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The effects of fire and cover on seedling establishment in a neotropical savanna

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Summary

1 It was hypothesized that if facilitation is important for seedling establishment in savanna, then fire should reduce seedling establishment.

2 This was tested in the cerrado savanna of Brazil with a factorial experiment designed to evaluate the effects of cover and prescribed burning on seedling establishment.

3 Seeds of 12 species of trees and shrubs were sown in plots located in sites providing three densities of woody cover and four times since last burning.

4 Seedling establishment generally was greater under the crowns of trees than in open grassland, but individual species responded differently to cover. Eight of the 12 species responded favourably to cover, but a single species showed reduced establishment with increasing cover.

5 Burning had an overall negative effect on seedling establishment in the first year following burning. By the second year following burning, establishment returned to control levels.

6 An irrigation experiment with two species demonstrated that rain-free periods within the wet season had negative effects on seedling establishment.

7 A litter-removal experiment with *Miconia albicans* revealed that, at least for this species, litter has a negative effect upon seedling establishment in densely wooded sites and positive effects in open grassland.

Keywords: cerradão, cerrado, facilitation, litter, woody plant

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Introduction

Disturbance is known to play an important role in ecosystem dynamics. As typically perceived, disturbance reduces the dominance of established plants and increases resource availability for seedlings. Additionally, disturbance may remove litter and humus which act as barriers to seedling establishment. As a result, disturbance is frequently followed by increased establishment and growth of seedlings. By reducing the negative effects of established individuals, disturbance improves conditions for seedling establishment.

However, established individuals do not always have a net negative effect on seedling establishment. Facilitation has been shown to occur in salt marshes (Bertness & Hacker 1994; Castellanos *et al.* 1994), desert (Turner *et al.* 1966; Jordan & Nobel 1979), prairie (Petranka & McPherson 1979), and savanna (Kellman & Miyanishi 1982; Kellman 1985; Callaway & D'Antonio 1991; Callaway 1992; Nyandiga & McPherson 1992; Bowman & Panton 1993). In all of the above studies, the presence of living individuals

improved the establishment and/or growth of seedlings. Numerous factors may be responsible for improved establishment under a canopy, such as improved temperature and water regimes, nutrient enrichment of soil by litter, or reduced predation (Hunter & Aarssen 1988).

In situations where beneficial plant interactions are important for seedling establishment, disturbance would be expected to play a different role from that which is typically observed. In this case, disturbance, by reducing the dominance of established individuals, should also reduce the beneficial effects provided by these established individuals. Therefore, it is expected that disturbance should reduce seedling establishment in environments where facilitation is important for seedling establishment.

It was in this context that I examined the effects of cover and fire on seedling establishment in the cerrado of Brazil. The cerrado is a savanna ecosystem occupying $\approx 2000\,000\text{ km}^2$ or nearly one quarter the area of Brazil (Adámoli *et al.* 1985). In the cerrado, grasses and forbs form a continuous herbaceous layer with

trees and shrubs forming a spatially heterogeneous woody layer varying in canopy height and stem density. Physiognomy varies continuously along a gradient of tree and shrub density from open grassland to closed woodland, or *cerradão*.

It is not known how establishment of trees and shrubs is affected by this extremely heterogeneous environment. Establishment of tree seedlings under natural conditions has long been an enigma of *cerrado* ecology. Many have considered reproduction by seed to be a rare event. P.W. Lund, in the last century, considered reproduction by seed to be an exception (Warming 1908). More recently, Ferri (1961) and Rizzini & Herringer (1962) confirmed the scarcity of woody plant seedlings. These authors considered that establishment of seedlings is infrequent and insignificant in comparison to vegetative reproduction by root suckers. While several studies have shown that seeds of *cerrado* species have high viability and germinate well under laboratory conditions (Rizzini & Herringer 1962; Rizzini 1971; Felipe & Silva 1984), there has been little corroborating field data. Recently Oliveira & Silva (1993), working with two species of *Kielmeyera*, showed that seeds germinated readily in the *cerrado* and the resulting seedlings had high survivorship despite the intense dry season typical of the *cerrado*, and burning, which occurred in the first year.

Although there is little information on seedling establishment in the *cerrado*, data from other tropical savannas indicate that forest trees have higher establishment under canopy cover than in open grassland (Kellman & Miyaniishi 1982; Kellman 1985; Bowman & Panton 1993). It is unknown if this response is limited to forest trees, or if it also applies to woody plants typical of savanna.

One objective of this study was to examine the role of woody cover on seedling establishment of trees and shrubs in the *cerrado*. Establishment was predicted to be highest at intermediate densities of canopy cover. Under a dense canopy, the negative effects of low light availability and a thick litter layer were expected to outweigh the beneficial effects of cover.

The second objective of this study was to determine the effects of fire on seedling establishment in the *cerrado*. Fire is the most widespread form of disturbance in the *cerrado*. Although little is known about the natural frequency of fire in the *cerrado*, there is little doubt that fire is currently much more frequent than before the arrival of humans. At present, fire intervals of two or three years are common in the *cerrado*. Although fire causes little mortality to established plants, it reduces the size of individuals, and reduces tree, herbaceous, and litter cover. It was predicted that if seedling establishment benefits from canopy cover, then fire will have a negative effect on seedling establishment.

