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Fire drives the reproductive responses of herbaceous plants in a Neotropical swamp

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Abstract Palm swamps (*veredas*) are unique and diverse plant communities associated with the headwaters of streams in central Brazil, and they are frequently subjected to fires. We evaluated the effect of fire and the role of different fire-related cues on inducing reproduction by palm swamp vegetation. We compared the responses of species in burned plots, in plots in which the aboveground vegetation was clipped and then removed, and in unburned and unclipped control plots. Both the number of reproductive species and the total number of flowers/fruits produced by all species monthly were significantly greater in the burned than in the clipped and control plots, and greater in the clipped than in the control plots. For 34 of the 48 individual species analyzed the number of flowers/fruits produced per m^2/month was greater in the burned than in the control plots, whereas the clipping treatment significantly increased the reproductive rate of only six species. This indicates that increased light availability was not the only factor inducing plant reproduction. Most likely, plant reproduction was also stimulated by the availability of soil nutrients whose concentrations increased significantly after burning. Although our results indicate that most plant species that occur in palm swamps are fire-recruiters, care must be taken in using fire as management tool, especially as the frequency of human-induced fires in palm swamps have increased dramatically in recent years.

Keywords Cerrado · Fire · Savannas · Hydrophilic flora · Induced reproduction · Phenology

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Introduction

Fire can stimulate the flowering of a wide variety of plant taxa via cues that are either direct (e.g., heat, smoke, ethylene) or indirect (e.g., enhanced nutrient availability) (Coutinho 1990; Mistry 1998; Main and Barry 2002; Miranda et al. 2009; Lamont and Downes 2011). However, other physical factors may also affect whether or not plants flower or fruit. These include the clearing of aboveground biomass and surface litter (Lamont and Downes 2011), which may be

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particularly important for smaller annual species that are unable to grow under dead vegetation (Canales et al. 1994). The extent to which this is generally true, however, remains unclear. Studies to date have often focused on only a limited number of species, and few have used experiments to evaluate the relative importance of different agents of disturbance that could influence reproduction.

Throughout much of South American *Cerrado* or the savanna biome, palm swamps (*veredas*) are a highly conspicuous plant community associated with the headwaters of streams. They are named due to their characteristic groves of *Mauritia flexuosa* palms (Oliveira-Filho and Ratter 2002), but also support a high diversity of hydrophilic herbaceous species (Araújo et al. 2002). These swamps are threatened by widespread and frequent fires and cattle grazing, both of which remove plant biomass and may affect the unique flora in palm swamps (Meireles et al. 2004). Despite their conservation status and ecological uniqueness surprisingly little is known about the factors that influence reproduction in palm swamps. Here we experimentally evaluated the relative influence of fire and aboveground biomass removal on inducing plant reproduction in palm swamps.

Methods

We examined a 70 ha and well-preserved palm swamp located in Uberlândia, Brazil (18°59′41″S; 48°18′18″W) (Fig. 1). The experiment was conduct in just one palm swamp given the inherent difficulties of obtaining a permit to burn a natural area. Nevertheless, this swamp is representative of others in terms of both its size and species composition (Araújo et al. 2002). An area of 12 × 210 m was marked and divided into four 3 × 210 m sections (Fig. S1). All vegetation in the second and fourth sections was clipped using a gas-powered brush cutter and then manually removed. The vegetation in the third section was burned with the assistance of the municipal fire brigade. Vegetation in the first section remained untreated as a control. These four contiguous sections traversed from one margin of the palm swamp to the opposite margin (Fig. 1). Because of the variable soil conditions in the different topographic zones of the swamp (Ramos et al. 2006) and to a lower extent in the opposite margins of the stream, the study area was divided into six blocks. Two blocks were located in the most elevated zone, near the limit between the Cerrado savanna and the palm swamp. Two blocks were in the intermediate zone, and two blocks were in the bottom zone (Fig. S1). Three plots were marked within each block, one within each vegetation treatment. Plots in the elevated and intermediate zones were 2 x 10 m, whereas those in the bottom zone were larger (2 x 18 m) because this zone was much larger.

