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Population biology and regeneration of forbs and shrubs after fire in Brazilian *Campos* grasslands

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Abstract Fire is an important factor in several ecosystems, affecting plant population biology. *Campos* grasslands are under constant influence of disturbance, mostly grazing and fire. However, few studies evaluated the effect of fire on plant population biology of grassland species. Therefore, we aim to analyze the effect of fire on the 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 in southern Brazil: frequently burned (FB) and excluded from fire since 6 years (E). All plots were subjected to controlled burns during summer. Before experiments, populations were sampled. Further observations were carried out after 90 and after 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 the bud bank of the following species: *E. ligulaefolium* and *V. flexuosa*. The obligate seeder species had all individuals killed by fire and established only after 1 year. Resprouters, however, showed new stems immediately after fire. *E. ligulaefolium* and *V. flexuosa* showed only vegetative regeneration from belowground organs and more individuals in excluded sites 1 year after the fire. The bud bank of *E. ligulaefolium* tended to be larger in excluded sites, whilst *V. flexuosa* showed an opposite result. High temperatures did not enhance nor kill seeds from both studied species. Vegetative regeneration was the most important strategy for all studied species, except for *H. psiadioides*, the obligate seeder species. Fire thus, plays an important role on population structure and demography, being also important for plant recruitment.

Keywords Obligate seeder · Plant population structure · Resprouter · Bud bank · Heat shock experiment

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Introduction

Fire is an important event in many ecosystems. It shapes vegetation, maintains physiognomy and structure, as well as diversity of several ecosystems (Bond and Keeley 2005). Fire size, shape and spatial patterns affect recovering and seedling colonization of burned sites (Lavorel et al. 1998). Furthermore, shoot recovery might be influenced by fire intensity and temperature (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 damages plants and stimulates vegetative regrowth (Pfab and Witkowski 1999). Vegetative reproduction is high, while sexual reproduction appears not to be so important for the population growth rate (Hoffmann 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 (e.g. better microsite conditions after fire events, Satterthwaite et al. 2002) or negative (e.g. the reduction of safe sites and seed availability, Hoffmann 1996) correlation with fire events.

Campos grasslands in southern Brazil are unique ecosystems, maintained mostly by grazing and fire events (Overbeck et al. 2007). Unfortunately, in Brazil plant population studies on grassland species are scarce (see Fidelis et al. 2008).

We aim to study the plant population in *Campos* grasslands in southern Brazil and its responses to fire events, 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 the laboratory and analyzed the bud bank of chosen species.

Materials and methods

Study area

The study was carried out in natural subtropical grassland sites on Morro Santana, a granitic hill located in 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 grassland 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, with return intervals of 2–5 years. It has been present throughout the past 1200 years according to palynological studies conducted in the area (Behling et al. 2007). Nowadays, fires are mostly set by local residents to clean the area, 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, with a dominance of C_4 caespitose grasses although C_3 grasses are also present, together with a large number of small forbs belonging to different botanical families (Overbeck et al. 2005). Shrubs are also present and their importance increases with longer intervals of fire.

Two sites were chosen for this study: frequently burned grassland (FB, last fire occurred 2 years before experiments) and excluded from fire since 6 years (E). Site FB is characterized by a continuous grass matrix and by a large cover of forb species, with the presence of several small grassland shrubs. The excluded site shows a higher percentage of shrub cover and dead biomass.

Population biology study

Four species from the same botanical family (Asteraceae) were chosen for this study, since this botanical family is well represented in these grasslands (for more details see Boldrini 1997; Matzenbacher 2003). *Vernonia flexuosa* is a perennial forb, 30–80 cm in height, flowering from October to April (Matzenbacher 2003). It shows large rhizophores (belowground stem system, for more information see Hayashi and Appezzato-da-Glória 2005) and clonal growth (pers. obs.). *Chaptalia runcinata* (no belowground organ) is a perennial rosette (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. It flowers from January until April (Matzenbacher 2003).

Seven plots (1 × 2 m) were randomly established on both sites mentioned above 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 25 m^2 in order 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. Differences in fire intensities between sites can be explained by available fine biomass which were distinct for both areas. Temperatures at soil level varied from 61.6 to 319.11°C (site FB) and from 48.3 to 537.4°C (site E). After fire, nearly all aboveground biomass was consumed (Fidelis et al. submitted a).