The final objective was to determine the role of litter and drying soil upon seedling establishment. These are factors that are likely to have large effects

on seedling establishment, and are also likely to be affected by woody cover and burning. Litter accumulation is generally greater under denser vegetation, and fire improves seedling establishment in some ecosystems by consuming thick litter, which may act as a physical barrier to seedling establishment. However, litter can also serve to prevent water loss from the soil. Rain-free periods during the wet season are frequent in the *cerrado* (Cochrane *et al.* 1988). Seedlings may be sensitive to these periods, as they occur at a time when seedlings are quite young. Woody cover may play an important role in reducing water loss during at these times.

The three objectives presented above were investigated with a series of field experiments.

Methods

STUDY SITE

This study was conducted in the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (Ecological Reserve of the Brazilian Institute of Geography and Statistics) and the Jardim Botânico de Brasília (Botanical Garden of Brasília). These two reserves are contiguous and lie within the Federal District of Brasília at 15°52'S, 47°51'W. These reserves host a large fire project entitled 'Effects of Fire Regimes on the Structure and Dynamics of Cerrado Communities in Brasília', hereafter referred to as the Fire Project. The Fire Project offers a large number of 10-ha plots located along the entire physiognomic gradient from open grassland to *cerradão*. Since 1991, each plot has been subjected to one of several fire regimes or left unburned.

The average annual rainfall at the site is ≈ 1500 mm, with a distinct dry season from mid May to mid September. Oxisols underlie the site.

EXPERIMENT 1. EFFECTS OF CANOPY COVER AND BURNING ON SEEDLING ESTABLISHMENT

Twelve species of trees and shrubs were selected to include species typical of both forest and savanna. Three species, *Alibertia macrophylla*, *Ocotea pomaderroides*, and *Pera glabrata* are species typical of *cerradão* (closed woodland) and riparian forest, being found very infrequently in more open physiognomies. The remaining nine species, *Brosimum gaudichaudii*, *Guapira noxia*, *Kielmeyera coriacea*, *Miconia albicans*, *Myrsine guianensis*, *Periandra mediterranea*, *Roupala montana*, *Rourea induta* and *Zeyheria montana*, are typical of open savanna, but may also be found in the *cerradão*. A summary of growth habit and fresh seed mass of these species is provided in Table 1. Of these species, only *M. albicans*, *M. guianensis* and *P. mediterranea* have long-lived seeds that could potentially form a seed bank.

Thirty-six 0.25-m² plots were established for each

Table 1 Summary of habitat, growth habit, seed mass, and number of seeds sown per plot for the 12 species of expt 1

Species	Family	Growth habit	Dispersal mechanism	Mean seed fresh mass (g)	Number of seeds per plot
<i>Alibertia macrophyllum</i> K. Schum.	Rubiaceae	shrub/tree	mammal/bird	0.019	15
<i>Brosimum gaudichaudii</i> Trécul.	Moraceae	shrub/tree	mammal/bird	1.895	15
<i>Guapira noxia</i> (Netto) Lundell	Nyctaginaceae	tree	bird	0.044	35
<i>Kielmeyera coriacea</i> Mart.	Guttiferae	tree	wind	0.042	10
<i>Miconia albicans</i> Steud.	Melastomataceae	shrub	bird	0.0027	1368*
<i>Myrsine guianensis</i> Aubl.	Myrsinaceae	tree	bird	0.027	30
<i>Ocotea pomaderroides</i> Mez.	Lauraceae	tree	bird	0.143	20
<i>Pera glabrata</i> Poepp.	Euphorbiaceae	tree	indet. animal	0.025	28
<i>Periandra mediterranea</i> Taub.	Leguminosae	shrub	ballistic	0.036	25
<i>Roupala montana</i> Aubl.	Proteaceae	tree	wind	0.022	21
<i>Rourea induta</i> Planch.	Connaraceae	shrub	bird	N/A	5
<i>Zeyheria montana</i> Mart.	Bignoniaceae	shrub	wind	0.033	16

*The seeds of 60 fruit were sown in each plot. Number of seeds sown was estimated based on a mean of 22.8 seeds per fruit.

species, following a factorial design. The two factors, time since burning and density of cover, were represented by four and three levels, respectively. Thus, for each combination of cover and time since burning, three plots were established per species, except for *Myrsine guianensis* and *Periandra mediterranea* for which there are only two replicates for some of the treatments due to shortage of seed. The four times since burning were: 0 years – the site was burned during the dry season preceding sowing (i.e. less than 5 months prior to sowing); 1 year – the site was burned during the dry season of the previous year; 2 years – the site was burned in the dry season 2 years earlier; and control – the site had not been burned for at least seven years. Additionally, each seedling plot was located in a site with one of three categories of woody cover: open, intermediate and dense. These categories correspond to sites in open grassland, sites beneath the crown of a single tree within open savanna, and sites beneath the canopy of cerradão, respectively. To control for differences in cover within categories, criteria were established for site selection. In open sites, woody vegetation could not extend more than 30° above the horizon. In intermediate sites, the canopy from a single tree must allow only diffuse light at midday, but must allow full sun to strike the plot in early morning and late afternoon. In dense sites, a closed canopy must allow only diffuse sun throughout the entire day. Although the criteria for the latter two categories appear rather arbitrary, the difference in canopy cover between dense and intermediate sites is quite marked. To control for changes in density of cover due to burning, plot locations were chosen after the woody plants leafed out following burning, so that plot location could be selected to give woody cover appropriate for the required category. Each plot location was chosen by first selecting four sites with the appropriate density of woody cover and subsequently choosing one of the four sites at random for the seedling plot. To avoid contamination of the plots by background seed rain, plots were not placed in sites near fruiting adults.

