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Post-Establishment Seedling Success in the Brazilian Cerrado: A Comparison of Savanna and Forest Species[1]

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ABSTRACT

Due to frequent fire, low nutrient availability, and prolonged drought, tropical savanna is a stressful environment for the survival and growth of woody plant seedlings. To understand why forest species do not succeed in this environment while savanna species are able to persist, the effects of fire and woody cover on seedlings of these two functional groups were investigated in the Brazilian Cerrado. Seedlings were established in experimental plots under three densities of woody cover, in sites protected from fire and sites to be subjected to fire. There was a clear difference in the ability of savanna and forest species to survive fire. None of the three forest species were able to survive fire during the first two years of life, whereas eight of the nine savanna species were able to resprout following fire. The small seed size of the ninth savanna species, *Miconia albicans,* predisposed its seedlings to be sensitive to fire, because there was a strong positive correlation between seed size and survivorship. Savanna species were less dependent on woody cover than were forest species, which exhibited higher growth and survival under tree canopies than in open grassland. The low rates of establishment and survival of forest trees in savanna, combined with high sensitivity to fire, appear sufficient to prevent the expansion of forest into savanna under current fire regimes in the Cerrado.

RESUMO

Devido ao fogo frequente, baixa disponibilidade de nutrientes, e estresse hídrico prolongado, a savana tropical é um ambiente severo para sobrevivência e crescimento de plântulas lenhosas. Para entender porque espécies de floresta não prosperam nesse ambiente enquanto que as espécies de savana persistem, foi investigado os efeitos de fogo e cobertura lenhosa nesses dois grupos funcionais no Cerrado do Brasil. Plântulas foram estabelecidas em áreas experimentais em baixo de três densidades de cobertura lenhosa, em áreas protegidas do fogo e áreas a serem queimadas. As espécies de floresta e as espécies de savana exibiram uma diferença nítida na capacidade de sobreviver o fogo. Nenhuma das três espécies de floresta mostrou a capacidade de sobreviver fogo durante os primeiro dois anos da vida, enquanto oito das nove espécies savânicas rebrotaram depois do fogo. As semantes pequenas da nona espécie de savana se predispõe a ser sensível ao fogo, porque houve um correlação forte entre sobrevivência e tamanho de semente. As espécies de floresta foram mais dependentes em cobertura lenhosa para sobrevivência do que as espécies de savana, mostrando menor crescimento e sobrevivência em savana aberta do que em baixo de cobertura lenhosa. A baixa taxa de estabelecimento e sobrevivência das espécies floristais em savana, junto com a alta sensibilidade ao fogo, são suficientes para virtualmente eliminar a expansão da floresta em áreas de Cerrado sob regimes atuais de fogo.

Key words: *Brazil; Cerrado; facilitation; fire; savanna; seedling; seed size; shrub; tree; tropical forest.*

THROUGHOUT MUCH OF THE WET–DRY TROPICS, the landscape is composed of a mosaic of savanna and forest vegetation. These two vegetation types are floristically distinct (Taylor & Dunlop 1985, Adejuwon & Adesina 1992, Felfili & da Silva 1992, Haridasan 1992), with most woody plant species occurring almost exclusively in one environment or the other. High temperatures, water stress, and low nutrient availability all may be important constraints for forest species in savanna. Woody cover, which ameliorates the savanna microclimate and improves soil nutrient availability (Kellman 1979, Belsky *et al.* 1989, Isichei & Muoghalu 1992, Mordelet *et al.* 1993), has been shown to facilitate the establishment and growth of forest trees in savanna (Kellman & Miyanishi 1982, Kellman 1985); however, it is not clear that forest species differ fundamentally from savanna species in their dependence upon woody cover for establishment. For example, Hoffmann (1996) demonstrated that some savanna species are similar to forest species in that they establish poorly in open grassy sites in the Brazilian Cerrado. That study, however, examined neither growth nor survival beyond the first growing season. To argue that the stressful environment

