboratory of Plant Anatomy, Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, Brazil
[c] Laboratory of Quantitative Ecology, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil
[d] Chair of Vegetation Ecology, Technische Universität München, Freising, Germany

ARTICLE INFO

Article history:
Received 25 May 2013
Accepted 12 December 2013
Edited by R. Lösch
Available online 8 January 2014

Keywords:
Fire
Grazing
Brazilian *Campos* grasslands
Resprouter
Xylopodium

ABSTRACT

Brazilian *Campos* grasslands are ecosystems under high frequency of disturbance by grazing and fires. Absence of such disturbances may lead to shrub encroachment and loss of plant diversity. Vegetation regeneration after disturbance in these grasslands occurs mostly by resprouting from belowground structures. We analyzed the importance of bud bank and belowground bud bearing organs in *Campos* grasslands. We hypothesize that the longer the intervals between disturbances are, the smaller the size of the bud bank is. Additionally, diversity and frequency of belowground organs should also decrease in areas without disturbance for many years. We sampled 20 soil cores from areas under different types of disturbance: grazed, exclusion from disturbance for two, six, 15 and 30 years. Belowground biomass was sorted for different growth forms and types of bud bearing organs. We found a decrease in bud bank size with longer disturbance intervals. Forbs showed the most drastic decrease in bud bank size in the absence of disturbance, which indicates that they are very sensitive to changes in disturbance regimes. Xylopodia (woody gemmiferous belowground organs with hypocotyl-root origin) were typical for areas under influence of recurrent fires. The diversity of belowground bud bearing structures decreased in the absence of disturbance. Longer intervals between disturbance events, resulting in decrease of bud bank size and heterogeneity of belowground organs may lead to the decline and even disappearance of species that relay on resprouting from the bud bank upon disturbance.

© 2014 Elsevier GmbH. All rights reserved.

Introduction

Vegetation disturbance rather often removes plant biomass (Grime, 1979) and in most of cases, stimulates vegetation regeneration, based on new plant establishment by germination of seeds from the local seed bank or favoring species with the ability to resprout from above- and/or belowground buds (Klimešová and Klimeš, 2003) that are stored in so-called bud bank (Harper, 1977; Klimesová and Klimes, 2007). In particular the high capacity of grassland ecosystems to respond rapidly to disturbance might be linked to their capacity of fast re-growth, mainly from the bud bank (Clarke et al., 2013; Knapp and Smith, 2001). The bud bank plays, in this case, nearly the same function as the seed bank for seedling recruitment: it maintains plant propagules in a dormant way, until environmental conditions are optimal for resprouting. In such cases the composition of the aboveground plant community and shoot population dynamics are more tightly connected with the bud bank than with a soil seed bank (Dalgleish and Hartnett, 2009; Zhang et al., 2009). Bud-bearing organs can maintain large carbohydrate storage pools. Therefore, resprouting shoots easily are able to outcompete seedlings (Verdaguer and Ojeda, 2002).

Besides its great importance for vegetation regeneration, it is not easy to access the bud bank of the entire plant community and to distinguish buds belonging to different functional groups (Benson and Hartnett, 2006; Benson et al., 2004; Dalgleish and Hartnett, 2009, 2006; Lee, 2004; Zhang et al., 2009). Moreover, few studies are devoted to assessment of belowground organs for a whole community and its relation to disturbance events (Klimesova et al., 2011; Sosnová et al., 2010; Wellstein and Kuss, 2011). Costs and tradeoffs associated with maintaining buds are not well known (Clarke et al., 2013; Vesk and Westoby, 2004), but there are indications that a change in the disturbance regime of a vegetation type my cause changes in species composition, being related to the costs in terms of biomass and energy investment which a bud bank will bring about (Bellingham and Sparrow, 2000; Midgley, 1996).

Subtropical grasslands in southern Brazil (also known as "Campos") are ecosystems under high frequency disturbances, mainly resulting from grazing and fire (Overbeck et al., 2007). They are

* Corresponding author. Current address: Instituto de Biociências, Departamento de Botânica, UNESP – Universidade Estadual Paulista, Av 24A, 1515, CEP 13506-900 Rio Claro, Brazil. Tel.: +55 19 35264208; fax: +55 19 35264201.
E-mail address: afidelis@rc.unesp.br (A. Fidelis).

