Plant Ecol (2009) 202:149–158
DOI 10.1007/s11258-008-9537-4

Fire responses of three co-occurring Asteraceae shrubs in a temperate savanna in South America

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Received: 10 October 2007 / Accepted: 14 October 2008 / Published online: 12 November 2008
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Abstract South American temperate savannas have undergone significant woody plant encroachment through changes in their disturbance regimes. We studied fire strategies and the spatial variation in individual fire responses of *Eupatorium buniifolium*, *Baccharis medullosa* and *B. dracunculifolia,* the dominant shrub species at El Palmar National Park, in areas with different fire history. In recently burnt sites, all *Baccharis dracunculifolia* individuals died, whereas all *E. buniifolium* and *B. medullosa* individuals sprouted. The relative growth rate was higher in *E. buniifolium,* which invested more biomass in shoots, and in *B. medullosa,* which invested more biomass in leaves. At the unburnt site, *B. dracunculifolia* showed the highest growth rate and leaf biomass. *B. medullosa* produced capitula immediately after fire, whereas *E. buniifolium* reproduction was delayed for 1 year. In both species, production of capitula and reproductive effort were higher in recently burnt sites. For *B. dracunculifolia*, production of capitula was lower and the reproductive effort was higher in burnt than in unburnt sites. Seedling establishment was extremely low for *E. buniifolium*, low for *B. medullosa* and high for *B. dracunculifolia in both recently burnt sites*. *E. buniifolium* behaved as a sprouter, *B. medullosa* as facultative sprouter and *B. dracunculifolia* as obligate seeder species. In order to control the increase and/or attain desirable population levels of these species, fire management practices in these savannas should consider individual species' responses, particularly to the time since the last fire.

Keywords Obligate seeders · Savanna · Shrub encroachment · Sprouters

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Introduction

Human activities have influenced the physiognomy of savanna ecosystems through changes in the disturbance regimes such as fire suppression, eradication of native herbivores or the introduction of grazing

livestock or exotic trees (Archer 1994; Sankaran et al. 2005). As a result, areas that were once grassland or savanna may be now shrublands or woodlands and vice versa (Scholes and Archer 1997; Archer et al. 2001). For example, in some North American savannas, fire-tolerant woody species which were present at low densities increased their abundance as a consequence of decreasing fire frequency (Peterson and Reich 2001). In contrast, in Brazilian central savannas woody plant encroachment was produced by fire-sensitive species (Moreira 2000), whereas in Venezuelan savannas, where fire was suppressed and grazing excluded, it was brought about by both fire-tolerant and fire-sensitive species (Silva et al. 2001).

South American savannas have been historically submitted to frequent fires and native herbivores. Over the last century, these savannas have experienced a significant increase in abundance and distribution of native shrubs and exotic tree species. It has been suggested that this process would be associated with changes in their disturbance regimes, since in areas where fire was controlled or suppressed and herbivores excluded or replaced by grazing livestock, the abundance of shrub species increased (Moreira 2000; Silva et al. 2001; Cabral et al. 2003; Altesor et al. 2006). If these plant communities have undergone these land management practices, then fire and/or grazing would seem the factors controlling shrub encroachment. The existence of areas in which one or both factors have been registered and documented for long periods of time, offers the opportunity to evaluate the role of these factors on the species' life cycle processes so as to identify the possible causes of changes in their distribution and abundance.

In the protected areas of these regions such as the National Parks, some of the land management policies have been fire suppression and grazing exclusion (Somma 1994). However, in some of them, fire suppression has been very difficult to accomplish. Thus, some protected areas periodically undergo either fire brought about by human activities or by natural causes. This would suggest that species whose abundance and distribution have increased in these areas, have the capacity to respond to fire (i.e. sprouting, seedling recruitment), in the same way as those present in fire-prone ecosystems (Moreno and Oechel 1994; Whelan 1995; Bond and van Wilgen 1996).

The aim of this paper was to study fire regeneration strategies and the spatial variation in individual fire responses of the three dominant native shrubs in areas with different fire histories at El Palmar National Park. In this protected area, as in others in this region, there is spatial and temporal variation in fire occurrence generating a spatial mosaic with different fire histories. We expected these species to be fire resistant and to have short-term individual fire responses, i.e. we expected to find the time-since-last-fire to be the most important fire regime characteristic for species' life history traits regardless of differences between sites with different fire histories. In such scenario, the species' responses would be more related to their fire regeneration strategies than to their habitat fire history. Knowledge of these shrubs' fire regeneration strategies will be useful for understanding shrub encroachment in this temperate savanna and for implementing adequate land management policies.