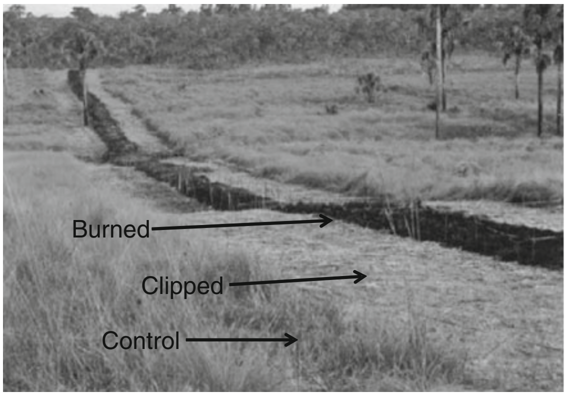

Fig. 1 View of the palm swamp studied and the experimental treatments applied to the herbaceous vegetation: burning, clipping + aboveground biomass removal, control

We applied our treatments at the end of the 2011 dry season (early October). We then recorded the number of species that were reproductive and the total number of flowers and fruits produced by each species within each plot monthly until May 2002. We recorded reproduction per species (no. flowers/fruits produced by each species per m^2/month) rather than at the individual level because grasses and sedges in our study system are nearly identical morphologically and grow in densely packed clumps with underground connections, making it impossible to distinguish reproductive and non-reproductive individuals. Although this measure does not provide the proportion of the population flowering or per-capita likelihood of reproduction, it does provide a comparable value for the production of flowers and fruits in each treatment.

In the control plots and the burning treatments two soil samples (depth = 0–5 cm) were taken for chemical analyses 15 days after the fire event. Analyses were performed using the procedures adopted by the Brazilian Agricultural Research Corporation (Embrapa 1997).

We compared the number of reproductive species and the flower/fruit production—total and by species—

among the different treatments using one-way randomized-block ANOVA. Comparisons at the species level were restricted to those species that produced more than 100 flowers or fruits over the 8 months of observation. We used paired *t* tests to test for differences in soil characteristics between the control and burning treatment. All statistical analyses were performed using square-root or log-transformed data, except for those comparing pH values for which no transformation was necessary.

Results

We recorded 141 reproductive species, of which 136 were in the burned plots, 102 in the clipped and 76 in the control plots (Appendix S1). The mean number of reproductive species was significantly greater in the burned than in the clipped and control plots ($F_{2,10} = 17.0$, $p = 0.001$). On average 81.8 species reproduced in each burned plot, which was nearly double that in the control plots (41.8 species) (Fig. 2a). In addition, the community-wide flower/fruit production (number of flowers/fruits produced by all species per m^2/month) was significantly greater in the burned plots than the clipped and control ones, and greater in the clipped plots than control plots ($F_{2,10} = 30.1$, $P < 0.001$) (Fig. 2b). Similarly, for 34 of the 48 species analyzed, flower/fruit production was significantly greater in the burned than in the control plots (Table 1). Another 13 species showed a similar but not statistically significant trend. *Trimezia juncifolia* (Iridaceae), in contrast to all other species, only reproduced in the control plots. Clipping significantly increased – relative to the control plots – the flower/fruit production of six of the 48 species analyzed. In most cases, mean flower/fruit production was smaller in the clipped plots than in plots that were burned. However, this difference was significant for only 11 of the 48 species analyzed (Table 1).

Burning increased the soil content of P, K, Ca, Mg, and decreased Al, but did not significantly affect soil pH and organic matter (Table 2).