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TABLE 1. *Summary of study species.*

Species	Family	Habitat	Growth form	Seedlings studied
Alibertia macrophylla K. Schum.	Rubiaceae	Forest	Shrub/Tree	75
Ocotea pomaderroides Mez.	Lauraceae	Forest	Tree	146
Pera glabrata Poepp.	Euphorbiaceae	Forest	Tree	33
Brosimum gaudichaudii Trécul.	Moraceae	Savanna	Shrub/Tree	206
Guapira noxia (Netto) Lundell	Nyctaginaceae	Savanna	Tree	312
Kielmeyera coriacea Mart.	Guttiferae	Savanna	Tree	67
Miconia albicans Steud.	Melastomataceae	Savanna	Shrub	1035
Myrsine guianensis Aubl.	Myrsinaceae	Savanna	Tree	143
Periandra mediterranea Taub.	Leguminosae	Savanna	Shrub	243
Roupala montana Aubl.	Proteaceae	Savanna	Tree	210
Rourea induta Planch.	Connaraceae	Savanna	Shrub	15
Zeyheria montana Mart.	Bignoniaceae	Savanna	Shrub	75

is a primary constraint for the success of forest trees in savanna, it becomes necessary to demonstrate that forest species are more sensitive than savanna species to the savanna environment.

Fire is another factor that may be responsible for the scarcity of forest trees in savanna. At present, moist savannas throughout the tropics commonly burn at intervals of one to three years (Lacey *et al.* 1982, Trollope 1984, Coutinho 1990, Stott 1990, Russell-Smith *et al.* 1997), primarily due to anthropogenic causes. This frequent burning may be responsible for the elimination of forest species from savanna. In contrast, fire typically does not penetrate far into undisturbed forest.

This study is a continuation of previously published work examining the effects of fire and cover on seedling establishment in savanna (Hoffmann 1996), in which establishment was defined as successful germination and survival to the end of the first wet season. Here, I focused on subsequent survival and growth of the same established seedlings. To understand the ecological differences between savanna and forest species, and to understand what factors limit forest seedling survival in savanna, I studied the effects of fire and cover on established seedlings of both groups of species. I predicted that forest species would be more dependent on woody cover and more sensitive to fire than savanna species.

METHODS

Research was conducted within the Reserva Ecológica do Instituto Brasileiro de Geografia e Estatística (IBGE) and the adjacent Jardim Botânico de Brasília (JBB). The site is *ca* 35 km south of Brasília, D.F., Brazil, at 15°56′S and 47°53′W. Mean annual rainfall (1980–1994) at the site is 1480 mm, of which 91 percent occurs in the summer months of October to April. Mean annual temperature (1980–1994) is 21.8°C. The soils are deep and well-drained Oxisols. A large fire project was established at the study site in the early 1990s. The experimental area was divided into six blocks of five 10-ha plots. Each plot within a block was subjected to one of four fire regimes or was left unburned. The vegetation within the fire project ranges from open shrub savanna (campo sujo) to closed savanna woodland (cerradão). The latter physiognomy is not as dense as true forests in the area, and contains savanna species along with forest species. Cerradão, however, was used rather than true forests because there is little difference in hydrology and soil properties between this vegetation and savanna (Haridasan 1992, Moreira 1992).

Twelve common species of trees and shrubs were chosen for this study (Table 1). Nine species are typical of savanna and three are typical of forest. The latter three also are encountered in the cerradão woodlands at the study site, indicating that they may be less sensitive to the savanna environment than many other forest species.