Materials and methods

Study area

The study was carried out at El Palmar National Park (31°55′ S, 58°17″ W), an 8,500-ha protected area (Entre Ríos province, Argentina). The climate is temperate and wet, the mean annual temperature is 19 ± 3.8°C, and the mean annual precipitation is 1,346 ± 291 mm, with 58% falling during the warm season (October–April) (Goveto 2005). The study area was located on well drained, fine, sandy-loam soils, dominated by the three shrub species under study: *Eupatorium buniifolium*, *Baccharis medullosa*, and *B. dracunculifolia*.

In March 2000, four sites with different fire histories were selected, designated A, B, C and D. These sites were adjacent to each other and separated by a fire break. Sites A and B (A: burnt in 1992, 1997; B: burnt in 1992) underwent a wildfire in January 2000, whereas in site C the last fire occurred in 1997, and site D has undergone no fires since 1965. All fires were intense summer fires with flame heights ranging from 2 to 4 m (Maranta, personal communication) and resulted in complete aerial biomass consumption. Whilst replication of individuals and plots occurred within each of the four sites, there

were no true replicate sites for the different fire histories under study and the design of this study is thus pseudoreplicated (Hurlbert 1984). General conclusions can therefore be drawn about patterns of variation among sites, but not about the effects of burning regimes per se (Morgan 2001).

Study species and sampling

Eupatorium buniifolium, *B. medullosa* and *B. dracunculifolia* (Asteraceae) are widespread perennial shrubs up to 2–3 m in height that are native to Argentina, Brazil, Uruguay, Paraguay and Bolivia (Zuloaga and Morrone 1999). *E. buniifolium* is hermaphrodite, whereas, *B. dracunculifolia* and *B. medullosa* are dioecious. Flowering typically occurs in summer (December–March). Several achenes (hereafter referred to as seeds) are produced per capitulum, and wind-dispersed in summer-autumn (February–May) (Burkart 1974).

To identify the fire strategies and spatial variation in their fire responses, for each species we monitored: individual survival, relative growth rate, biomass allocation (leaf/shoot biomass ratio), capitula production, reproductive effort (capitula/total aerial biomass ratio) and seedling establishment (emergence and survival). At each study site, a 30 × 30 m^2 plot was delimited at random, in which at least ten adult individuals of each species were randomly selected, permanently marked and measured at 3-month intervals during 2 years (March 2000–2002). Marked individuals were at least 2 m apart from each other. Adult individuals could still be identified at species level after fire based on bark characteristics. In each individual, we measured total number of live shoots, and the height and basal diameter of three randomly tagged shoots. Aboveground biomass was estimated by non-destructive methods applying allometric equations that related height and basal diameter with shoot biomass. Allometric equations were constructed using nearby individuals in which we measured the height and basal diameter of shoots. These shoots were harvested and the dry weight was obtained after drying for 72 h at 70° (at least 80 shoots/species). Total aboveground biomass of each individual was estimated by multiplying the total number of shoots by the mean shoot biomass per plant. The relative growth rate was estimated as: $RGR = [(\ln(B_{t2}) - \ln(B_{t1})]/T2 - T1$, where B_{t2} was the aboveground biomass at time T2 and B_{t1} was the aboveground biomass in the previous time T1.

We estimated the total number of capitula and the capitula biomass/total aerial biomass ratio per plant in March 2000, 2001 and 2002. For it, we counted the total number of flowering branches per individual and three of them were randomly selected, harvested and taken to the laboratory for further processing. Total number of capitula per plant was estimated by multiplying the mean number of capitula per branch by the total number of flowering branches. Since *B. dracunculifolia* and *B. medullosa* are dioecious species, only female individuals were selected for this study. As reproductive variables may vary with plant size, for *E. buniifolium* and *B. medullosa* we used the area of the underground perenneting structures (xylopodes) as a proxy estimator of the individual size. This area was calculated as the product of $\pi \times D1 \times D2/4$, where D1 and D2 are the two largest diameters of the underground structure perpendicular to one another (Cruz and Moreno 2001).

To register seedling establishment at each site, we randomly delimited 30 (2 × 2 m^2) quadrants separated at least by 2 m. In March 2000, 2001 and 2002, we identified and tagged all newly established seedlings. Total seedling emergence for each year was recorded separately, and seedling survival was calculated as the proportion of total seedling emergence that survived after 2 years.

