

Tree topkill, not mortality, governs the dynamics of savanna–forest boundaries under frequent fire in central Brazil

WILLIAM A. HOFFMANN,^{1,5} RYAN ADASME,¹ M. HARIDASAN,² MARINA T. DE CARVALHO,³ ERIKA L. GEIGER,¹
MIREIA A. B. PEREIRA,⁴ SYBIL G. GOTSCH,¹ AND AUGUSTO C. FRANCO³

¹Department of Plant Biology, Campus Box 7612, North Carolina State University, Raleigh, North Carolina 27695-7612 USA

²Departamento de Ecologia, Caixa Postal 04457, Universidade de Brasília, Brasília, DF 70904-970 Brazil

³Departamento de Botânica, Caixa Postal 04457, Universidade de Brasília, Brasília, DF 70904-970 Brazil

⁴Departamento de Agronomia, Universidade Federal do Tocantins, Gurupi, TO 77404-970 Brazil

Abstract. Tropical savanna and forest are recognized to represent alternate stable states, primarily determined by feedbacks with fire. Vegetation–fire dynamics in each of these vegetation types are largely determined by the influence of the vegetation on fire behavior, as well as the effects of fire behavior on tree mortality, topkill (defined here as complete death of the aerial biomass, regardless of whether the plant recovers by resprouting), and rate of growth of resprouts. We studied the effect of fire on three savanna–forest boundaries in central Brazil. Fire intensity was greater in savanna than forest, as inferred by a twofold greater height of stem charring. Despite lower fire intensity, forest tree species exhibited higher rates of topkill, which was best explained by their thinner bark, relative to savanna species. Following topkill, there was no tendency for sprouts of savanna trees to grow faster than those of forest species, contrary to expectations, nor was whole-plant mortality higher in forest than in savanna. This contrasts with observations of high rates of postburn mortality in many other tropical forests. The low tree mortality in these transitional forests suggests that the dynamic of these natural savanna–forest boundaries is fundamentally different from that of forest boundaries originating from deforestation in the humid tropics. The forests studied here appear to be much more resilient to occasional incursion of fire from the savanna, despite being unable to invade frequently burned savanna. The thin bark of forest species makes them particularly susceptible to the “fire trap,” whereby repeated topkill of small trees prevents recruitment into adult size classes. Rapid growth will be particularly important for forest species to escape the fire trap, so we predict that, where fire is frequent, forests should be restricted to high-resource sites. Here, Mg²⁺ and Ca²⁺ concentrations had particularly strong effects on postburn growth rates, suggesting that these elements may most strongly limit the distribution of forest in these fire-prone savannas.

Key words: alternate stable states; Cerrado, Brazil; evergreen forest; fire ecology; gallery forest; hysteresis; positive feedback; riparian forest; savanna; topkill.

INTRODUCTION

The savanna–forest boundary represents the “natural” limit of distribution of tropical forest, and therefore offers an opportunity to understand how the extent of tropical forest will respond to changing climate and disturbance regimes. Climate, fire, hydrology, herbivory, and soil characteristics can all be important in determining the distribution of savanna and forest (Tinley 1982, Furley 1992, Hopkins 1992, Ruggiero et al. 2002). Of these factors, fire is perhaps the most universal determinant of savanna–forest boundaries worldwide. Savanna vegetation is very flammable, and may burn at intervals of 1 to 3 years, whereas evergreen forest is typically less flammable due to a dense canopy that

excludes grasses (Hennenberg et al. 2006, Banfai and Bowman 2007) and maintains a more humid understory. Most savanna fires do not penetrate far into undisturbed evergreen forest (Biddulph and Kellman 1998, Hennenberg et al. 2006), so the higher fire frequency in savanna tends to sharpen the savanna–forest boundary. Under fire exclusion, forest commonly expands into savanna (Bowman and Fensham 1991, Hopkins 1992, Swaine et al. 1992, Brook and Bowman 2006), resulting in a more diffuse boundary.

The savanna–forest boundary is characterized by a transition not only in tree density, but also in species composition, with few tree species being common to both savanna and forest (Adejuwon and Adesina 1992, Felfili and Silva 1992). Savanna species tend to have a lower leaf area index than forest species, even when growing under similar conditions, so stands of savanna species may be unable to develop the dense canopies that are responsible for the low flammability of evergreen forest (Hoffmann et al. 2005). If succession from

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⁵ E-mail: william_hoffmann@ncsu.edu

savanna to closed-canopy forest is dependent on the presence of forest tree species, then any differences in the fire response of savanna and forest species should play a fundamental role in vegetation dynamics.