Before conducting the controlled burns, all populations were sampled (number of stems, plant height and diameter on rosette plants, as well as presence of flowers/fruits, T0). Populations were grouped according to the following classes: juveniles (individuals $\leq$10 cm height for shrubs species, individuals $\leq$5 cm diameter for forbs), non-flowering (individuals >10 cm height for shrubs and >5 cm diameter for forbs) and flowering individuals. Since 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 (*H. psiadioides*). Instead, we evaluated the regeneration strategy of these species only after fire experiments, considering thus, seedlings and resprouts for the analysis. Observations were carried out 2 months (T60) and 1 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 *H. psiadioides* and *V. flexuosa*. *E. ligulaefolium* did not flower during the study period (observations were carried out in March and December) and only a few individuals of *C. runcinata* flowered, so that the number of seeds was not sufficient for experiments. Seeds were collected on plant canopies from different populations during summer. They were weighed before germination experiments.

Seeds were subjected to different heat shock temperatures each lasting 1 min: 60, 80, 100 and 120°C. Each species and treatment had five 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 a germination chamber. Since this study aimed to reproduce real conditions from the field a temperature between 20/30°C and, 12/12 h dark/light conditions were chosen.

Seed were kept moist and observations were performed every 3 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 banks from a shrub (*E. ligulaefolium)* and a forb (*V. flexuosa*) were analyzed. Three plots (1 m^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 the 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 traits and buds on different sites.

We used the same test to analyze differences between temperatures in germination experiments for the chosen species. Randomization tests were used (Pillar and Orlóci 1996) applied to Euclidean distances (10000 iterations), since there is no restriction on normal distribution of data (for more details about method, see Manly 2007). In order to avoid serial correlation, 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 observation where 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, Stasoft).

Results

Population biology

In general, more individuals were sampled in the frequently burned site, except for *H. psiadioides* before experiments (Fig. 1). Its populations showed more individuals in excluded sites ($P = 0.05$). Two months after the fire, no individuals of *H. psiadioides* could be observed. One year later, seedlings were found in site E. *E. ligulaefolium* had more individuals in site FB before fire experiments ($P = 0.018$) and showed the same tendency after experiments ($P > 0.05$). The same pattern could be observed for *C. runcinata* ($P > 0.05$). *V. flexuosa* tended to show more individuals in site FB before and 2 months after fire experiments, but after 1 year, site E tended to have more individuals ($P > 0.05$).

H. psiadioides was the only species with flowering individuals, but only in excluded sites (49.24). Populations of *E. ligulaefolium* contained a higher proportion of non-flowering individuals in site FB (63.86%) and the opposite result in site E: 61.1% juveniles and 39.9% non-flowering individuals.

Forb species showed different patterns. Two months after fire, populations of *C. runcinata* had more juveniles than non-flowering individuals in both sites (55.7% in FB and 85.71% in E), whilst populations of *V. flexuosa* showed a higher proportion of non-flowering individuals (72.34% in FB and 60% in E). Flowering individuals were present in both species 2 months after fire. *C. runcinata* showed flowering individuals in both sites and *V. flexuosa* only in excluded site.

Populations of *H. psiadioides* had new individuals only 1 year after fire experiments (all juveniles). *E. ligulaefolium* showed well-established populations, most with non-flowering adult individuals in FB (82.15%) and E (91.18%), with few juveniles 1 year after fire. Populations of *V. flexuosa*, on the other hand, showed a high proportion of juveniles in frequently burned sites (66.67%), but the same proportion of juveniles and non-flowering individuals in excluded sites (45%). In addition, 1 year after fire, flowering individuals were also observed in excluded sites (less than 10%). Populations of *C. runcinata* showed a different pattern: more non-flowering individuals in FB (55.36%) and more juveniles in E (59%). Flowering individuals were found only two months after fire.

Both *V. flexuosa* and *E. ligulaefolium* showed only vegetative regeneration. New stems resprouted from belowground organs. No resprouting from epicormic buds was observed. *C. runcinata* showed 98% of new rosettes arising from vegetative regeneration. Two months after the fire experiments only 2% of all individuals were seedlings. However, 1 year after the fire, no seedlings could be observed. *H. psiadioides* showed 100% of seedlings emerging 1 year after fire experiments, exclusively in site E.