0367-2530/$ – see front matter © 2014 Elsevier GmbH. All rights reserved.
http://dx.doi.org/10.1016/j.flora.2013.12.003

very rich in species (ca. 2500 plant species, Boldrini et al., 2009), but there is a decrease in species richness when areas are excluded from disturbance (Fidelis et al., 2012; Overbeck et al., 2005). Mechanisms that maintain plant diversity there are not well known, but the frequent removal of aboveground biomass and, consequently, the opening of new gaps for recruitments (mostly by resprouting) certainly play a crucial role in grassland dynamics (Fidelis et al., 2012). When *Campos* grasslands are excluded from disturbance, shrub species resprouting from belowground organs are replaced by shrubs that regenerate via seedling establishment (Fidelis et al., 2012, 2010), and forb species dominating in disturbed areas (Fidelis et al., 2012; Overbeck et al., 2005) start to disappear due to the shading effect caused by cespitose grasses (Fidelis et al., 2012). Both, forbs and shrubs usually have belowground bud bearing organs (Canadell et al., 1998), which might imply costs when the disturbance regime is relaxed.

To elucidate how abundant are resting buds of *Campos* grassland, and which and how numerous bud bearing organs do occur belowground, we studied those parameters at sites under different disturbance regimes – grazing each year, exclusion from burning for 2, 6, 15, and 30 years – that were previously grazed annually and burned every 2–3 years. We determined the number of belowground buds and described the diversity of bud bearing organs in the different areas. We also describe the number of buds of the different functional groups (graminoids, forbs and shrubs) in the areas under different disturbance regimes.

Materials and methods

Study area

We used a space-for-time substitution approach (e.g. Walker et al., 2010) and selected five disturbance regimes occurring in four different grassland areas in southern Brazil (Table 1). They are species-rich grasslands (Boldrini et al., 2009; Overbeck et al., 2007), with a high fine-scale diversity (Overbeck et al., 2005), containing both C3 and C4 grasses (Fidelis, 2010). If no disturbance occurs in the area, there is a decrease in species richness, mostly of forb species, that are outcompeted by grasses and shrubs (Fidelis et al., 2012; Overbeck et al., 2005).

It is difficult to find true replicated grassland areas with the same management and with the same disturbance regime. Additionally, sites under long-term exclusion of fire and grazing are rare. Therefore, we chose these areas representing the different disturbance regimes, but we are aware of the problems associated with pseudo-replication (Hurlbert, 1984). Therefore, we just describe the number of buds and the type of belowground organs in each site, and compare only the different functional groups in each site, in order to avoid pseudo-replication.

All sampling was performed during summer in all sites. In the field, cores were sampled randomly (20 cores/areas, 0.2 m × 0.2 m × 0.2 m) and stored in plastic bags. In the laboratory, all belowground biomass was sorted into different growth forms (graminoids, and forbs and shrubs). When there was no aboveground biomass and/or if correct identification of growth forms was not possible, the sample was labeled undetermined and buds were not considered for the analysis (less than 3% of total sample). Belowground plant structures were washed and fixed in FAA 70 (formalin–acetic acid–alcohol), dehydrated in a graded ethylic series and finally conserved in alcohol 70%. Buds with leaf primordia were easily identified and counted with the help of a stereomicroscope. When the protrusions of underground organs did not have leaf primordia, longitudinal sections were performed and the slides studied using a light microscope.

Table 1
Location of study sites, and description of climate (Cfa – temperate humid with hot summers, Cfb – temperate humid with mild summers), altitude, disturbance regime, dominant vegetation and plant species, and methods used (Livi, 1999; Waechter et al., 1984).

Study site	Coordinates	Altitude (m)	Climate	Disturbance reqime	Dominant vegetation	Dominant species	Methods
Morro Santana (MS)	30°03′ S, 51°07′ W	311	Cfa	Exclusion of grazing, exclusion of fire for two years (**E2**) and six years (**E6**)	E2: continuous grass matrix, rich in forb species; E6: higher percentage of shrub cover	*Aristida flaccida*; *Vernonia flexuosa*; *Baccharis leucopappa*	20 samples (20 × 20 × 15) in E2 and E6. Shrubs ≤ 1.5 m.
Experimental Station of the Universidade Federal do Rio Grande do Sul (ESUFRGS)	30°05′ S, 51°40′ W	20–70	Cfa	Long-term grazing (**Gr**)	Fine-scale mosaic of intensively grazed and ungrazed patches	*Paspalum notatum*	20 samples (20 × 20 × 15): grazed patches. Shrubs ≤ 1.5 m.
Aparados da Serra National Park (ASNP)	30°04′ S, 51°06′ W	720	Cfb	Exclusion of both grazing and fire for 15 years (**E15**)	Tussock grasses dominate the area (almost 80 cm tall), with isolated shrub individuals	*Andropogon lateralis*; *Sorghastrum setosum*	20 samples (20 × 20 × 15). Shrubs ≤ 1.5 m.
Ecological Station of Aracuri (ESA)	28°13′ S, 51°10′ W	900	Cfb	Exclusion of both grazing and fire for 30 years (**E30**)	Short shrubland dominated by *Baccharis* species	*Baccharis uncinella*	20 samples (20 × 20 × 15): between shrubs, where typical grasslands species could still be observed. Shrubs ≤ 1.5 m.