Statistical analyses

RGR, leaf/shoot biomass ratio, number of capitula and capitula/total aerial biomass ratio per plant were analysed by repeated-measured ANCOVA model. Sites (S) were considered the main effects, months of the year (T) as the repeated measures and the area of the xylopodes for *E. buniifolium* and *B. medullosa* as a covariant. For all analyses we modelled the covariance structure within subjects and selected the structure with the best fit by comparing AIC and BIC statistics (Littell et al. 1996). The Unstructured and the Heterogeneous first-order Autoregressive structure were used in our analysis. We specified the Kenwardroger method for computing the denominator degrees of freedom for the tests of fixed effects. The individual values of different levels of each variable were compared to a post hoc test (LS means

with the Sidak method for correcting alfa). Data were analysed with the Mixed Models procedure (Proc Mixed) using the SAS 8.2 statistical package (SAS Institute Inc 1989).

Site effect on both seedling emergence and seedling survival was analysed using a generalised linear model, assuming a Poisson response variable with a log link function for seedling emergence and a binomial response variable with a logic link function for seedling survival. In both cases we used Least Square means for multiple comparisons (LSMEANS; PROC GENMOD, SAS Institute Inc 1989). Inspection of residuals was carried out to check for normality and homoscedasticity and when necessary, analyses were run on transformed data.

Results

In recently burnt sites (A and B), all *B. dracunculifolia* individuals died after fire and none of them were able to sprout during the studied period. In contrast, all individuals of *E. buniifolium* and *B. medullosa* produced abundant new shoots immediately after fire.

RGR in all species was significantly different among sites (*E. buniifolium*: $F_{SxT(21,179)} = 13.35$, $P < 0.0001$; *B. medullosa*: $F_{SxT(21,150)} = 4.6$, $P < 0.0001$ and *B. dracunculifolia*: $F_{SxT(7,21.9)} = 7.68$, $P = 0.0001$; Fig. 1a–c). In *E. buniifolium* and *B. medullosa*, RGR in sites A and B were initially higher than in the other two sites (*E. buniifolium*: 0.654 vs. 0.080 g $g^{-1}mo^{-1}$, *B. medullosa:* 0.430 vs. 0.050 g $g^{-1}mo^{-1}$). RGR for *B. dracunculifolia* could not be calculated for sites A and B since all individuals died after fire. However, RGR in the unburnt site (D) was initially six times higher compared to the site burnt in 1997 (C) (0.258 vs. 0.043 g $g^{-1}mo^{-1}$, respectively). For all three species these differences decreased with time. The area of the xylopodes did not affect the RGR in *E. buniifolium* ($F_{1,140} = 0.2$, $P = 0.657$) and *B. medullosa* individuals ($F_{1,110} = 0$, $P = 0.985$).

For leaf/shoot biomass ratio, we found significant differences among sites (*E. buniifolium*: $F_{SxT(24,65)} = 3.62$, $P < 0.0001$; *B. medullosa*: $F_{SxT(24,52.1)} = 5.49$, $P < 0.0001$ y *B.* d*racunculifolia*: $F_{SxT(8,35.5)} = 5.68$; $P = 0.0001$; Fig. 2a–c). In *E. buniifolium*, the ratio was initially lower in sites A and B but increased with time, whereas sites C and D showed relatively constant ratios, although values were higher in site C. In contrast, leaf/shoot ratio for *B. medullosa* individuals was initially higher in both sites A and B than in the other sites, but these differences tended to disappear with time. Differences between sites for *B. dracunculifolia* were only visible at the end of the study; leaf/shoot ratio was higher in site D than in site C. The xylopodes area did not affect the leaf/shoot biomass ratio in *E. buniifolium* ($F_{1,40} = 0.07$; $P = 0.797$) and *B. medullosa* ($F_{1,34} = 0.76$; $P = 0.767$).