I established a series of subplots within the fire project to study seedling establishment and growth. Each subplot was established in a site with one of three categories of woody cover: open, intermediate, and dense. These categories corresponded to sites in open grassland, sites beneath the crown of a single tree within open savanna, and sites beneath the canopy of cerradão woodland. To reduce variation within cover 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 of a single tree must allow only diffuse sunlight at midday, but must allow direct sunlight to strike the subplot during early morning and late afternoon. In dense sites, a closed canopy must allow only diffuse sun during the entire day. Each subplot location was chosen by first selecting four sites with the appropriate density of woody cover and then randomly selecting one of the four sites. Thirty-six subplots were established for each of the 12 species in 1993. Thirty-five additional subplots were established for *Miconia albicans* and *Roupala montana* in 1992, and 36 additional subplots established for *Periandra mediterranea* and *Myrsine guianensis* in 1994. The 1992 subplots were 1.00 m^2 and the 1993 and 1994 subplots were 0.25 m^2. In any one year, no two subplots of the same species and the same density of cover were established within the same 10-ha plot of the fire project; however, two or three subplots of different cover densities often were established within the same 10-ha plot, but never placed within 15 m of each other.

Seeds from all 12 species were collected within a few kilometers of the seedling subplots, and were sown within two weeks of collecting. No site preparation was performed, and the seeds were scattered directly on the natural substrate. The number of seeds sown per subplot varied among species, depending upon seed availability. As a result of variable seed number and variable establishment success (Hoffmann 1996), the number of seedlings available for study differed considerably among species (Table 1).

I marked each seedling with an aluminum tag when less than one year old. I conducted censuses of these subplots in 1993, 1994, 1995, and 1996, during the dry season. At each census, I measured the height of each individual. Because of scheduled burning in the fire project and an unplanned wildfire in 1994, approximately half of the seedlings for each species were burned during the first dry season, when less than one year old. Some of the remaining unburned seedlings were burned in subsequent years, but too few for statistical comparisons. Therefore, I examined survival of only one-year-old seedlings. All survival rates presented are for the one-year period beginning at the end of the first wet season. To test for effects of fire and cover on survival of each species, Fisher's exact test was used. To test for a significant relationship between fresh seed mass and survival probability, I used the nonlinear regression procedure of SYSTAT 5.01. For this, the least squares method was employed to fit the logistic equation to the survival probabilities, which were obtained by pooling the data from all three cover types. To test for differences in survival between forest and savanna species, ANCOVA was used, with fresh seed mass as the covariate.

Growth was examined only in the unburned subplots. One-way ANOVA was used to test for the effect of cover on seedling height. This analysis was repeated for the first three years, which was the age of most seedlings when the study was discontinued.

The seedling subplots initially were established to examine factors controlling seedling establishment. As a result of this design, these subplots were subjected to treatments that are not being examined here. For example, half of the 1992 subplots for *M. albicans* and *R. montana* were watered during dry periods within the first wet season, but this treatment was discontinued before the current data were collected. Additionally, the 1993 and 1994 subplots were placed in experimental plots with varying fire histories. Any effect of these factors on subsequent growth or survival would not influence the interpretation of the current analysis, since these treatments were applied in balanced factorial designs and distributed evenly among the cover treatments.

RESULTS

Savanna and forest species differed significantly in their ability to survive fire, with savanna species exhibiting higher survival (Fig. 1a; $F_{1,9} = 16.95$, $P = 0.003$). Eight of the nine savanna species were able to survive fire when less than one year old. In contrast, not a single one-year-old seedling of the three forest species survived fire. Similarly, no two-year-old forest seedlings survived fire ($N = 27$, data not shown). Among the savanna species, survival of burned seedlings was positively correlated to seed mass (Fig. 1a; $R^2 = 0.60$, $P < 0.05$). *Miconia albicans*, the one savanna species unable to survive fire as seedlings, was also the species with the smallest seed mass.

In unburned plots, there was no significant difference in survival between savanna and forest species (Fig. 1b; $F_{1,9} = 1.04$, $P = 0.335$). Among savanna species, there was a positive correlation between seed mass and survivorship in unburned plots ($R^2 = 0.61$, $P < 0.05$), but this relationship was nonsignificant when forest species were included ($R^2 = 0.26$, NS).