After fire experiments, all individuals of *H. psiadioides* died (Table 1). All forb species and the other shrub species, *E. ligulaefolium* showed a very high shoot recruitment in both sites 2 months after the experiments (T60). However, stem mortality was also high at T360, mostly in site FB. *V. flexuosa* showed the highest rates of stem death 1 year after fire in site FB (81%). Both forb species displayed no stem death 1 year after the experiments in excluded sites, and stem establishment was still high, mostly for populations of *C. runcinata* (increased in 328% from T60 to T360). *E. ligulaefolium* also had a higher rate of stem death in site FB than in site E (68 and 29%, respectively).

Plant traits from populations also showed significant differences between sites and time. Individuals of *V. flexuosa* tended to be taller in excluded sites before fire experiments than in frequently burned sites ($P > 0.05$, Table 2). One year after experiments, individuals were still smaller than before experiments

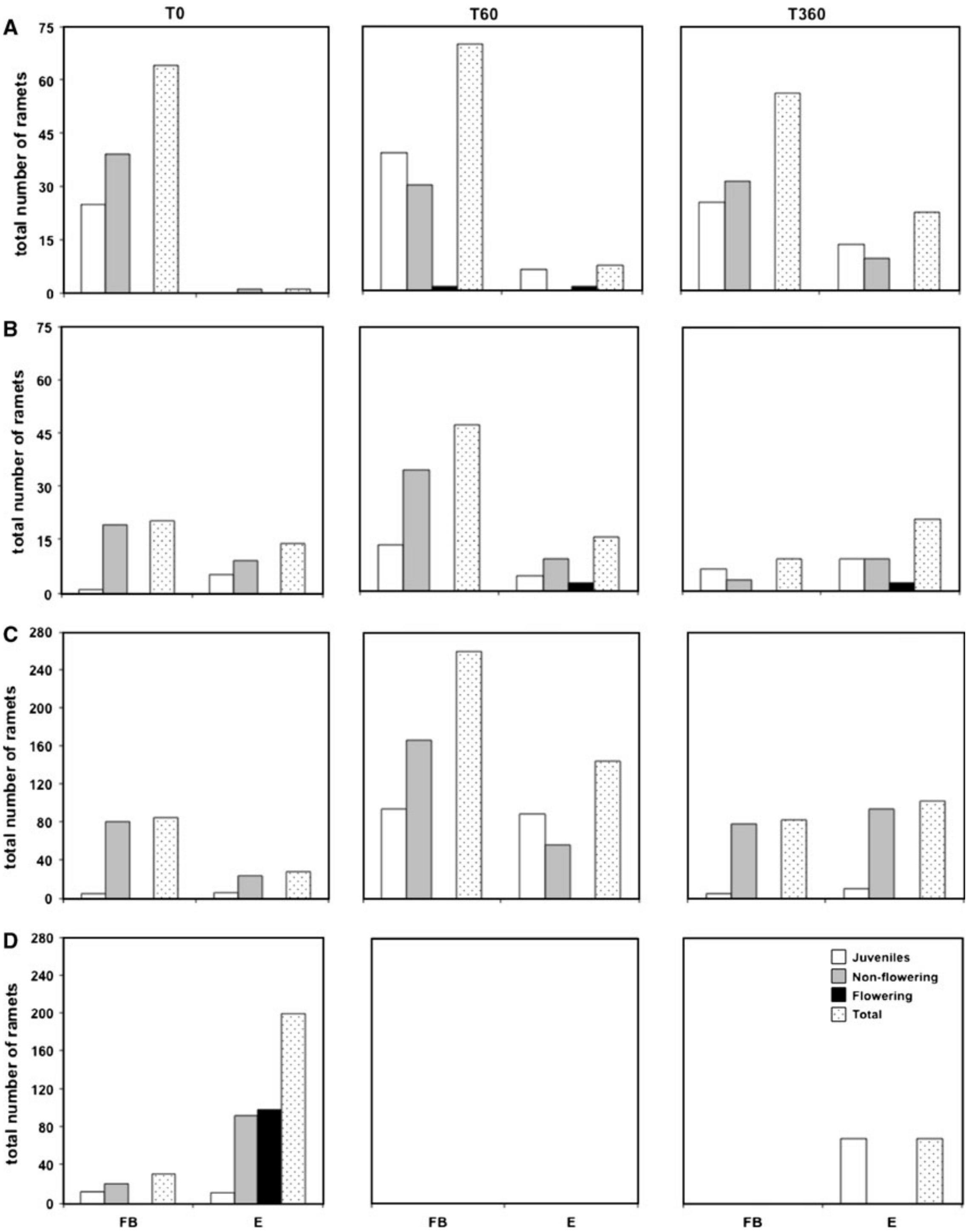

Fig. 1 Number of individuals (ramets) in different age classes: juveniles (individuals ≤10 cm height for shrubs species, individuals ≤5 cm diameter for forbs); non-flowering individuals; flowering individuals; and, total number of individuals in sites FB (frequently burned) and E (excluded from fire for the previous 6 years) on Morro Santana, southern Brazil. **a** *Chaptalia runcinata*, **b** *Vernonia flexuosa*, **c** *Eupatorium ligulaefolium* and **d** *Heterothalamus psiadioides*