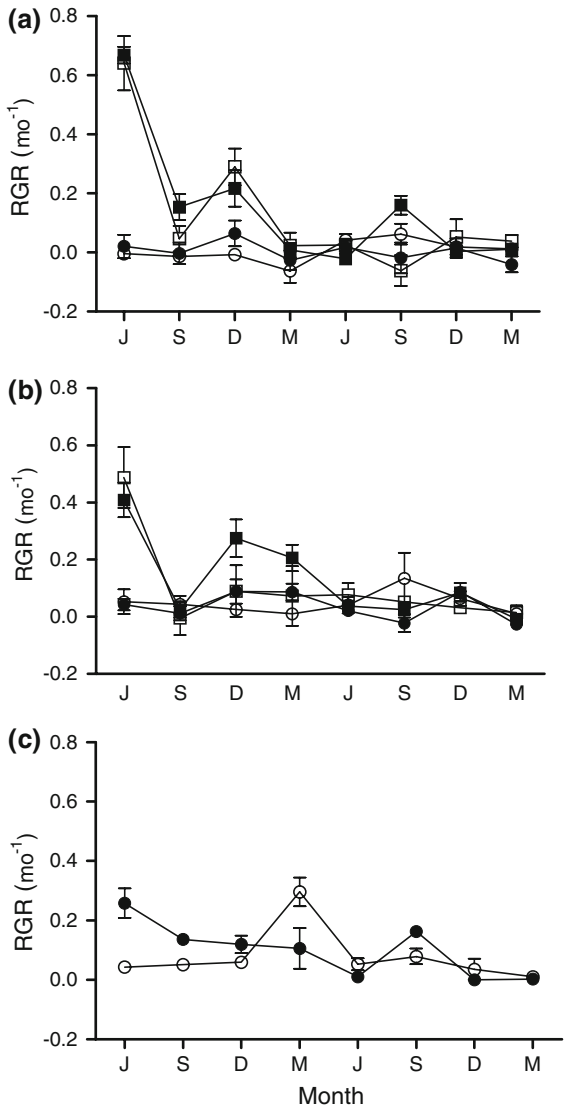

Fig. 1 Relative growth rate per plant (mean ± SE) of **a** *E. buniifolium*, **b** *B. medullosa* and **c** *B. dracunculifolia* at each site (■: A, □: B, ○: C and ●: D) measured at 3 months interval (J: stands for June) during the period 2000–2002

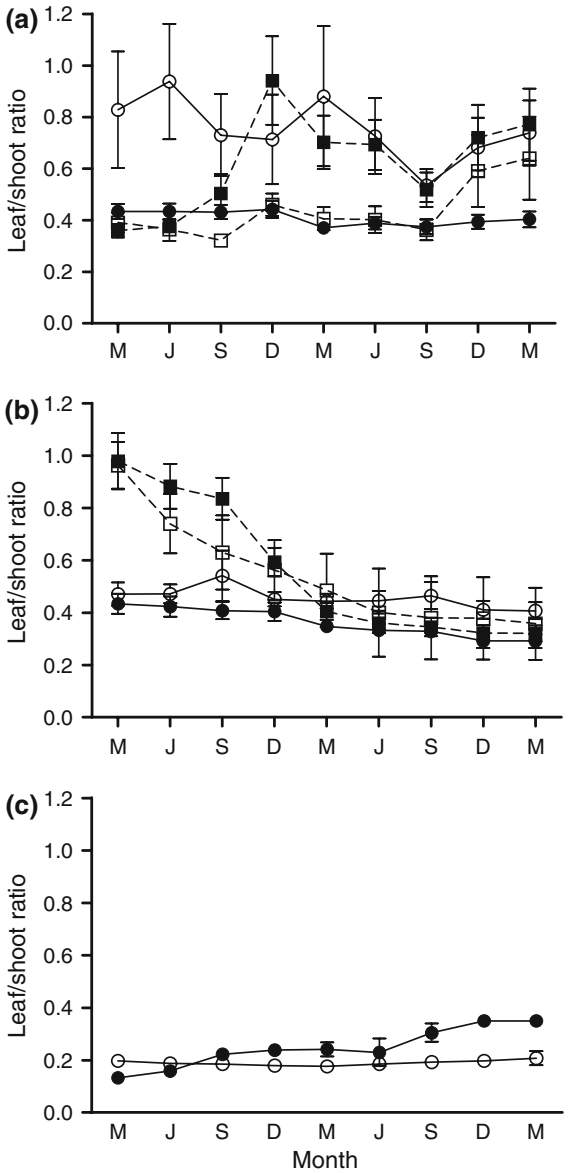

Fig. 2 Leaf/shoot biomass ratio per plant (mean ± SE) of **a** *E. buniifolium*, **b** *B. medullosa* and **c** *B. dracunculifolia* at each site (■: A, □: B, ○: C and ●: D) measured at 3 months interval (M: stands for March) during the period 2000–2002