Burning had a significant negative effect on the survival of all species except *Rourea induta* and *Kielmeyera coriacea* (Fig. 1); however, it must be noted that the sample size for *R. induta* was quite

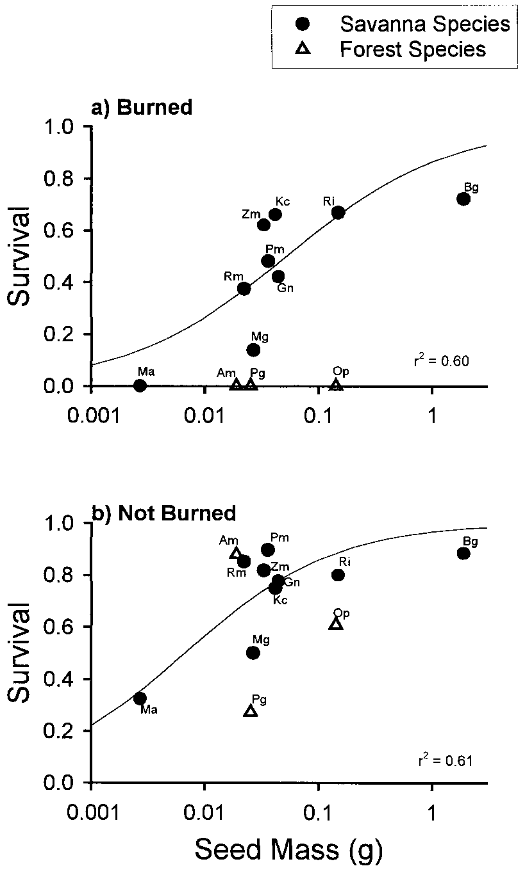

FIGURE 1. First-year survival rates of savanna and forest seedlings. (a) Survival in plots burned during first dry season. (b) Survival in unburned plots. The logistic curves in both graphs were obtained by a least squares fit to the data for only the savanna species. Species codes: Am, *Alibertia macrophylla*; Bg, *Brosimum gaudichaudii*; Gn, *Guapira noxia*; Kc, *Kielmeyera coriacea*; Ma, *Miconia albicans*; Mg, *Myrsine guianensis*; Op, *Ocotea pomaderroides*; Pg, *Pera glabrata*; Pm, *Periandra mediterranea*; Rm, *Roupala montana*; Ri, *Rourea induta*; Zm, *Zeyheria montana.*