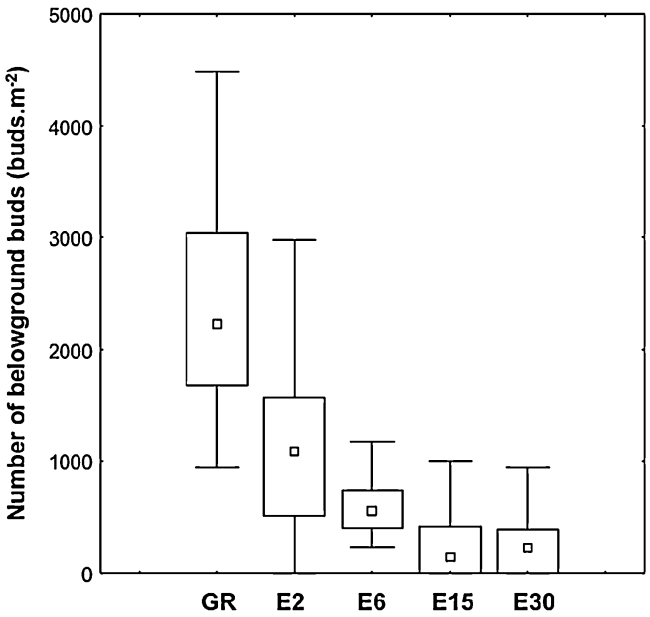

Fig. 1. Number of belowground buds (buds m^{-2}) in the study areas under different disturbance types and regimes: GR – grazing, E2 – exclusion from disturbance for two years, E6 – exclusion from disturbance for six years, E15 – exclusion from disturbance (grazing + fire) for 15 years, and E30 – exclusion from disturbance for 30 years. The box-plots present the median, 25% – interquartiles, and maximum and minimum values.

Belowground organs were identified and classified, but we used only the cores from E2 and E30 for this part of the analysis. 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: bulbs, corms, tuberous roots, underground stems, xylopodia, rhizophores and rhizomes. Since bulb and corm, as well as rhizophores and rhizomes have the same function, they were grouped for the statistical analyses. For a more detailed discussion about belowground bud bearing organs, see Appezzato-da-Glória et al. (2008).

Statistical analyses

Since we have no true replication of areas, we only describe the number of buds per square meter on each locality. To compare the bud bank size between growth forms (graminoids, forbs and shrubs) for each disturbance type and regime, we used one-way analysis of variance (factor: growth forms), which was tested by randomization test (Manly, 2007). The software MULTIV (Pillar, 2005) was used for analysis of variance.

Results

Bud bank analysis

The bud bank found in grazed areas tended to be larger than in other areas, as shown by Fig. 1 (2408 buds m^{-2}). On the other hand, the bud banks in areas with longer intervals of disturbance were almost 10-fold smaller than in the vegetation under grazing (398 buds m^{-2} for E15 and 292 buds m^{-2} for E30, respectively). The areas excluded from disturbance since 2 (E2) and six years (E6) showed 1122 and 1018 buds m^{-2}, respectively.

At the regularly grazed and fire-excluded for two years areas (GR and E2), the forb bud bank was large, but the graminoid bud bank exceeded it somewhat. In sites completely excluded from disturbance for two years, the largest bud bank was from forbs ($p = 0.0001$, Fig. 2A), contributing to more than 80% of the total bud bank (shrubs = 16%, graminoids = 0.8%). In grasslands excluded from disturbance for six years (E6), the number of forb buds decreased, but still showed a high contribution to the total bud bank (68%), though being very variable depending on plots, while the graminoid bud bank was almost absent in these grasslands (1%, Fig. 2B).

Table 2
Number of bud bearing organs assessed per square meter (average ± SD) in subtropical grasslands excluded from fire for two (E2) and 30 years (E30) in Southern Brazil.

Bud bearing organ	E2	E30
Xylopodium	48.6 ± 36.9	11.9 ± 20.3
Bulb	30.6 ± 33.8	6.0 ± 15.6
Rhizome	23.6 ± 21.8	8.3 ± 18.3
Tuberous roots	33.3 ± 39.3	16.7 ± 35.6
Underground stems	4.2 ± 9.6	8.3 ± 24.2

The larger the intervals of disturbance, the less important was the contribution of the forb bud bank to the total bud bank. Importance of the graminoid bud bank in these sites (E15 and E30, Fig. 2C and D) increased, contributing to 29 and 6%, respectively. Though with a much lower density, forbs were still responsible for 43 and 54% of the total buds in sites excluded from disturbance for 15 and 30 years. On the other hand, the shrub bud bank showed a low density in both sites (15.8 buds m^{-2} for sites E15 and 91.6 buds m^{-2} for sites E30), respectively.