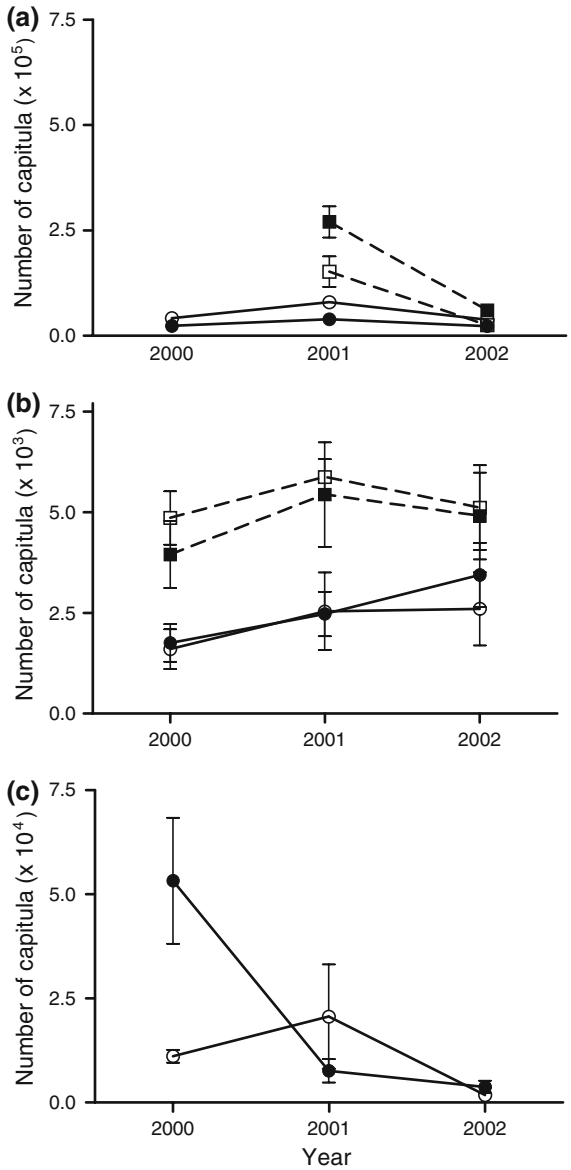

Fig. 3 Number of capitula per plant (mean ± SE) of **a** *E. buniifolium*, **b** *B. medullosa* and **c** *B. dracunculifolia* at each site (■: A, □: B, ○: C and ●: D) and studied year

Capitula production per plant differed by two orders of magnitude among sites. In sites A and B, all *B. medullosa* individuals produced capitula immediately after fire (in Autumn 2000), whereas for *E. buniifolium* sexual reproduction was delayed for 1 year (in 2001). For both species we found significant differences among sites (*E. buniifolium*: $F_{SxT(6,67.7)} = 417.6$, $P < 0.0001$ and *B. medullosa*: $F_{SxT(6,52)} = 3.4$, $P = 0.041$; Fig. 3a, b). *E. buniifolium* produced approximately 3.5 times more capitula in sites A and B (211047 capitula/plant), whereas for *B. medullosa* it was 2.5 times higher in sites A and B (on average 4,209 capitula/plant) than in C and D sites. In *B. dracunculifolia,* the individuals growing in site C produced capitula for the first time in 2000, and this production was significantly lower than in site D (11,151 capitula/plant and 53,285 capitula/

plant, respectively) ($F_{SxT(2,13.7)} = 4.8$, $P = 0.025$; Fig. 3c). However, for the three species these differences disappeared by the third year of study (2002). Only for *E. buniifolium*, the xylopodes area significantly affected the capitula production ($F_{1,48.8} = 7.96$, $P = 0.007$), increasing positively with the structure's size.

The peak reproductive effort for all species occurred during the first reproductive season (Fig. 4). For *E. buniifolium*, the capitula biomass/total aerial biomass ratio was significantly higher in site A than in sites C and D, approximately two times greater ($F_{SxT(6,77.3)} = 7.0$, $P < 0.0001$; Fig. 4a), whereas for *B. medullosa*, it was three to four times higher in both sites A and B than in the other two sites ($F_{SxT(6,53.4)} = 7.97$, $P < 0.0001$; Fig. 4b). For *B. dracunculifolia*, individuals growing in site C allocated significantly more biomass to capitula production per unit of aerial biomass than in site D ($F_{SxT(2,19.6)} = 46.73$, $P < 0.0001$; Fig. 4c). In *E. buniifolium* and *B. medullosa*, the investment in capitula decreased significantly in the following years, whereas for *B. dracunculifolia* reproductive effort was maintained high until 2001; its second reproductive period. Only for *E. buniifolium*, the xylopodes area significantly affected the reproductive effort ($F_{1,63.3} = 4.56$, $P = 0.037$), increasing positively with structure's size.