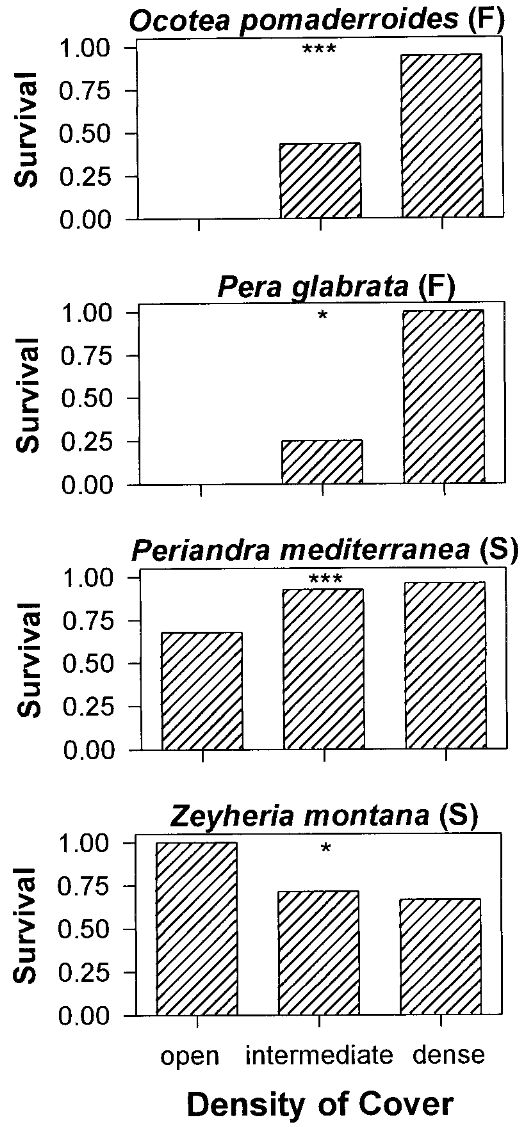

FIGURE 2. Effect of cover on survival of forest (F) and savanna (S) seedlings in unburned plots. Data for species without a significant response to cover are not shown. Significance was tested with Fisher's exact test. Asterisks indicate significance level: *$0.01 < P < 0.05$; **$0.005 < P < 0.01$; ***$P < 0.005$.

small (Table 1), so the statistical test had little power to detect a fire effect for this species.

Seedling survival also was affected by woody cover. In unburned plots, cover had a positive effect on the survival of two forest species, *Ocotea pomaderroides* and *Pera glabrata* (Fig. 2). Of the savanna species, *P. mediterranea* exhibited increased survival under woody cover, whereas *Zeyheria montana,* exhibited reduced survival under woody cover (Fig. 2).

Cover had a significant effect on the ability of several species to survive fire. For *K. coriacea* and *Z. montana,* cover reduced the ability of seedlings to survive fire, while the opposite was true for *P. mediterranea* (Fig. 3).

Cover had a significant positive effect on the heights of all three forest species at the end of the first growing season (Fig. 4). In subsequent years, there was only a single forest seedling surviving in open sites, permitting comparisons only between intermediate and dense sites. In the second and

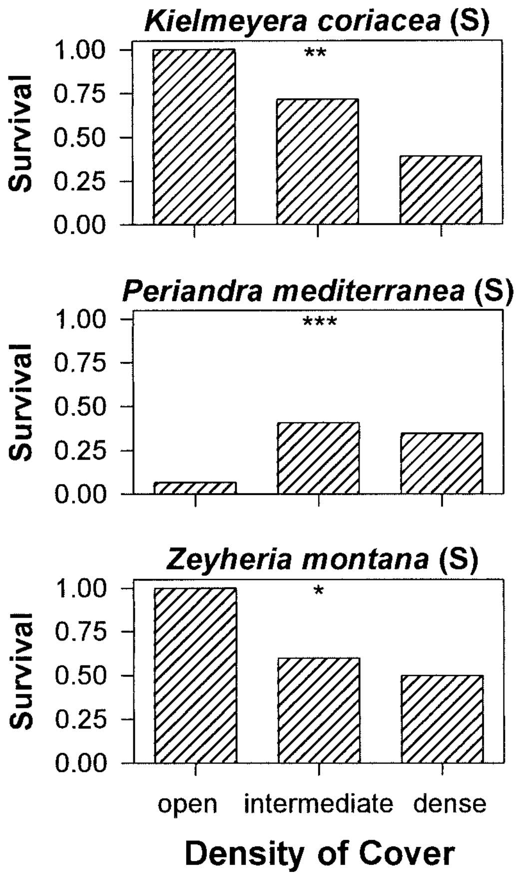

FIGURE 3. Effect of cover on survival of forest (F) and savanna (S) seedlings in plots burned during the first dry season. Data for species without a significant response to cover are not shown. Significance was tested with Fisher's exact test. Asterisks indicate significance level: *0.01 < P < 0.05; **0.005 < P < 0.01; ***P < 0.005.