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 6 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	–

in site FB ($F = 7.73$, $P = 0.01$) and tended to be smaller in the excluded site ($P > 0.05$). Individuals of *C. runcinata* were taller in frequently burned sites at T0 ($P = 0.03$). After 1 year, rosette heights showed no significant differences ($F = 0.04$, $P = 0.84$). Plant diameter neither showed significant differences between sites nor before and after 1 year of fire.

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

Heat shock experiments

High temperatures neither enhanced germination nor damaged seeds. There were no significant differences between control and the treatments for all tested species (Table 3).

*Heterothalamus psiadioide*s showed the highest germination rates ($\geq 75\%$), whilst rates of *V. flexuosa* did not reach 40%. Additionally, seeds from *H. psiadioides* germinated first (after 5 days). *V. flexuosa* started to germinate only after 10 days.

Bud bank analysis

The bud bank of *E. ligulaefolium* tended to be larger in excluded sites ($P > 0.05$, Fig. 2a). *V. flexuosa*, however, showed the opposite tendency: a larger bud bank in frequently burned sites ($P > 0.05$, Fig. 2b). Stem density followed the bud bank pattern for *V. flexuosa*, but not for *E. ligulaefolium*: there were more stems in frequently burned than in excluded sites ($P = 0.02$).

Discussion

Population structure and dynamics

Before fire experiments, all species showed more individuals in frequently burned sites (FB), except for *H. psiadioides*. This shrub species is an obligate seeder, which invades 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 on other granitic hills (pers. obs.). Reasons for this patchiness of *H. psiadioides* are not clear, but could be related to seed dispersal. Fruits of this species have no special dispersal structures (e.g. pappus), which could be a problem for long-distance dispersal. They are probably dispersed near the mother plant.

Since fire is recurrent in site FB, individuals of *H. psiadioides* probably did not have enough time to develop flowers and seeds. The seed bank is probably transient and due to the short period between fires, it is not refilled. Hence, in these sites, no new recruitments could be found, even 1 year after the fire experiments. In the excluded site, a large number of flowering individuals could still be found near

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 6 years) at different times (T0—before experiments, T60—2 months and T360—1 year after fire)

Site	Species	Plant height (cm)			Plant diameter (cm)		
		T0	T60	T360	T0	T60	T360
FB	*Chaptalia runcinata*	4.9 ± 3.65 aA	1.37 ± 0.9aA	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 ± 0 bA	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	–	–	–

Randomization tests used Euclidean distances (10000 iterations) between sites. Repeated measures analysis was performed for between times. Different small letters mean significant differences between time of observations and different capital letters mean differences between sites ($P \leq 0.05$)

experimental plots and seeds might come from seed rain from neighbouring plants. Observations showed that individuals do not flower before 2 years (pers. obs).

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) and post-fire soil temperatures (Christensen 1985; Knox and Clarke 2006). Germination experiments showed a high rate of germination and seeds emerged very fast. Therefore, the long time needed for seedling establishment of *H. psiadioides* 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 may seldom occur, since seeds coming from neighbouring plants are needed.

E. ligulaefolium (shrub and resprouter) showed different patterns. 100% of individuals were topkilled. All new resprouters came from belowground buds. Fire might have destroyed epicormic buds and formation of new buds occurred only on the surface of the xylopodium. Two months after fire, 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. Knox and Clarke (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 2-year intervals might not be enough to replenish these reserves in order to achieve an optimal resprouting capacity. Other studies also found different optimal fire intervals for populations of shrubs, but most of them agreed that, frequent burns decrease populations of woody species (e.g. Heelemann et al. 2008; Quintana-Ascencio et al. 2002; Satterthwaite et al. 2002).