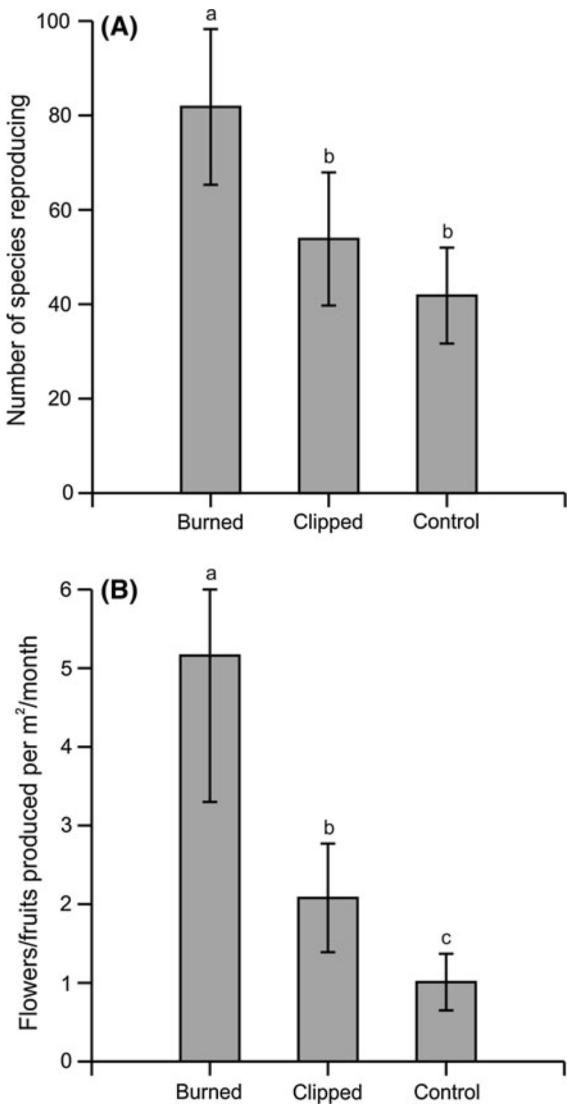

Fig. 2 Mean ± S.E. number of reproductive species (**a**) and mean number of flowers/fruits produced per m^2/month (**b**) in plots where the herbaceous vegetation was burned, clipped and removed, or not manipulated (control)

Discussion

Significantly more species reproduced in plots that were burned indicating that fire positively affects the reproduction of most plant species in Brazilian palm swamps. In fact, for over 70 % of the species analyzed the number of flowers and fruits produced per m^2/month was much higher in the burned plots. Of the 48 most common species, only *Trimezia juncifolia* (Iridaceae) was negatively affected by the fire and clipping treatments. It is important to notice that the observed differences in flower/fruit production may reflect differences in the abundance of species in our different plots, rather than the effects of the treatments

Table 1 Number of flowers/fruits produced per m^2/month ($n = 8$ consecutive monthly observations) by different plant species in plots that were burned, in which vegetation was clipped, or in which there was no manipulation (controls)