At grazed sites graminoids showed the greatest contribution to the bud bank (1418 buds m^{-2}, 59% of the total bud bank, Fig. 2E), followed by a likewise high number of buds belonging to the forb bud bank (978.4 buds m^{-2}, 40.5% of the total bud bank, $p = 0.2$). The shrub bud bank was significantly lower ($p = 0.001$, 11.6 buds m^{-2}), representing only 0.5% of the total bud bank.

Belowground organs

Belowground structures exhibited a high diversity. Bulbs and corms were usually found with no aboveground biomass (Fig. 3A and B). Graminoid rhizomes were not very abundant (less than 5% of total rhizomes found, Fig. 3C) in comparison to rhizomes of forbs. Xylopodia and tuberous roots (Fig. 3D–F, respectively) were present in many samples, sometimes together in the same structure. Xylopodium structures of some species showed their surface covered by viable buds, sometimes up to 100 buds/xylopodium (Fig. 3G). In E30 a decrease in composition and number of the belowground organs could be observed (Table 2). A tendency to higher numbers of xylopodia and tuberous roots were found in frequently burned grasslands, whilst the other types of belowground organs were barely found in fire-excluded areas (E30).

Discussion

Bud bank and disturbance

A tendency in decreasing the number of buds and diversity of bud bearing organs could be observed in relation to the time since last disturbance (exclusion since 2, 6, 15 and 30 years). This resulted primarily from a decrease of the forb bud bank.

The graminoid bud bank was the most important one in the grazed area, where it contributed almost 60% to the total bud bank. In these sites, the graminoid bud bank was composed predominantly by *Paspalum notatum*, a typical rhizomatous grass that is widespread in grazed areas in southern Brazil. Rhizomatous and stoloniferous grass species dominate generally the pastures in southern Brazil. After grazing exclusion they decrease in dominance and are mostly replaced by tussock grasses, e.g. *Andropogon lateralis* (Boldrini and Eggers, 1997, 1996).