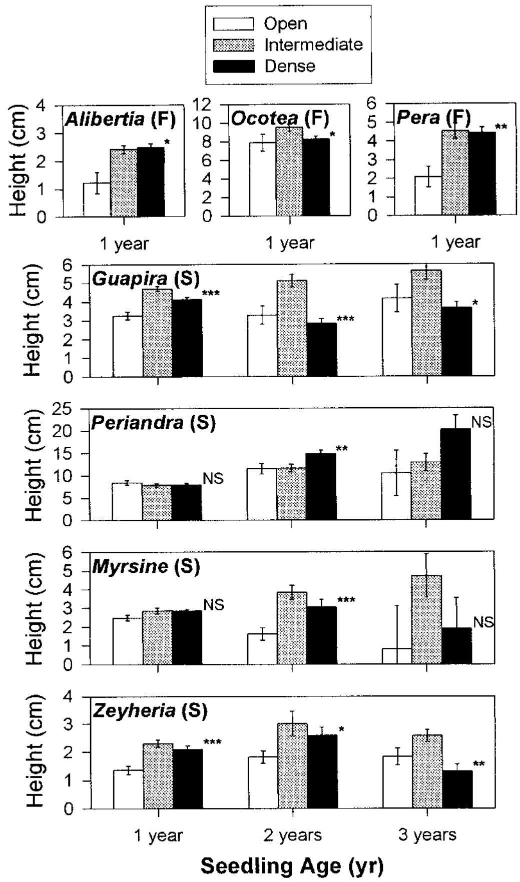

FIGURE 4. Effect of woody cover on seedling growth in unburned plots. Data for species without a significant response to cover are not shown. Cover effects were tested with ANOVA. Second- and third-year data for the forest species are not shown because few or no seedlings were available for open sites. Asterisks indicate significance level: *0.01 < P < 0.05; **0.005 < P < 0.01; ***P < 0.005. Note that scales of the Y-axes vary.

third years, there were no significant differences in the height of forest species between intermediate and dense sites (data not shown). Of the nine savanna species, five exhibited no significant response to cover (data not shown). Cover had a significant positive effect on the heights of two savanna species, *Guapira noxia* and *Z. montana,* at the end of the first growing season (Fig. 4). In subsequent years, dense cover had a negative effect on height relative to intermediate cover, so that seedling heights were greatest under intermediate cover. For two savanna species, *M. guianensis* and *P. mediterranea,* the effect of cover was significant only after two years of growth. For the former, height was greatest under intermediate cover; for the latter, height was greatest under dense cover (Fig. 4).

DISCUSSION

Ability to survive burning is essential for success in tropical savannas, especially in moist savannas in which fire typically occurs at intervals of one to three years. This study indicates that savanna and forest species differ fundamentally in their ability to survive fire. Not a single forest seedling survived burning in the first two years of life, while eight of the nine savanna species were able to survive fire at such an early age (Fig. 1a). The remaining savanna species, *M. albicans,* was unable to survive fire as seedlings because its small seed size predisposes it to be sensitive to fire. Ability to resprout after burning was positively correlated to seed size, as has been shown for resprouting following herbivory (Dalling *et al.* 1997, Harms & Dalling 1997). The low survival of forest species, however, cannot be attributed to small seed size, as savanna species with similar seed size were able to survive fire.

In contrast to these results, Bowman and Panton (1993), studying two monsoon forest species in the savannas of northern Australia under irrigated and fertilized conditions, found that some forest seedlings survived burning. Although I found that none of the three forest species survived burning as seedlings, adults of many forest species of the Cerrado region are able to resprout following burning (including *O. pomaderroides* and *P. Glabrata*; Hoffman, pers. obs.). It is not clear how large an individual must be to survive burning.

Even in the absence of fire, forest trees do not perform well in savanna. All three forest species exhibited lower growth rates, and two exhibited lower survivorship in open sites relative to sites with woody cover (Figs. 2, 4); however, *Ocotea* exhibited reduced growth under dense cover relative to intermediate cover. All three forest species also were shown by Hoffmann (1996) to exhibit lower rates of germination in open sites than under cover, thus reinforcing the trends presented here. This is consistent with the results of others that forest species are sensitive to the microclimate and/or edaphic conditions of open savanna (Kellman & Miyanishi 1982, Kellman 1985, Bowman & Panton 1993). Several factors may be involved. The soil in open grassland may have lower nutrient status (Kellman 1979, Belsky *et al.* 1989), lower moisture content during dry periods (Belsky *et al.* 1989, Bowman & Panton 1993), and higher temperatures (Belsky *et al.* 1989). Also, biotic factors such as mycorrhizae abundance (Bowman & Panton 1993) or herbivory may play important roles.