When it does occur, fire causes much higher rates of tree mortality in humid lowland tropical forest than in savanna (Hoffmann and Moreira 2002), but data are lacking for forests near savanna, where historical exposure to frequent fire is expected. Even if postburn mortality is low in these forests, fire can govern vegetation dynamics by creating a bottleneck for tree recruitment into large size classes. Frequent fire may create a “fire trap” by causing topkill (defined here as complete death of the aerial biomass, regardless of whether the plant later recovers by resprouting), thereby maintaining trees in suppressed, nonreproductive size classes. Large individuals may avoid topkill due to thick bark, but small individuals cannot (Rutherford 1981, Hoffmann and Solbrig 2003) because bark thickness is largely dependent on stem diameter (Uhl and Kauffman 1990, Hoffmann and Solbrig 2003, Hoffmann et al. 2003). Increases in tree cover therefore require fire-free intervals of sufficient duration to allow recruitment into fire-resistant size classes. In turn, the minimum interval required for adult tree recruitment largely depends on growth rates of resprouting saplings and the size at which fire resistance is attained (Gignoux et al. 1997, Bond and Midgley 2000), the latter being determined largely by bark thickness (Hoffmann and Solbrig 2003).

The importance of the fire trap for determining tree density in tropical savannas has been well described, but to our knowledge its role in governing the balance of savanna and forest has not been examined. We expect the fire trap to play a particularly important role in the dynamics of savanna–forest boundaries because of differences in the response of savanna and forest tree species to fire. Specifically, we hypothesized that savanna species would exhibit (1) higher rates of postburn survival than forest species, (2) lower rates of topkill than forest species, with this being demonstrably related to greater bark thickness among savanna species, and (3) greater rates of regrowth following topkill than forest species.

If supported, these hypotheses would point to the importance of the fire trap in governing the distribution of forest within savanna landscapes. But species characteristics alone should not determine susceptibility to the fire trap. In particular, soil resources, by determining the growth rate of resprouting trees, should influence the time needed to reach a fire-resistant size. Therefore where soil resources are locally abundant, higher growth rates should reduce susceptibility to the fire trap, increasing the probability of succession from savanna to forest. Therefore we also test the hypothesis that, within species, the rate of regrowth is positively correlated to soil nutrient availability.

To test these hypotheses, we studied the effect of fire on whole-tree mortality and stem mortality (topkill) at

three savanna–forest boundaries in the Brazilian Cerrado. We also compared the growth rate of resprouts for 15 congeneric species pairs containing a savanna species and a forest species, all of which were growing within savanna environments due to long-term fire suppression. Measurements of bark thickness, soil nutrients, and height of stem charring were used to infer causes of variation in tree responses to fire as relevant to the dynamics of savanna–forest boundaries.

METHODS

The study was performed at the IBGE (Instituto Brasileiro de Geografia e Estatística) Ecological Reserve, near Brasília, DF, Brazil, at an elevation of ~1100 m. Mean annual rainfall on the reserve was 1426 mm for 1993–2002, with a distinct dry season from May to September and mean annual temperature of 22.5°C. Fire has been suppressed on the reserve since the early 1970s, but it had been subject to frequent wildfires before that (Braulio F. S. Dias, *personal communication*). In 1994 and 2005, wildfires spreading from nearby reserves burned over roughly half of the reserve. Both fires occurred in September, at the end of the dry season, when dry conditions allowed them to spread into gallery (riparian) forests. Our study began in June 2006, one growing season after the 2005 fire.

Studies at savanna–forest boundaries

To test the hypotheses that forest species would exhibit higher rates of whole-plant mortality and higher stem mortality (topkill), we set up seven transects in June and July 2006, at three savanna–gallery forest boundaries that had burned the previous year. We selected locations occurring well upslope of the stream, where the entire transect occurs on well-drained soils. These forests are evergreen but some species are deciduous or brevideciduous (i.e., remaining leafless only briefly while leaves are being replaced). Each transect was 5 × 100 m, aligned perpendicularly to the forest edge, with at least 100 m between transects. Each transect was centered at the forest edge, which we defined as the farthest point at which savanna grasses could be found along the transect. Three transects each were placed along the Roncador and Monjolo streams and a single transect was placed along the Pitoco stream, as it was not possible to find additional sites where the fire had penetrated sufficiently far into the latter forest.

We censused all trees in the transects that had a preburn stem diameter >4 cm at 30 cm height. As is typical for fires in this region, the sites had all been burned by surface fires, so woody stems were not fully consumed, making it possible to measure diameter and height of the original stem. We measured stem diameter at 30 cm from the ground and the height of each preburn stem and of the largest stem resprouting from this individual. We recorded char height as the highest point exhibiting blackening of 50% of the circumference of the original stem. A stem was scored as topkilled if there

was no evidence of living branches or sprouting from any point >30 cm. This definition therefore included individuals that resprouted from <30 cm, as well as those that failed to resprout at all. In total, 858 stems were censused in these transects, all of which we assumed were living prior to the fire, for the purpose of estimating topkill and mortality.