Family	Species	Burned	Clipped	Control
Achantaceae	*Justicia polygaloides*	0.117 (0.056)^{a}	0.068 (0.038)^{ab}	0.017 (0.010)^{b}
Cyperaceae	*Ascolepsis brasiliensis*	0.070 (0.033)^{a}	0.042 (0.016)^{ab}	0.015 (0.009)^{b}
	Eleocharis capillacea	0.054 (0.020)^{a}	0.012 (0.008)^{ab}	0^{b}
	Eleocharis filiculmis	0.061 (0.029)^{a}	0.020 (0.010)^{ab}	0^{b}
	Exochlogyne amazonica	0.059 (0.025)^{a}	0.075 (0.028)^{a}	0^{b}
	Lipocarpha humboldtiana	0.072 (0.034)^{a}	0.025 (0.009)^{a}	0.011 (0.004)^{a}
	Rhynchospora emaciata	0.072 (0.034)^{a}	0.013 (0.006)^{a}	0.005 (0.003)^{a}
	Rhynchospora globosa	0.074 (0.025)^{a}	0.082 (0.025)^{a}	0.027 (0.009)^{b}
	Rhynchospora robusta	0.071 (0.025)^{a}	0.024 (0.008)^{ab}	0.003 (0.002)^{b}
	Rhynchospora rugosa	0.055 (0.028)^{a}	0.016 (0.008)^{ab}	0^{b}
	Rhynchospora velutina	0.056 (0.020)^{a}	0.037 (0.016)^{a}	0.017 (0.008)^{a}
	Scleria hirtella	0.056 (0.027)^{a}	0.018 (0.009)^{a}	0.016 (0.008)^{a}
Eriocaulaceae	*Paepalanthus flaccidus*	0.097 (0.024)^{a}	0.063 (0.008)^{a}	0.049 (0.015)^{a}
	Paepalanthus scholiophyllus	0.071 (0.032)^{a}	0.013 (0.008)^{ab}	0^{b}
	Syngonanthus nitens	0.070 (0.033)^{a}	0.044 (0.014)^{a}	0.027 (0.013)^{a}
	Syngonanthus xeranthemoides	0.072 (0.030)^{a}	0.010 (0.006)^{b}	0^{b}
Iridaceae	*Trimezia juncifolia*	0^{a}	0^{a}	0.081 (0.041)^{b}
Lentibulariaceae	*Utricularia bicolor*	0.063 (0.021)^{a}	0.021 (0.011)^{b}	0.019 (0.007)^{b}
	Utricularia purpureocaerulea	0.070 (0.030)^{a}	0.017 (0.009)^{a}	0.013 (0.007)^{a}
Melastomataceae	*Cambessedesia hilariana*	0.051 (0.020)^{a}	0.017 (0.009)^{b}	0.011 (0.007)^{b}
Poaceae	*Anthaenotiopsis trachystachya*	0.088 (0.041)^{a}	0.049 (0.029)^{ab}	0.007 (0.004)^{b}
	Andropogon ternatus	0.097 (0.037)^{a}	0.036 (0.017)^{a}	0.026 (0.012)^{a}
	Anthaenantia lanata	0.071 (0.035)^{a}	0.042 (0.018)^{a}	0^{a}
	Arundinella hispida	0.083 (0.032)^{a}	0.055 (0.018)^{a}	0.025 (0.012)^{b}
	Axonopus chrysoblepharis	0.083 (0.035)^{a}	0.037 (0.012)^{ab}	0.022 (0.007)^{b}
	Axonopus fissifolius	0.088 (0.043)^{a}	0.052 (0.023)^{ab}	0.012 (0.006)^{b}
	Axonopus siccus	0.053 (0.031)^{a}	0.035 (0.019)^{ab}	0.023 (0.014)^{a}
	Axonopus marginatus	0.062 (0.027)^{a}	0.019 (0.008)^{ab}	0.011 (0.005)^{b}
	Ctenium brevispicatum	0.142 (0.064)^{a}	0.094 (0.044)^{ab}	0.026 (0.016)^{b}
	Echnolaena inflexa	0.062 (0.014)^{a}	0.048 (0.013)^{b}	0.034 (0.010)c
	Elionurus muticus	0.049 (0.025)^{a}	0.020 (0.013)^{a}	0^{a}
	Ichnanthus procurrens	0.085 (0.018)^{a}	0.064 (0.017)^{b}	0.034 (0.009)c
	Panicum caaguazense	0.034 (0.014)^{a}	0.022 (0.014)^{ab}	0.010 (0.007)^{b}
	Panicum cayennense	0.071 (0.030)^{a}	0.028 (0.015)^{ab}	0.016 (0.008)^{b}
	Paspalum cordatum	0.050 (0.017)^{a}	0.012 (0.009)^{b}	0.025 (0.009)^{ab}
	Paspalum flaccidum	0.048 (0.021)^{a}	0.038 (0.015)^{ab}	0.012 (0.006)^{b}
	Paspalum gardnerianum	0.080 (0.028)^{a}	0.025 (0.012)^{b}	0.015 (0.007)^{b}
	Sorgastrum pillitum	0.060 (0.024)^{a}	0.021 (0.009)^{b}	0.017 (0.007)^{b}
	Sporobolus cubensis	0.047 (0.017)^{a}	0.033 (0.009)^{a}	0^{b}
Polygalaceae	*Pollygala bracteata*	0.075 (0.025)^{a}	0.014 (0.005)^{b}	0^{b}
	Pollygala longicaulis	0.062 (0.023)^{a}	0.030 (0.011)^{ab}	0^{b}
	Pollygala paniculata	0.00 (0.00)^{a}	0.00 (0.00)^{ab}	0.00 (0.00)^{b}
	Polygala timoutoides	0.050 (0.012)^{a}	0.020 (0.010)^{a}	0.011 (0.005)^{a}
Rapateaceae	*Cephalostemon angustatus*	0.062 (0.028)^{a}	0.027 (0.012)^{ab}	0.018 (0.007)^{b}