In contrast to forest species, most of the savanna species showed no response to cover. Those that did respond to cover exhibited a range of responses, with some responding positively and others responding negatively (Figs. 2, 3, 4). The latter seem particularly well adapted to the conditions of open savanna. For example, *Kielmeyera* and *Zeyheria* both experienced greater mortality under cover (Figs. 3, 4), and neither showed a significant response to cover in the establishment phase (Hoffmann 1996). For these species adapted to the high light environment of savanna environments, it appears that the negative effects of low light may exceed the positive effects of woody cover. Other species exhibited an intermediate response to cover, with seedling height being greatest under intermediate cover.

The three forest species are at an extreme disadvantage within the savanna environment because they are sensitive to both fire and the physical environment of the savanna. Savanna species are able to persist despite being sensitive to one or the other of these two factors. For example, *P. mediterranea*, a savanna species, is common in savanna despite the fact that its seedlings are sensitive to the conditions of open savanna. It exhibited lower growth and survival in open savanna than under cover, and germination of this species was lower in open savanna than under cover (Hoffmann 1996). That *P. mediterranea* is common in open savanna despite these traits weakens the argument that microclimatic and edaphic constraints are sufficient to prevent expansion of forest species into savanna, provided that woody cover is available. Similarly, *M. albicans*, despite having fire-sensitive seedlings, persists in savanna because it can invade quickly when a prolonged fire-free interval occurs (Hoffmann 1999). Forest species do eventually invade the Cerrado savannas when protected from fire (Ratter 1992), but the low rate of establishment combined with the high probability of burning, makes it highly unlikely that much succession of savanna to forest would be observed under current fire regimes.

In the absence of fire, survival of both savanna and forest species was quite high when pooled over all cover types (Fig. 1b). These first-year survival rates were compiled for the one-year period beginning at the end of the first growing season, and thus include survival during the first dry season. In 1994, the year in which most of the first-year survival data was obtained, the dry season was particularly long. In this year, the seedlings exhibited high rates of survival despite a 134-day period during which the study site received a total of only 2 mm of rainfall. All species except *K. coriacea* retained green leaves throughout the dry season, although there was a reduction of leaf area in many cases.

Savanna species typically have a deep taproot that develops very quickly in seedlings (Rizzini 1965, Moreira 1992, Oliveira & Silva 1993). This taproot undoubtedly plays an important role in the high drought tolerance of savanna seedlings. Franco *et al.* (1996), working at a nearby site, found that soil water potential at 60-cm depth did not drop below -1.6 MPa at any point during the dry season of 1995, indicating a permanent source of water within reach of a deep taproot. This same taproot, by storing carbohydrate, would permit resprouting following fire. Thus, the taproot is able to reduce the impact of fire and drought, two important constraints to seedling establishment in the Cerrado. Early rapid growth of this taproot is likely dependent on resources stored in the seed. As a result, larger-seeded species exhibited a higher capacity to survive fire and drought.

The ability of seedlings to survive fire is an important trait for success in tropical savannas, but it must be noted that this alone does not guarantee that a species will thrive under current fire regimes. Fire affects all aspects of the demography of Cerrado plants, including plant size, adult survival, seed production (Hoffmann 1998), vegetative reproduction (Hoffmann 1998), and seedling establishment (Hoffmann 1996). For a species to thrive under frequent burning, all of these stages of the life history are important. Nonetheless, the seedling is a critical stage of the life cycle and is likely the most sensitive to fire and environmental stress.

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