Soil samples were collected for each transect from 0 to 10 cm depth at the forest edge and at 20 and 40 m into both the savanna and forest vegetation. Soil pH was measured in 1:2.5 soil–water suspension and in 1 mol/L KCl. Exchangeable Ca, Mg, and Al were determined in extracts of 1 mol/L KCl and K, P, Fe, Mn, Zn, and Cu in Mehlich's extract of a diacid mixture of 0.05 mol/L HCl and 0.025 mol/L H₂SO₄. The cations were determined by atomic absorption spectrophotometry and P by colorimetry (Allen 1989). Total N was determined by Kjeldahl digestion and distillation. Soil organic carbon was determined by the Walkley and Black method (Allen 1989).

We measured canopy light transmission using a SunScan probe (Delta-T, Cambridge, UK), which measures average photosynthetic photon flux density (PPFD) over an array of 64 photodiodes spaced along a 1-m wand. Incident PPFD was measured in open savanna, and then transmitted PPFD was measured at a height of 1 m at 5-m intervals along the transects. These measurements were collected within one hour of solar noon on cloudless days in June 2008. Because these measurements were performed approximately three years after the fire, these measurements are meant only to characterize savanna–forest boundaries rather than represent the light environment prior to burning or during resprouting.

Comparative studies on congeneric savanna and forest species pairs

At the study site there are 56 genera containing both savanna and forest tree species (Pereira et al. 1992), offering an excellent opportunity for comparative studies. Furthermore, the long history of fire prevention has allowed many forest species to establish and grow within the savanna environment, allowing these two species types to be compared under similar light and soil conditions and burning histories. To test the hypothesis that savanna species would exhibit more vigorous resprouting, we identified 15 such species pairs for which we were able to locate, in savanna, at least 10 individuals that had experienced topkill in 2005 and had subsequently resprouted. For each individual, we measured diameter and height of all preburn stems and the five largest resprouting stems in the dry seasons of 2006 and 2007. To allow us to test the hypothesis that resprout vigor is positively correlated with soil nutrient availability, we collected a surface soil sample (0–10 cm) near each tree or group of neighboring trees. Soils were analyzed as described before.

We measured bark thickness and stem diameter of at least 10 unburned individuals of each of these species (excluding *Alibertia* spp.) and nine additional congeneric species pairs. Hoffmann et al. (2003) presented bark thickness data for 10 congeneric species pairs, so here we add 12 additional pairs to the previous analysis to permit a more complete comparison.

Literature survey of fire effects

We compiled published data to compare postfire mortality of tropical savanna and forest trees and to test for a relationship between annual precipitation and postfire mortality. We utilized data only for which community-wide mortality rates were reported. We excluded studies in which topkilled trees were considered dead even if they resprouted. When a single study presented mortality rates for multiple sites within close proximity, these values were averaged to provide a single estimate. To compare patterns of bark thickness with that of an Amazonian forest we used the program xyExtract Graph Digitizer 2.3 (W. P. Silva, Campina Grande, Brazil) to extract data of bark thickness and stem diameter from a figure of Uhl and Kauffman (1990).

Analysis

Analyses were performed with JMP 7.0 (SAS Institute, Cary, North Carolina, USA). For the analyses of community responses to fire at the seven savanna–forest transects, data were pooled for all 111 woody plant species present along the transects. Logistic regression was used to test for effects of species type (savanna vs. forest), char height, and stem diameter on topkill and on whole-plant mortality of trees. Individual trees were used as the sampling unit, which can overinflate Type I error rates when spatial autocorrelation is present in the data, so we also performed autologistic regression. For this approach, we included an additional independent variable equal to the mean response of eight neighboring trees. In other words, this autoregressive variable was simply the fraction of neighboring trees that had survived. We performed an equivalent analysis to test for the relationship between bark thickness and topkill of trees along these transects. To estimate bark thickness of each individual, we used species-specific regression equations for the relationship between stem diameter and bark thickness of unburned trees. These relationships were available for the 44 species in Table 1 and for 14 additional species (W. A. Hoffmann, *unpublished data*). Because these data were not available for all species, this analysis included only 56% of the stems in the transects.

We performed linear regressions to test the relationship between each environmental variable and position along the transect. The soil variables tended to be highly correlated among each other, so a MANOVA was utilized to perform a comprehensive test of soil differences among savanna, forest, and border positions.

TABLE 1. Congeneric species pairs included in the study of resprout growth and bark thickness in savanna-forest boundaries in central Brazil.