Table 1 continued

Family	Species	Burned	Clipped	Control
Xyridaceae	*Xyris asperula*	0.103 (0.027)[a]	0.029 (0.011)[b]	0.031 (0.012)[b]
	Xyris savanensis	0.063 (0.027)[a]	0.021 (0.009)[a]	0.018 (0.008)[a]
	Xyris tenella	0.095 (0.034)[a]	0.016 (0.005)[b]	0.006 (0.004)[b]
	Xyris tortula	0.049 (0.023)[a]	0.035 (0.014)[a]	0.014 (0.004)[a]

Values represent mean ± SE; means followed by different letters are significantly different from each other

Table 2 Differences in soil characteristics between control and experimentally burned plots 15 days after burning

Soil characteristic	Burned	Control
pH (H_2O)	5.34 ± 0.15[a]	5.24 ± 0.06[a]
P (mg/dm^3)	9.68 ± 3.87[b]	4.29 ± 1.08[a]
K^+ (cmol$_c$/dm^3)	55.11 ± 13.78[b]	40.08 ± 12.17[a]
Ca^{2+} (cmol$_c$/dm^3)	0.37 ± 0.10[b]	0.13 ± 0.01[a]
Mg^{2+} (cmol$_c$/dm^3)	0.16 ± 0.14[b]	0.06 ± 0.02[a]
Al^{3+} (cmol$_c$/dm^3)	1.64 ± 0.10[a]	2.07 ± 0.32[b]
Organic matter (%)	22.76 ± 21.00[b]	16.99 ± 7.4[b]

Values represent mean ± SE; means followed by different letters are significantly different from each other

per se. However, given our study design—in which the treatments were applied across the entire swamp in plots immediately adjacent to each other—the likelihood of inter-treatment variation in the relative abundances of the different species is, in our view, minimal.

Fire-induced reproduction usually occurs in response to a combination of factors, especially light and soil nutrients (Lamont and Downes 2011). By removing herbaceous and shrubby biomass fire increases the amount of light reaching the soil surface and increases the availability of nutrients via ash deposition. Although differences in the average production of flowers/fruits between the clipping and burning treatments were significant for only some species, there was a clear trend towards finding more flowers and fruits per unit of area in burned than in clipped plots. This suggests that, for most species, increased light availability was not the only factor inducing plant reproduction in response to fire. Most likely, their reproduction was also stimulated by the availability of soil nutrients, whose concentrations increased significantly following our experimental burning treatment. Palm swamp soils are poor in nutrients (Ramos et al. 2006) and there is strong evidence that in the Cerrado many grasses and other species with superficial roots take advantage of the nutrients contained in plant ash (Coutinho 1990). In addition, ethylene, which is released during a fire and penetrates into the soil, has also been shown to induce flowering in some species (Mistry 1998; Miranda et al. 2009).

Previous studies have indicated that for at least some species clipping can be as effective as burning in inducing reproduction (Abrahamson 1999; McConnell and Menges 2002). Similarly, here we found that flower/fruit production of species such as *Arundinella hispida*, *Sporobolus cubensis*, *Exochogyne amazonica*, and *Rhynchospora globosa* was as high in the clipped as in the burned plots. This suggests that increased light is perhaps the most critical factor for reproduction of these species (Abrahamson 1999; Huffman and Werner 2000).

Despite the fact that this experiment is un-replicated results are so strikingly different among the treatments that we regard this as strong evidence that fire has a major effect on the reproduction of most plant species in palm swamps. Furthermore, the long term persistence of these species is contingent upon the occurrence of occasional fires, which is not altogether surprising given that fire is common in the Cerrado, and many species have evolved fire-adapted traits (Simon et al. 2009). Nevertheless, it is important to note that the frequency of fires have changed dramatically as a result of increased human activity in this biome (Pivello 2011). In this sense, future studies should evaluate the effects of fire frequency on the reproductive performance of palm swamp species. These studies are essential if we are to devise strategies to use fire as a management tool (Pivello 2011) for conservation of these unique and highly threatened Neotropical ecosystems.

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