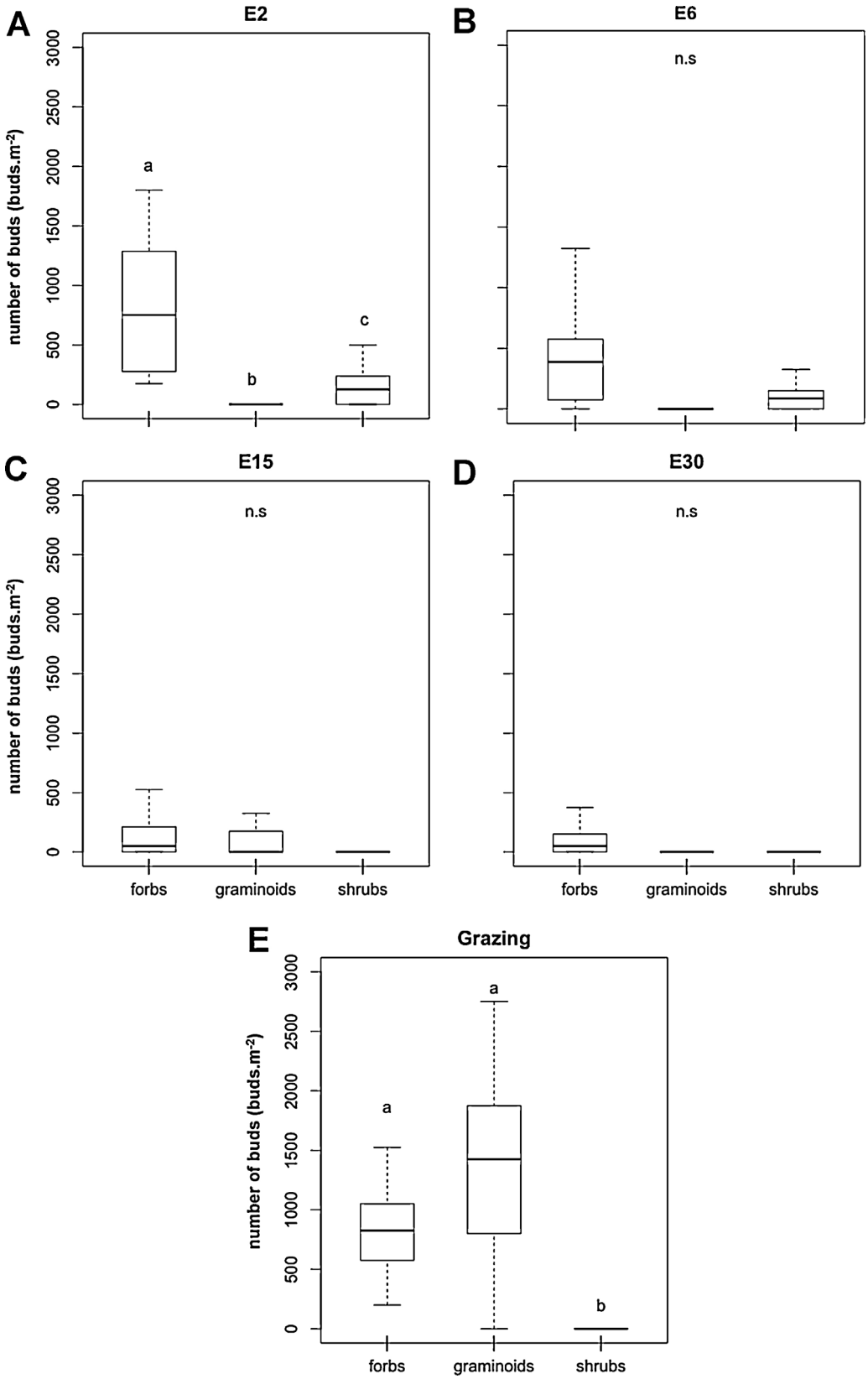

Fig. 2. Number of buds assessed per square meter for forbs, graminoids and shrubs in subtropical grasslands in southern Brazil with different disturbance types and regimes: (a) exclusion from disturbance for two years, (b) exclusion from disturbance for six years, (c) exclusion from disturbance for 15 years, (d) exclusion from disturbance for 30 years, and (e) grazing. Different letters means significant differences between growth forms ($p \leq 0.05$). The box-plots present the median, 25% – interquartiles, and maximum and minimum values.