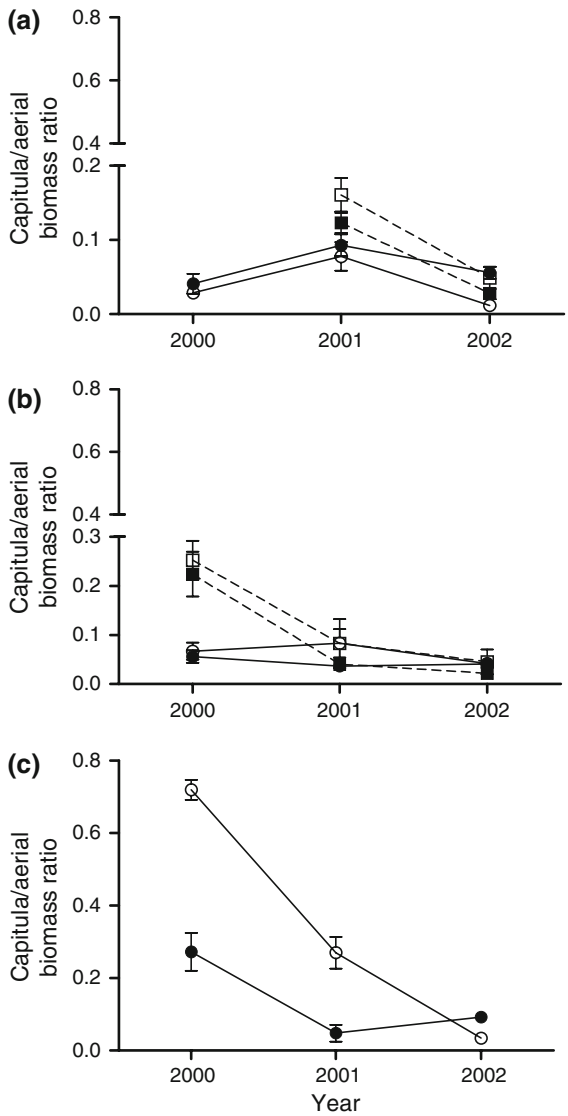

Fig. 4 Capitula biomass/total aerial biomass ratio per plant (mean ± SE) of **a** *E. buniifolium*, **b** *B. medullosa* and **c** *B. dracunculifolia* at each site (■: A, □: B, ○: C and ●: D) and studied year

Seedling emergence for each species during March 2000–2001 was significantly different among sites (*E. buniifolium:* $F_{3,110} = 19.92$, $P < 0.0001$, *B. medullosa*: $F_{3,110} = 13.10$, $P < 0.0001$ and *B. dracunculifolia*: $F_{3,110} = 42.83$, $P < 0.0001$; Fig. 5a–c). For *E. buniifolium* and *B. medullosa* the mean number of seedlings/m^2 was higher in site B (*ca.* 2.5 and 9 seedlings/m^2, respectively) compared to the other sites, whereas *B. dracunculifolia*, produced 20–30 times more seedlings in both sites A and B (*ca.* 30–32 seedlings/m^2), compared to the other two sites. In the period 2001–2002, seedling emergence remained significantly different among sites for each species (*E. buniifolium:* $F_{3,110} = 10.34$, $P < 0.0001$, *B. medullosa*: $F_{3,110} = 19.73$ $P < 0.0001$ and *B. dracunculifolia*: $F_{3,110} = 15.21$, $P < 0.0001$; Fig. 5a–c). For *E. buniifolium* and *B. dracunculifolia,* the number of seedlings was higher in site B (0.8 and 4 seedlings/m^2, respectively). For *B. medullosa*, the number of seedlings was higher in site A (1.6 seedlings/m^2) and no seedling emergence was registered in site D. Seedling's survival varied during the first study year, which precluded to detect any differences in survival percentage among sites for either *E. buniifolium* or *B. medullosa* ($F_{3,30} = 2.08$, $P = 0.12$ and $F_{3,13} = 0.51$, $P = 0.68$, respectively; Fig. 5d, e). Survival of *B. dracunculifolia* seedlings differed significantly among sites ($F_{3,76} = 11.16$, $P < 0.0001$, Fig. 5f), being two to four times higher in sites A and B (76–84%, respectively) compared to the other two sites (15–33%). Seedling survival for those emerged during 2001–2002 was low for all species (*ca.* <40%, Fig. 5c, d, f) and no