Since the Fire Project at the research site offers a large number of replicate plots for each of the four burn treatments used in this experiment, sufficient plots were available to prevent pseudoreplication. For a given density of cover, no two seedling plots of the same species were located within the same 10-ha experimental plot of the Fire Project.

The number of seeds sown per plot varied between species (Table 1), the exact number being determined by availability of seeds. All seeds were collected within 5 km of the Fire Project. Seed were collected and sown between 1 September and 23 December 1993, depending on the period of natural seed dispersal for each species. Sowing involved scattering the seeds in the plots without any treatment to either the soil or the seeds.

Establishment success was defined as proportion of sown seeds producing seedlings that survived until May 1994, the end of the first wet season. Establishment success was transformed using the arcsine transformation and subsequently analysed with three-factor ANOVA with species as a random factor and cover and fire treatments as fixed factors. To understand further which burn treatments and cover densities contributed to overall burn and cover effects, planned orthogonal comparisons were made. As there are three levels of canopy cover, two independent orthogonal comparisons could be made. The first compares establishment in the open sites with the average of intermediate and dense sites. The second compares intermediate sites with dense sites. Likewise, as there are four burn treatments, three independent orthogonal comparisons could be made. The first compares newly burned plots with the average of the other three treatments. The second compares control plots with the average of plots burned 1 year previously and plots burned 2 years previously. The last compares plots burned 1 year previously with plots burned 2 years previously. A two-factor ANOVA was performed for each species, with cover and time since burning as the two factors.

EXPERIMENT 2. EFFECTS OF IRRIGATION AND
CANOPY COVER ON SEEDLING
ESTABLISHMENT

Thirty-five plots were established for each of two species, *Roupala montana* and *Miconia albicans*, for which sufficient seeds were available. Plots were placed in unburned sites with the three categories of canopy cover used in expt 1. Plots were established in 15 open sites, 15 intermediate sites and five dense sites for each species. To ensure independence of the seedling plots, no more than one plot of a given cover density was located within each experimental plot of the Fire Project. Each plot consisted of two subplots, one of which was randomly chosen for irrigation. In the *R. montana* plots, each subplot had an area of 1 m², in which 18 seeds were scattered on 17–19 November 1992. Each *M. albicans* subplot had an area of 0.25 m² in which the seeds of 60 fruit were scattered on 2–5 December 1992. This is the equivalent of 1368 seeds, based on an average of 22.8 seeds per fruit ($n = 100$). For both species, the seeds were scattered on the unmodified soil surface.

Irrigation subplots were watered during rain-free periods between the date the seeds were sown and 31 March 1993. Watering was done at three-day intervals within these rain-free periods, beginning on the third day without rain. The quantity of water supplied during each irrigation episode was 4 L m⁻².

Establishment success was defined as proportion of sown seeds producing seedlings that survived until May 1993, the end of the first wet season. Establishment success was transformed with the arcsine transformation and were analysed as a split-plot design with cover as the main plot factor.

EXPERIMENT 3. EFFECTS OF LEAF LITTER ON
SEEDLING ESTABLISHMENT.

The role of leaf litter in the establishment of *Miconia albicans* was studied, as this species appeared to establish poorly in deep litter. Eighteen plots were established in unburned cerrado, with six in each of the three classes of canopy cover described for expt 1. Each plot consisted of two 50-cm × 50-cm subplots. One of the two subplots was randomly chosen and all leaf litter and standing dead herbaceous biomass was removed. The other subplot was left untouched. The seeds from 60 fruit of *M. albicans* were scattered in each quadrat on 20 January 1994. At 2-month intervals until the end of the wet season, newly fallen litter was removed from the appropriate subplots and seedlings were counted. Litter was dried at 60 °C to constant mass and weighed.

Establishment success was defined as proportion of sown seeds producing seedlings that survived until May 1994, the end of the first wet season. Establishment success was transformed with the arcsine transformation and analysed using split-plot ANOVA

with cover as the main plot factor. Litter biomass between cover categories was compared with a single-factor ANOVA using log-transformed mass.

Results

EXPERIMENT 1

Establishment success differed among species ($P < 0.0001$, Table 2). Among species, average seedling establishment was positively correlated with log seed mass ($r^2 = 0.56$, $n = 11$, $P = 0.008$).

Overall, cover had a significant effect on seedling establishment ($P < 0.0001$, Table 2). Seedling establishment in open sites was lower than in dense and intermediate sites ($F_{1,277} = 57.60$, $P < 0.0001$). There was no difference in seedling establishment between dense and intermediate sites ($F_{1,277} = 1.28$, $P = 0.26$).

Species differed in response to cover, as is indicated by the significant interaction of species and cover effects ($P = 0.007$, Table 2). Nine of the 12 species showed significant effects of cover on seedling establishment (Table 3). Most of these species showed increased establishment in sites with woody cover. All three cerrado species and four of the nine savanna species experienced significantly lower establishment in open sites than sites with cover (Table 3a, Fig. 1). Only *Roupala montana* showed improved establishment in dense sites relative to intermediate sites (Table 3b). A single species, *Miconia albicans*, showed negative effects of cover (Table 3, Fig. 1g).

