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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

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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.

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).

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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 regime	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.