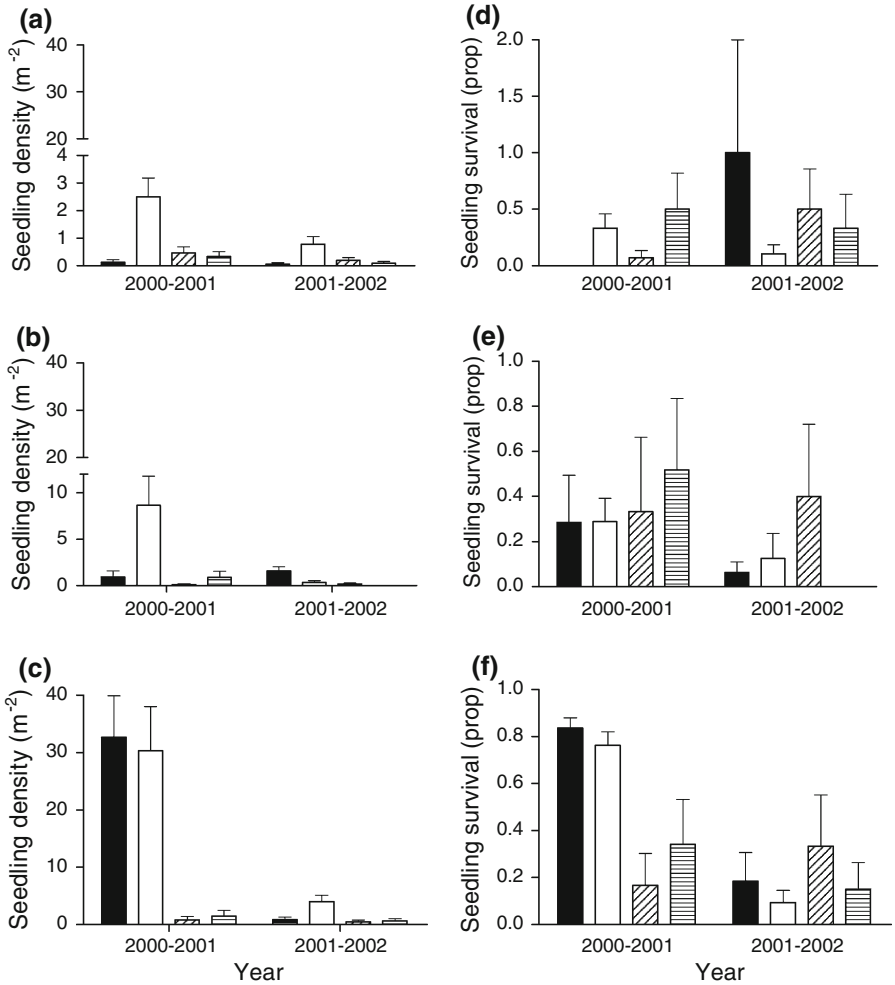

Fig. 5 Seedling emergence and seedling survival (mean ± SE) of **a**, **d** *E. buniifolium*, **b**, **e** *B. medullosa* and **c**, **f** *B. dracunculifolia* at each site (■: A, □: B, //: C and ≡: D) during the periods 2000–2001 and 2001–2002

differences were found among sites (*E. buniifolium:* $F_{3,14} = 2.61$, $P = 0.09$, *B. medullosa*: $F_{2,18} = 1.51$ $P = 0.25$ and *B. dracunculifolia*: $F_{3,46} = 1.26$, $P = 0.30$).

Discussion

After-fire regeneration is determined by interactions between the disturbance regime and the species biology (Pickett and White 1985). Some plants regenerate after fire by sprouting, others by producing new seedlings and still others by a combination of both strategies (Keeley and Zedler 1978; Whelan 1995). As we expected, at El Palmar National Park the species under study were fire resistant species since they exhibited the same responses as species living in fire prone ecosystems. Thus, after fire all selected *E. buniifolium* and *B. medullosa* individuals sprouted from underground structures, while all individuals of *B. dracunculifolia* died and their regeneration depended exclusively on their seedling establishment.