Time since burning affected seedling establishment ($P < 0.0001$, Table 2). Seedling establishment in recently burned sites was lower than in the other treatments ($F_{1,277} = 42.89$, $P < 0.0001$). Establishment did not differ significantly between control plots and plots burned one or 2 years previously ($F_{1,277} = 0.39$, $P = 0.55$). Likewise, establishment did not differ between plots burned 1 year previously and plots burned 2 years previously ($F_{1,277} = 2.03$, $P = 0.14$).

The lack of a significant interaction between time after fire and species ($P = 0.90$, Table 2) indicates that there was little interspecific difference in the response of seedling establishment to burning. All species showed a reduction in establishment in recently burned plots relative to all other plots (Fig. 2), but this was significant only for six species (Table 4a). In contrast, only two species showed significant differences in establishment among control plots, plots burned 1 year previously and plots burned 2 years previously (Table 4b,c). These results indicate that burning has a large negative effect on seedling establishment in the first year, but, by the second year, establishment success is not significantly different from control levels for most species. A notable exception to this trend is *Miconia albicans*, for which establishment declined significantly following the increase in establishment 1 year following burning.

There was no significant interaction between time

Table 2 Three-factor ANOVA testing for effects of burning, woody cover, and species on seedling establishment

Source	Sum of squares	d.f.	Mean square	F-ratio	P
Burn	2.12360	3	0.707865	21.381	< 0.0001
Cover	2.75951	2	1.37976	14.713	< 0.0001
Species	10.6695	11	0.969950	20.361	< 0.0001
Burn × cover	0.338909	6	0.056485	1.7089	0.1327
Burn × species	1.09252	33	0.033107	0.69498	0.8962
Cover × species	2.06305	22	0.093775	1.9685	0.0069
Burn × cover × species	2.18158	66	0.033054	0.69387	0.9619
Error	13.1955	277	0.047637		

Table 3 Results of ANOVA testing for effects of cover on seedling establishment. The Woody cover column indicates the result of the test for overall effects of cover on seedling establishment. (a) No cover vs. cover and (b) intermediate cover vs. dense cover (see text)

Species	Habitat	Woody cover	Orthogonal comparisons	
			(a)	(b)
<i>Alibertia macrophylla</i>	Cerradão	**	***	NS
<i>Ocotea pomederroides</i>	Cerradão	**	***	NS
<i>Pera glabrata</i>	Cerradão	NS	*	NS
<i>Brosimum gaudichaudii</i>	Savanna	**	***	NS
<i>Guapira noxia</i>	Savanna	**	***	NS
<i>Keilmeyera coriacea</i>	Savanna	NS	NS	NS
<i>Miconia albicans</i>	Savanna	**	**	**
<i>Myrsine guianensis</i>	Savanna	NS	NS	NS
<i>Periandra mediterranea</i>	Savanna	*	*	NS
<i>Roupala montana</i>	Savanna	*	NS	*
<i>Rourea induta</i>	Savanna	NS	*	NS
<i>Zeyheria montana</i>	Savanna	NS	NS	NS

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

and cover (Table 2). Likewise there was no significant third-order interaction between species, cover, and time since burning (Table 2).

EXPERIMENT 2

Establishment of *Roupala montana* showed a significant positive response to both irrigation ($F_{1,32} = 8.23$, $P = 0.007$) and woody cover ($F_{2,32} = 5.67$, $P = 0.008$). Average establishment success was 3.1% in open sites, 9.4% in intermediate sites and 15.6% in dense sites (Fig. 3). Likewise, irrigation improved establishment. Average establishment success was 7.0% in unirrigated subplots and 11.7% in irrigated subplots (Fig. 3). There was no significant interaction between cover and irrigation ($F_{2,32} = 1.72$, $P = 0.196$).

Irrigation also increased seedling establishment of *Miconia albicans* ($F_{1,32} = 8.58$, $P = 0.0062$). Average establishment in irrigated sites was 0.94% whereas in unirrigated sites average establishment was 0.26% (Fig. 4). There was no significant effect of cover on seedling establishment ($F_{2,32} = 1.55$, $P = 0.23$) nor a significant interaction between cover and irrigation ($F_{2,32} = 0.38$, $P = 0.69$).