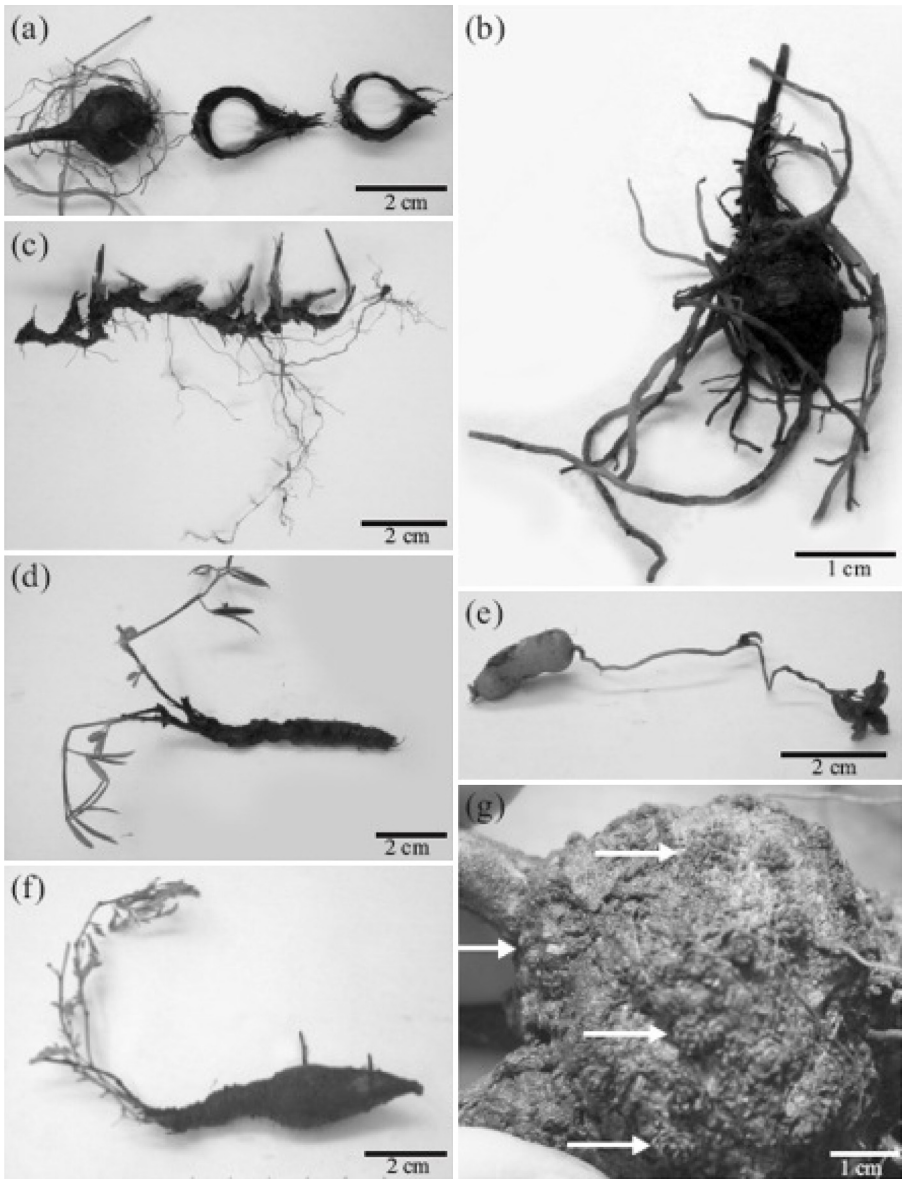

Fig. 3. Different bud-bearing belowground organs: (a) bulb, (b) corm, (c) graminoid rhizome, (d) xylopodium, and (e) tuberous root; (f) xylopodium and (g) details of viable buds of a xylopodium structure. White arrows show bud region.

In burned areas, there is a lack of rhizomatous and stoloniferous graminoid species (Overbeck and Pfadenhauer, 2007), which is confirmed by our results. In sites excluded from disturbance for longer intervals (E15 and E30) the belowground graminoid bud bank on rhizomes gained importance, even if the dominant graminoids in these sites are caespitose grasses, mostly *Andropogon lateralis* and *Sorghastrum setosum* (C4 grasses). We can speculate that rhizomatous grasses are able to survive only in communities with long periods between fires.

The forb bud bank seems to be most affected by lack of disturbance: its contribution to the total bud bank decreased from 80% on the site that was burned two years ago to 6% in sites excluded from fire and grazing for 30 years. The longer the intervals since the last fire, the smaller the forb bud bank is. Such effect can also be observed for the aboveground vegetation: in frequently burned areas, the number and cover of forb species is higher. In areas protected from fire cover and diversity of forbs decrease, this life form being outcompeted by tussock grasses and further, by grassland shrubs (Overbeck et al., 2005). An opposite tendency was found in the North American Tallgrass Prairie: the larger the intervals among disturbance events, the larger is the forb bud bank (Benson et al., 2004; Dalgleish and Hartnett, 2009) and the smaller is the graminoid bud bank. This is reflected also by the aboveground vegetation: annually burned grasslands shows a higher number of graminoid tiller, whilst infrequently burned areas have a higher density of forb ramets.

The shrub bud bank was not very important in the study areas with different disturbance types and regimes. In grazed and frequently disturbed areas, several resprouter shrubs can be found, such as *Eupatorium ligulaefolium*, *Baccharis cognata* and *Baccharis trimera* (all Asteraceae, usually <1.5 m), that contributed prominently to the higher number of buds in these sites. In areas excluded from disturbance, there is an increase in shrub cover (Müller et al., 2007; Oliveira and Pillar, 2004). However, the dominant shrubs on those sites are obligate seeders (i.e. *Baccharis uncinella*, *Heterothalamus psiadioides*) possessing no bud bank (Fidelis et al., 2010).

Our results emphasize the importance of a viable bud bank on the vegetation regeneration after disturbance in Brazilian *Campos*

grasslands. Since disturbance by fire and grazing is the major factor maintaining plant diversity in these grasslands, the bud bank plays a crucial role on the maintenance of the biodiversity and vegetation dynamics in southern Brazilian grasslands.

The ecological role of belowground bud bearing organs

The most abundant bud bearing organs were xylopodia. Xylopodia are woody gemmiferous belowground organs of mixed origin (with participation of hypocotyl and primary root) without pronounced carbon storage function (Appezzato-da-Glória and Estelita, 2000; Appezzato-da-Glória et al., 2008; Appezzato-da-Glória and Cury, 2011; Rizzini and Heringer, 1961). No storage parenchyma tissue is found in xylopodium structures (Appezzato-da-Glória and Estelita, 2000). However, they are usually combined with tuberous roots (Appezzato-da-Glória and Estelita, 2000; Milanez and Moraes-Dallaqua, 2003) that provide the nutrients necessary for a plant to resprout after fire or drought events. Buds are irregularly distributed all over the surface of the xylopodium (see Fig. 3G), but mostly found near the soil surface (Appezzato-da-Glória et al., 2008). Plants with xylopodia in Cerrado vegetation (Brazilian tropical savanna) usually lose the aboveground parts during the dry season. 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 pronounced dry season. As a consequence, the xylopodium function is exclusively related to the resprouting ability of plants after biomass loss due to fire events.