In recently burnt sites, *E. buniifolium* and *B. medullosa* showed higher relative growth rates during the first months after fire compared to the other sites. This immediate response to fire would allow both species to persist in the system (DeSouza et al. 1986; Nascimento 1996; Kennard et al. 2002), but most importantly, to keep the space occupied during the establishment phase. Fire frequency would not play a significant role, since, if we consider the number of fires experienced during the last 8 years (2 vs. 3 in sites A and B, respectively), both species showed the same sprouting and relative growth rate pattern. In contrast, for *B. dracunculifolia*, the relative growth

rate seemed to be dependent on plant age and density (Goveto 2005).

In relation to biomass allocation, *E. buniifolium* individuals allocated more biomass to shoots than to leaves in recently burnt sites compared to the other two sites, at least during the first 6 months. It has been suggested that a decrease in leaf/shoot biomass after disturbance is usually associated with an increase in height growth and competition for light (Vilà and Terradas 1995). In contrast, *B. medullosa* initially allocated more biomass to photosynthetic tissues relative to shoots in recently burnt sites compared to the other two sites, at least during the first 6 months. This differential allocation pattern may have made an important contribution, allowing *B. medullosa* individuals to reproduce sexually only 3–4 months after fire. Similar to growth rate, fire frequency would not have influenced biomass allocation patterns for most of the study period. For *B. dracunculifolia* we did not find differences in the leaf/shoot biomass ratio between sites until the end of the study, when individuals in the unburnt site showed a higher ratio than those in burnt sites. Taking into account that individuals in the unburnt site were older, and that a good proportion of the standing biomass consisted of dead branches, the observed increase in leaf/shoot ratio might be attributed to the new sprouts originating from buds near the base of the main shoot (Galíndez, personal observation).

Sexual reproduction in *E. buniifolium* was delayed for 1 year after fire. It has been documented that the sprouting process may demand resources causing a delay in flowering until enough biomass is build up to withstand reproduction (Hoffmann 1998; Hoffmann and Solbrig 2003). However, the damage caused by fire to aboveground parts of plants and the greater availability of light, water and nutrients after fire may stimulate the production of flowers (Whelan 1995; Bond and Wilgen 1996). This seems to be the case for *B. medullosa* in which sexual reproduction occurred immediately after fire. However, regardless of the year in which sexual reproduction started (2000 and 2001, respectively), both species showed higher numbers of capitula and reproductive effort in recently burnt sites, compared to the other sites. In *B. dracunculifolia*, after-fire reproduction commenced 3 years later in the site burnt in 1997. However, even though the total number of capitula per plant was higher in the unburnt site, the biomass allocated to sexual reproduction in relation to the total aerial biomass was higher in the site burnt in 1997, similar to the findings for the other species. This strategy to allocate more biomass to seed production would be an advantage in this environment where fire occurrence is unpredictable (Parker and Kelly 1989; Auld and Denham 2006).

Seedling establishment of *E. buniifolium* and *B. medullosa* was low in all sites and study years. This could be associated with the presence of a dense litter layer and a continuous dense canopy which would produce unfavourable conditions for both seed seedling emergence and survival (Morgan 2001; Williams et al. 2005). The exceptionally high emergence of *B. medullosa* in one of the burnt sites in 2000 (site B) could be attributed to the fact that most of the seeds produced by sprouting individuals were dispersed around the mother plant and germinated immediately after dispersal. However, this flush of emergence was not successful at establishing a relevant number of new individuals. In contrast, for *B. dracunculifolia*, seedling emergence and survival were high, particularly in both recently burnt sites immediately after fire. These results agree with those found for other obligate seeders (Keeley 1991).

We may conclude that *E. buniifolium* responded as a sprouter species, *B. medullosa* as a facultative sprouter, and *B. dracunculifolia* as an obligate seeder. Fire frequency does not seem to influence the individual fire responses of these species, being the time-since-last-fire the most important characteristic of fire regimen for species response. These results would support the idea that land management practices that included annual–biannual fires would have been one of the factors controlling the density and composition of the dominant shrub species, even though we do not deny the role neither of grazing nor of fire and grazing interacting together on shrub encroachment. According to this study, fire management practices of these savannas, should consider each species' responses, particularly to the time since the last fire, in order to control their increase and/or attain desirable population levels.

Acknowledgements We are grateful to Silvia Sühring for reviewing the manuscript and to Cristian Pereyra for his assistance in field. We also thank Cecilia Moraga and Mark Ooi for useful suggestions in the English version. This research was supported by the Agencia Nacional para la Promoción

Científica y Técnica (PICT 08-08962). Additional funds were provided by the University of Buenos Aires (UBACyT G 095), and PICT 2006–1979.

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