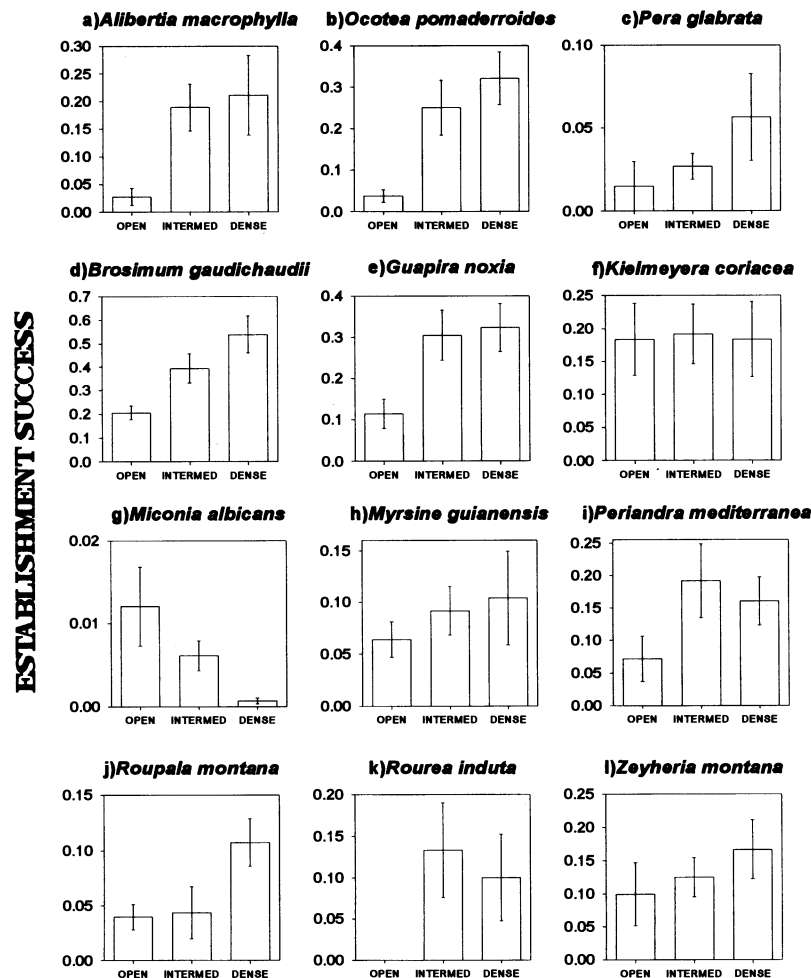
Irrigation, which was performed at three-day inter-

vals during dry spells, was necessary 10 times between 5 December 1992 and 31 March 1993. Although the total quantity of water applied during this time represented an equivalent of only 40 mm of rain, less than 3% of the mean annual rainfall, this amount resulted in a 67% increase in seedling establishment of *Roupala montana* and a 260% increase in establishment of *Miconia albicans*.

EXPERIMENT 3

The three categories of cover differed significantly in mass of accumulated litter ($F_{2,15} = 26.66$, $P < 0.0001$). Mean (\pm SE) litter mass per 0.25 m² was 79.3 \pm 13.8 g in open sites, 248.8 \pm 36.6 g in intermediate sites and 366.7 \pm 51.2 g in dense sites (d.f. = 6 in all cases).

In this experiment, cover had a significant effect on seedling establishment of *Miconia albicans* ($F_{2,15} = 6.13$, $P = 0.011$). Litter removal did not significantly affect seedling establishment when compared over all three densities of woody cover ($F_{1,15} = 0.048$, $P = 0.83$). This is due, at least in part, to a significant interaction between cover effects and litter effects ($F_{2,15} = 5.01$, $P = 0.022$). Indicating that



DENSITY OF WOODY COVER

Fig. 1 Effect of woody cover on seedling establishment of 12 species of trees and shrubs. Species a–c are typical of cerradão and forest, and species d–l are typical of savanna. Error bars represent ± 1 SE.

the effect of litter removal depended on cover density. When the effects of litter removal is analysed separately for each of the three densities of woody cover, results depended upon census date. For data collected in May 1994, litter removal had no effect for either open ($t_5 = 2.28$, $P = 0.07$), intermediate ($t_5 = 0.96$, $P = 0.38$), or dense ($t_5 = 2.236$, $P = 0.08$) sites (paired t -tests). However, for the census data obtained in March 1994, before considerable mortality had occurred, litter removal increased seedling establishment in dense sites ($t_5 = 3.98$, $P = 0.01$), had no effect in sites with intermediate cover ($t_5 = 0.62$, $P = 0.56$) and decreased seedling establishment in open sites ($t_5 = 3.38$, $P = 0.02$) (Fig. 5).

Discussion

Cover was shown to be important for seedling establishment in all three experiments. The beneficial effect of trees was probably due to a number of factors. Soil under savanna trees has been shown to have better nutrient status (Kellman 1979; Belsky *et al.* 1989;

Isichei & Muoghalu 1992; Mordelet *et al.* 1993) and higher moisture content during dry periods than nearby open grassland (Joffre & Rambal 1988; Belsky *et al.* 1989; Ko & Reich 1993). Likewise, tree cover reduces soil surface temperatures (Belsky *et al.* 1989; Franco & Nobel 1989; Callaway *et al.* 1991; Ko & Reich 1993). Differences in temperature and moisture may result in lower water stress for seedlings in covered sites. Grasses, which are similar to young seedlings in that they tend to have shallow root systems (Frost *et al.* 1986), have been shown to have higher leaf water potential under tree clumps in savanna (Mordelet 1993). The amelioration of water stress under trees is likely to be a particularly important factor in the cerrado. Dry spells of several days or more occur frequently during the wet season in the cerrado region (Cochrane *et al.* 1988). These commonly occur during germination or shortly thereafter, when seedlings are most sensitive to drying soil. The effect of these dry spells was demonstrated in expt 2. Irrigation resulted in a 67% increase in seedling establishment of *Roupala montana* and a 260%