The other organs found in this study (bulbs, rhizomes and tuberous roots) are typical storage organs (Dong and Pierdominici, 1995; Suzuki and Stuefer, 1999), but this must not so apply for the underground stems. Bud bearing organs in frequently burned sites of *Campos* grassland may represent 30% of belowground biomass (Fidelis et al., 2006). With fire exclusion, the number of belowground organs decreases, but they still can be found with viable buds and lacking aboveground parts. These organs can survive belowground for many years, without allocation of resources to shoot formation, as it was found for many species in different ecosystems (Shefferson, 2009).

Conclusions

Campos grasslands in southern Brazil are ecosystems under frequent disturbance, mainly grazing and fire. Resprouting is the most important strategy of site occupation after disturbance, being totally supported by the large bud bank. A high amount of belowground organs with high bud numbers and carbon storage potential characterizes this vegetation type. Data of present study show that, the longer the intervals among disturbance events are, the smaller is the bud bank and the diversity and frequency of belowground organs. This apparently implies that there are costs connected with forming a belowground bud bank, which may lead to decline of species that possess an obligate bud bank in cases where disturbances are reduced.

Acknowledgments

We greatly thank the security guards of the Universidade Federal do Rio Grande do Sul for accompanying us during field work. We are also thankful to Marcel Tust and Maximiliano de Oliveira for collecting soil cores, and Marli Kazue Misaki Soares for helping with the pictures of belowground structures. We also thank three anonymous reviewers for their valuable suggestions on a former version of this manuscript. Finally, we thank Susana Bautista for helping us with data analyses. This project was supported by the German Research Foundation (DFG – PF 120/10-2).