No flowering individuals and seedlings of *E. ligulaefolium* could be found. Flowering time begins in February. 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

Table 3 Seed weight and germination rates of two grassland species under different heat shock treatments in southern Brazil (means ± SE)

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

No significant differences could be found ($P \leq 0.05$)

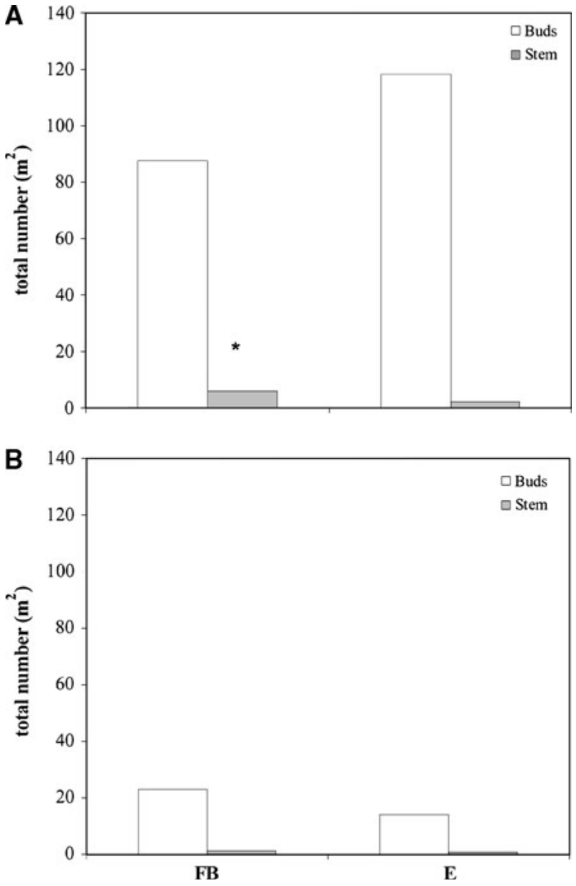

Fig. 2 Total number of belowground buds (buds/m^2) and stems (stem/m^2) from **a** *Eupatorium ligulaefolium* (shrub) and **b** *Vernonia flexuosa* (forb). *Asterisk* means significant difference between study sites (FB—frequently burned, E—excluded since 6 years, $P \leq 0.05$)

sites. However, after 1 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. Individuals of *C. runcinata* showed no evident belowground storage organ, but they were able to resprout immediately after fire. In another study, most individuals of this species showed flowers (Fidelis and Blanco in preparation) 1 month after fire (in summer). Therefore, 2 months after fire, some 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. Asteraceae species in *Campos* grasslands showed no enhancement in germination after exposition to high temperatures (Overbeck et al. 2006). Therefore, we do not believe that seeds from *C. runcinata* exhibit dormancy. Although this species shows no belowground bud-bearing organ, dead individuals remain in the site and fire should stimulate the development of new stems from buds located at the soil level.

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 1 year after fire, populations showed a larger number of individuals than before experiments. This species showed the lowest rates of mortality, having thus, more advantage of post-fire site conditions for individuals and population growth than the other study species. Hence, *C. runcinata* individuals need open sites. The longer the intervals of fires, the smaller the population size due to competition with grasses and shrubs.

Finally, populations of *V. flexuosa* also showed great recruitment capacity, mostly in site FB. Its populations decreased drastically after 1 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).

Flowering individuals of *V. flexuosa* could be found in site E 2 months after fire, as well as in neighbouring sites. Carvalho and Dietrich (1993) verified oscillations in fructans contents in *Vernonia* species at different phases: there was a decrease in fructan during flowering and sprouting phases, whilst fructan accumulation occurred during summer, showing the role of fructans as reserve substance in flowering and sprouting processes.

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.

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) on the germination of plant species in fire-prone ecosystems. In *Campos* grasslands, Overbeck et al. (2006) could not find any relationship between higher temperatures and enhancement of germination for herbaceous species, 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. (submitted b) analyzed the bud bank in Brazilian *Campos* grasslands under different management (grazing, fire and exclusion) and found a relation between fire frequency and bud bank size. The larger the intervals of fire, the smaller the bud bank was.

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).

Conclusion

Recurrent fires are needed in order to maintain plant populations of study species in *Campos* grasslands, as showed by our study. Even *H. psiadioides*, which has no recruitment via vegetative regeneration, requires fires or another 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. Fire plays a major role not only in *Campos* grasslands, but also in other Brazilian ecosystems, such as Cerrado. Therefore, studies about the effects of fire on plant populations are of crucial importance in order to understand vegetation dynamics after fire events in such ecosystems and to be able to use fire as a management tool.

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