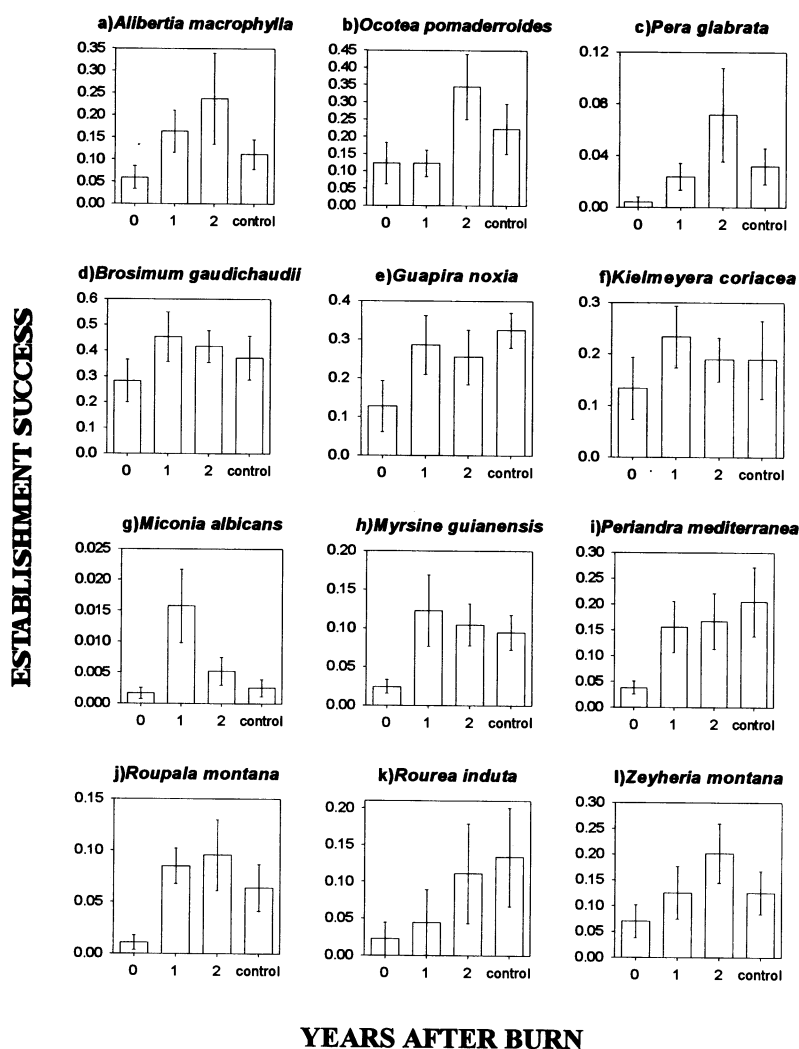


Fig. 2 Effect of burning on seedling establishment of 12 species of trees and shrubs. Species a–c are typical of cerradão and forest, and species d–l are typical of savanna. Error bars represent ± 1 SE.

Table 4 Results of ANOVA testing for effects of burning on seedling establishment. The Time since burning column indicates results of the test for overall effects of burning treatments on seedling establishment. (a) Newly burned plots vs. all other plots, (b) control plots vs. plots burned 1 or 2 years previously and (c) plots burned 1 year previously vs. plots burned 2 years previously (see text)

Species	Habitat	Time since burning	Orthogonal comparisons		
			(a)	(b)	(c)
<i>Alibertia macrophylla</i>	Cerradão	NS	NS	NS	NS
<i>Ocotea pomaderroides</i>	Cerradão	*	NS	NS	*
<i>Pera glabrata</i>	Cerradão	NS	*	NS	NS
<i>Brosimum gaudichaudii</i>	Savanna	NS	NS	NS	NS
<i>Guapira noxia</i>	Savanna	*	***	NS	NS
<i>Kiellmeyera coriacea</i>	Savanna	NS	NS	NS	NS
<i>Miconia albicans</i>	Savanna	**	*	*	*
<i>Myrsine guianensis</i>	Savanna	NS	*	NS	NS
<i>Periandra mediterranea</i>	Savanna	*	*	NS	NS
<i>Roupala montana</i>	Savanna	*	*	NS	NS
<i>Rourea induta</i>	Savanna	NS	NS	NS	NS
<i>Zeyheria montana</i>	Savanna	NS	NS	NS	NS

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.005$.

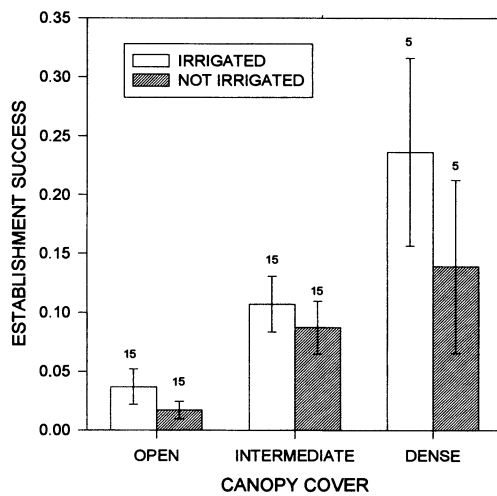


Fig. 3 Establishment success of *Roupala montana* under three densities of woody cover, with and without irrigation. Error bars represent ± 1 SE.