References

Appezzato-da-Glória, B., Cury, G., 2011. Morpho-anatomical features of underground systems in six Asteraceae species from the Brazilian Cerrado. Anal. Acad. Bras. Cienc. 83, 1–11.
Appezzato-da-Glória, B., Estelita, M.E.M.F.M., 2000. The developmental anatomy of the subterranean system in *Mandevilla illustris* (Vell.) Woodson and *M. velutina* (Mart. ex Stadelm.) Woodson (Apocynaceae). Rev. Bras. Botânica 23, 27–35.
Appezzato-da-Glória, B., Hayashi, A.H.H., Cury, G., Soares, M.K.M.K.M., Rocha, R., 2008. Underground systems of *Asteraceae* species from the Brazilian Cerrado. J. Torrey Bot. Soc. 135, 103–113.
Bellingham, P.J., Sparrow, A.D., 2000. Resprouting as a life history strategy in woody plant communities. Oikos 89, 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 Ecol. 187, 163–177.
Benson, E.J., Hartnett, D.C., Mann, K.H., 2004. Belowground bud banks and meristem limitation in tallgrass prairieplant populations. Am. J. Bot. 91, 416–421.
Boldrini, I.I., Eggers, L., 1996. Vegetação campestre do sul do Brasil: dinâmica de espécies à exclusão do gado. Acta Bot. Brasilica 10, 37–50.
Boldrini, I.I., Eggers, L., 1997. Directionality of succession after grazing exclusion in grassland in the South of Brazil. Coenoses 12, 63–66.
Boldrini, I.I., et al. (9 authors), 2009. Flora. In: Boldrini, I.I. (Ed.), Biodiversidade Dos Campos Do Planalto de Araucárias. MMA, Brasília, pp. 38–94.
Canadell, J., López-Soria, L., Lopez-Soria, L., 1998. Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Funct. Ecol. 12, 31–38.
Clarke, P.J., et al. (8 authors), 2013. Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. New Phytol. 197, 19–35.
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 Phytol. 171, 81–89.
Dalgleish, H.J., Hartnett, D.C., 2009. The effects of fire frequency and grazing on tallgrass prairie productivity and plant composition are mediated through bud bank demography. Plant Ecol. 201, 411–420.
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., 2010. South Brazilian Campos grasslands: biodiversity, conservation and the role of disturbance. In: Runas, J., Dahlgren, T. (Eds.), Grassland Biodiversity: Habitat Types, Ecological Processes and Environmental Impacts. Nova Science Publisher, New York, pp. 223–239.
Fidelis, A., Müller, S., Pillar, V.D., Pfadenhauer, J., 2006. Efeito do fogo na biomassa aérea e subterrânea dos Campos Sulinos. In: Campos, X.X.I.R.G. (Ed.), Desafios e Oportunidades Do Bioma Campos Frente à Expansão e Intensificação Agrícola. EMBRAPA – Clima Temperado, Pelotas.
Fidelis, A., Müller, S., Pillar, V., Pfadenhauer, J., 2010. Population biology and regeneration of forbs and shrubs after fire in Brazilian Campos grasslands. Plant Ecol. 211, 107–117.
Fidelis, A., Blanco, C., Müller, S., Pillar, V., Pfadenhauer, J., 2012. Short-term changes caused by fire and mowing in Brazilian Campos grasslands with different long-term fire histories. J. Veg. Sci. 23, 552–562.
Grime, J.P., 1979. Plant Strategies and Vegetation Processes. John Wiley and Sons, Chichester, UK.
Harper, J., 1977. Population Biology of Plants. Academic Press, London.
Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211.
Klimešová, J., Klimeš, L., 2003. Resprouting of herbs in disturbed habitats: is it adequately described by Bellingham–Sparrow's model? Oikos 103, 225–229.
Klimesová, J., Klimes, L., 2007. Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. Persp. Plant Ecol. Evol. Syst. 8, 115–129.
Klimesova, J., de Bello, F., Herben, T., 2011. Searching for the relevance of clonal and bud bank traits across floras and communities. Folia Geobot. 46, 109–115.
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 forests. Can. J. Bot. 82, 1468–1480.
Livi, F.P., 1999. Elementos do clima: o contraste de tempos frios e quentes. In: Menegat, R., Porto, M.L., Carraro, C.C., Fernandes, L.A.D. (Eds.), Atlas Ambiental de Porto Alegre. Editora da Universidade Federal do Rio Grande do Sul, Porto Alegre, pp. 73–78.
Manly, B.F.J., 2007. Randomization, Bootstrap, and Monte Carlo Methods in Biology. Chapman & Hall/CRC, Boca Raton.
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* (Wedd.) Parodi (Fabaceae). Rev. Bras. Botânica 26, 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 Ecol. 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 Ecol. 5, 197–202.
Overbeck, G.E., Pfadenhauer, J., 2007. Adaptive strategies in burned subtropical grassland in southern Brazil. Flora 202, 27–49.
Overbeck, G.E., Müller, S.C., Pillar, V.D., Pfadenhauer, J., 2005. Fine-scale post-fire dynamics in southern Brazilian subtropical grassland. J. Veg. Sci. 16, 655–664.
Overbeck, G.E., et al. (9 authors), 2007. Brazil's neglected biome: the South Brazilian Campos. Perspect. Plant Ecol. Evol. Syst. 9, 101–116.
Pillar, V.D., 2005. Multiv: Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling. Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.
Rizzini, C.T., Heringer, E.P., 1961. Underground organs of plants from some southern Brazilian savannas, with special reference to the xylopodium. Phyton 17, 105–124.
Rizzini, C.T., Heringer, E.P., 1962. Studies on the underground organs of trees and shrubs from some southern Brazilian savannas. Anal. Acad. Bras. Cienc. 34, 235–247.
Shefferson, R.P., 2009. The evolutionary ecology of vegetative dormancy in mature herbaceous perennial plants. J. Ecol 97, 1000–1009.
Sosnová, M., van Diggelen, R., Klimešová, J., 2010. Distribution of clonal growth forms in wetlands. Aquat. Bot. 92, 33–39.
Suzuki, J.-I., Stuefer, J.F., 1999. On the ecological and evolutionary significance of storage in clonal plants. Plant Species Biol. 14, 11–17.
Verdaguer, D., Ojeda, F., 2002. Root starch storage and allocation patterns in seeders and resprouter seedlings of two Cape *Erica* (Ericaceae) species. Am. J. Bot. 89, 1189–1196.
Vesk, P.P.A., Westoby, M., 2004. Funding the bud bank: a review of the costs of buds. Oikos 106, 200–208.
Waechter, J.L.L., Cestaro, L.A.A., Miotto, S.T.S., 1984. Vegetation types in the ecological station of Aracuri, Esmeralda, Rio Grande do Sul, Brazil. Phytocoenologia 12, 261–269.
Walker, L.R., Wardle, D.A., Bardgett, R.D., Clarkson, B.D., 2010. The use of chronosequences in studies of ecological succession and soil development. J. Ecol. 98, 725–736.
Wellstein, C., Kuss, P., 2011. Diversity and frequency of clonal traits along natural and land-use gradients in grasslands of the Swiss Alps. Folia Geobot. 46, 255–270.
Zhang, J., Mu, C., Wang, D., Wang, J., Chen, G., 2009. Shoot population recruitment from a bud bank over two seasons of undisturbed growth of *Leymus chinensis*. Botany 87, 1242–1249.