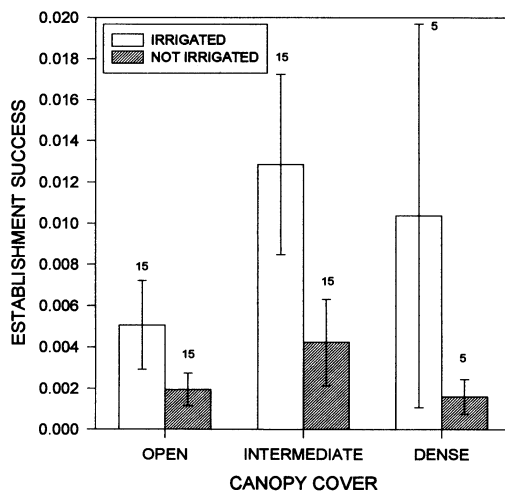


Fig. 4 Establishment success of *Miconia albicans* under three densities of woody cover, with and without irrigation. Error bars represent ± 1 SE.

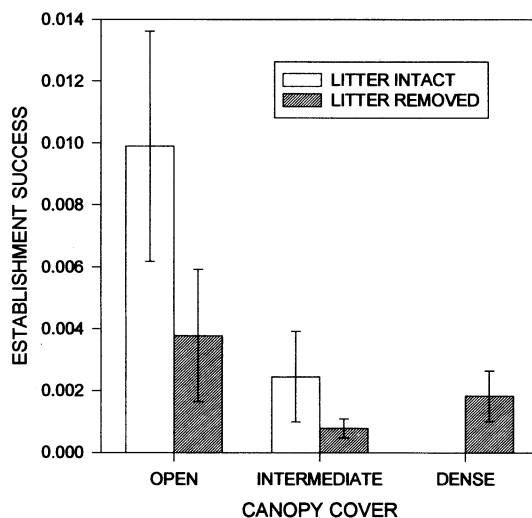


Fig. 5 Establishment success of *Miconia albicans* under three densities of woody cover, with and without removal of litter. Error bars represent ± 1 SE ($n = 6$ plots).

increase in establishment of *Miconia albicans*, even though the total amount of water applied was less than 3% on the mean annual rainfall. The timing of irrigation, which occurred at regular intervals during dry periods early in the life of the seedlings was important. Considering the sensitivity of seedling establishment to dry periods during the wet season, it is probably during these periods that amelioration of water stress by tree cover is most critical to the establishment of seedlings.

Canopy cover may have influenced seedling establishment indirectly by reducing the density of the competing herbaceous layer. This may have been important in dense sites, where the herbaceous layer is typically scant, but probably was not important for the difference between open and intermediate sites. There was little observable difference in density of the herbaceous layer between open sites and sites with intermediate cover. In fact, a single tree may facilitate the herbaceous layer in savanna (Belsky *et al.* 1989).

Additionally, predation upon seeds and seedlings may have differed among cover categories. Shade has previously been shown to reduce herbivory in other systems (Louda & Rodman 1996). In this study, herbivory affected few seedlings, and usually did not kill the seedling outright, so this probably contributed little to the observed trends. However, the effect of seed predation might have been important, and needs to be tested.

Establishment was not highest at intermediate levels of canopy cover as predicted. Rather, there was little difference in establishment between dense and intermediate sites. The failure to observe a decline in establishment at higher densities of cover may reflect the range of canopy densities tested. Although the dense sites used in this study had a closed canopy typical of cerradão, the canopy was less dense than that of riparian forests in the area. Individuals of savanna trees and shrubs are frequent in the understorey of cerradão, but are absent from riparian forest. Had the study included sites within riparian forest, it is likely that a negative response to high density would have been observed.

Although canopy cover improved seedling establishment of most species in this study, this response was not universal. All three forest species benefited from woody cover, supporting previous findings that tropical forest trees establish poorly in open savanna (Kellman & Miyanishi 1982; Kellman 1985; Bowman & Panton 1993). Additionally, five of the nine savanna trees and shrubs showed improved seedling establishment under tree cover, while one species showed reduced establishment under cover. Many factors may be responsible for differential response to cover, as species vary greatly in response to light, water stress, temperature, and nutrients (Kozłowski *et al.* 1991), all of which have been shown by others to differ between sites under trees and sites in open grassland. The fact that canopy cover facilitated establishment

of all three forest species, but not all savanna species, suggests that the forest trees are more susceptible to nutrient, water or temperature stress than are savanna trees. Forest trees have been shown to have lower root-shoot ratios than savanna trees of the cerrado (Moreira 1992), which may reduce their ability to obtain water and nutrients.

The benefit of an extensive root system early in life is also supported by the significant positive correlation between seed size and overall seedling establishment. Large seeds have ample reserves for the development of an extensive root system, probably conferring greater drought tolerance (Baker 1972; Leishman & Westoby 1994).

The present study addressed the role of woody cover for the establishment of seedlings only until the end of the first wet season. However, the beneficial role of cover may extend well beyond this period, particularly through the first dry season. Even after the first year of growth, the seedlings may benefit from adults. Kellman (1985) demonstrated that woody cover in savanna produced increased growth rates in seedlings of two forest tree species for several years. Although water relations are likely to be most critical early in establishment, improved growth later is probably dependant upon the improved nutrient status under woody cover.

Another factor found to influence seedling establishment in this study is fire. Although only six of the 12 species showed a significant reduction in seedling establishment in recently burned plots, the lack of a significant interaction between species effects and burning effects (Table 2) suggest that the failure of some species to show a significant response to burning is due to lack of statistical power, rather than large differences in species responses to fire. This is further corroborated by the fact that every species exhibited lowest seedling establishment in recently burned plots, even though this reduction was not always statistically significant.

Because woody cover is beneficial to seedling establishment, a negative effect of burning was expected. However, reduction in establishment due to burning cannot be entirely explained by a reduction in woody cover, as fire caused an overall reduction in establishment even though site selection controlled for density of woody cover. In the first year following burning, the litter layer is thin and herbaceous biomass is considerably lower than preburn levels, exposing seeds and seedlings to higher temperature and desiccation. Predation may have been greater in burned plots, however, burning can also reduce seed predation (Tyler 1995)

The negative effect of burning on seedling establishment contradicts trends observed in other fire-prone ecosystems. Fire has been shown to improve conditions for seedling establishment in Mediterranean shrublands (Wellington 1989; Keeley 1991; van Wilgen & Forsyth 1992; Tyler 1995), forest (Shea-

rer 1976; Mallik & Roberts 1994), and pine barrens (Little 1979), however, it must be noted that not all species in these ecosystems show improved establishment following burning. In these systems, burning removes the inhibitory effects of established vegetation, such as accumulated litter, a closed canopy, or allelopathic chemicals. Such factors appear to not play such an important negative role for most species in the cerrado.

Miconia albicans deviated greatly from the trend observed for the other species. In the 1993–94 season, it showed reduced establishment with increasing canopy cover. This response is due, at least in part, to thick litter which acts as a barrier to establishment, as is common for small-seeded species (Facelli & Pickett 1991). In dense sites, where the litter layer is greatest, litter removal had a positive effect on establishment of this species. However, in open sites, where leaf litter is scant and desiccation is greater, litter removal had a negative effect on establishment of *M. albicans*. In grassland, litter serves to reduce soil temperature and water loss (Facelli & Pickett 1991), a benefit which probably outweighs the negative effects of the thin litter layer of open sites. Interestingly, in 1992–93 (expt 2), establishment of *M. albicans* did not show a negative response to cover. Establishment in open sites was particularly poor in 1992–93, probably due to low rainfall during the period of seedling establishment. During the period of 1 December 1992–31 March 1993, the Ecological Reserve of IBGE received only 858 mm of rain as compared to 1172 mm received during the same months of 1993–94. More importantly, there were three rain-free periods of 9 or more days in length during these months of the 1992–93 wet season, whereas no rain-free period lasted for more than 6 days in the 1993–94 wet season. Thus the relative magnitudes of negative and positive effects of cover appear to depend upon rainfall. In dry years, the role of cover plays a particularly important role in ameliorating the environment, countering the negative effects of the thick litter associated with woody cover. This supports the hypothesis of Bertness & Callaway (1994) that positive interactions between plants are most important under conditions of physical stress.

Miconia albicans also differed from the other species in its response to burning. Although it exhibited reduced establishment in the first year following fire, as did other species, it alone had a peak in establishment in the second year. There was a subsequent decline in establishment. A similar trend in natural establishment of this species following fire was demonstrated by Miyanishi & Kellman (1986) in Belize. This reduction in establishment several years after burning appears to be due to inhibition by accumulated litter.

The thick litter of dense sites appears not to represent such a formidable barrier to establishment for the remaining species, all of which have larger seeds than *M. albicans*. However, the reduction of tem-

perature and water stress by litter is probably beneficial to these species, regardless of seed size.

Thus these results indicate that the roles of cover and fire depend on a number of factors. Although canopy cover plays an important role in ameliorating water, nutrient, and temperature stress, cover also has negative effects caused by shading. The effect of litter may be positive, but becomes negative if the litter layer is too thick. The relative magnitudes of the positive and negative effects of these multiple factors are dependant on the density of cover, but are most certainly influenced by species attributes such as seed size, requirements for germination, and drought tolerance.

Fire intervenes in this relationship between cover and germination by causing short-term reductions in canopy cover and litter. Repeated burning causes long-term reductions in woody cover (Ramos 1990; Moreira 1992). While fire results in a immediate flush of nutrients, it causes a net loss of P, N and S (Kauffmann *et al.* 1994), exasperating the low nutrient availability of cerrado soils. So, fire must reduce recruitment by reducing the availability of safe sites, in addition to direct effects of burning on young seedlings and seed availability.

The results of this study have considerable implications for vegetation dynamics of the cerrado and other tropical savannas. In particular, the importance of beneficial interactions between plants may compromise the stability of the tree-grass ratio in savannas. The beneficial effect of cover on establishment of seedlings results in a positive feedback loop. Where woody cover is present, seedling establishment is high, causing further increases in density. In open sites, seedling establishment is low, so increase in vegetation density is slow. This contrasts with forest ecosystems, in which competition for light results in a negative feedback loop in which areas of dense vegetation exhibit low plant growth and establishment relative to open areas. In forests, plant biomass develops towards a relatively even spatial distribution in which the negative feedback loop stabilizes vegetation density. Positive feedback loops, however, have a destabilizing effect (Puccia & Levins 1985). Because establishment of woody plants in the cerrado is greatest where woody plants are already present, there is a tendency for spatial variation in cover to increase, rather than decrease. Evidence of this is frequently seen in savannas, as woody plants in savanna are frequently found in clusters (San José *et al.* 1991; Archer 1995) which may expand in the absence of fire (Archer *et al.* 1988).

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