Savanna species	Forest species	Family	Resprout	Bark
<i>Aegiphila lhotzkiana</i>	<i>A. sellowiana</i>	Verbenaceae	X	X
<i>Alibertia sessilis</i>	<i>A. elliptica</i>	Rubiaceae	X	
<i>Aspidosperma tomentosum</i>	<i>A. subicanum</i>	Apocynaceae	X	X
<i>Byrsonima crassa</i>	<i>B. laxiflora</i>	Malpighiaceae	X	X
<i>Diospyros burchellii</i>	<i>D. hispida</i>	Ebenaceae	X	X
<i>Erythroxylum suberosum</i>	<i>E. daphnites</i>	Erythroxylaceae		X
<i>Guapira noxia</i>	<i>G. areolata</i>	Nyctaginaceae	X	X
<i>Hymenaea stignocarpa</i>	<i>H. courbaril</i>	Leguminosae		X
<i>Machaerium opacum</i>	<i>M. acutifolium</i>	Leguminosae	X	X
<i>Miconia pohliana</i>	<i>M. cuspidata</i>	Melastomataceae		X
<i>Myrcia rostrata</i>	<i>M. tomentosa</i>	Myrtaceae	X	X
<i>Myrsine guianensis</i>	<i>M. ferruginea</i>	Myrsinaceae	X	X
<i>Ouratea hexasperma</i>	<i>O. castaneaefolia</i>	Ochnaceae		X
<i>Piptocarpha rotundifolia</i>	<i>P. macropoda</i>	Asteraceae	X	X
<i>Pouteria ramiflora</i>	<i>Pouteria</i> sp.	Sapotaceae		X
<i>Qualea parviflora</i>	<i>Q. dichotoma</i>	Vochysiaceae	X	X
<i>Salacia crassifolia</i>	<i>S. elliptica</i>	Hippocrateaceae		X
<i>Schefflera macrocarpum</i>	<i>S. morotoni</i>	Araliaceae	X	X
<i>Styrax ferruginus</i>	<i>S. camporum</i>	Styracaceae	X	X
<i>Symplocos lanceolata</i>	<i>S. mosenii</i>	Symplocaceae	X	X
<i>Tabebuia ochracea</i>	<i>T. roseo-alba</i>	Bignoniaceae		X
<i>Vochysia thyrsoidea</i>	<i>V. tucanorum</i>	Vochysiaceae	X	X

Note: The last two columns indicate the genera for which we obtained data on resprout growth and bark thickness for both species.

All soil variables except pH, C, and N were log-transformed prior to analysis.

To test for differences between savanna and forest species in bark ratio (ratio of bark thickness to stem radius), we used a factorial ANOVA with species type as a fixed factor and genus as a random factor. A *t* test was also applied to each congeneric pair.

To quantify the vigor of resprouting, we utilized the allometric relationship between preburn size and the size of resprouts. We calculated an index of stem size, $S = \pi \times r^2 \times h$, equal to the volume of a cylinder with dimensions defined by stem height (*h*) and stem radius (*r*). For individuals with multiple stems, we summed all stems to obtain total plant size. To test if resprout size differed between savanna and forest species within each genus, we performed an analysis of covariance with $\log_{10}(\text{resprout size})$ as the dependent variable and $\log_{10}(\text{preburn size})$ as the covariate. For a pooled test of species type on resprout size across all genera, we specified genus as a random factor, with species type as fixed factor and preburn size as a covariate. We tested for effects of soil variables within species on $\log_{10}(\text{resprout size})$ using generalized linear models. $\log_{10}(\text{preburn size})$ was used as a covariate, and species was included as a random factor.

RESULTS

Studies at savanna-forest boundaries

There was a sharp transition in the abundance of savanna and forest tree species at the savanna-forest boundaries (Fig. 1). Only one individual of a savanna tree species was encountered >15 m into the forest, while forest species comprised 7% of the stems occurring

>15 m into the savanna. Soil characteristics were associated with vegetation type. The MANOVA revealed significant differences in soil characteristics among savanna, forest, and border positions (Pillai's trace = 1.34, $F_{24,44} = 3.76$, $P < 0.0001$). When each soil variable was tested individually, forest soils had significantly greater pH, C, N, P, Ca, Mg, Mn, K, and Zn and less available Fe and Cu than soils in adjacent savanna ($P < 0.01$; Fig. 1, Appendix). Al did not vary significantly along the transects (Appendix). However, there was considerable spatial variability in this overall trend, with two transects exhibiting little tendency for increased nutrient availability in the forest (Fig. 1). These occurred in two different gallery forests.

The mean height of stem charring was significantly greater in savanna than in forest (Fig. 1), reflecting differences in fire intensity. Topkill probability was positively correlated to char height ($\chi^2 = 16.10$, $P < 0.0001$) and negatively correlated to stem diameter ($\chi^2 = 272.5$, $P < 0.0001$; Fig. 2). Despite the lower mean char height in the forest, forest tree species had significantly greater probability of topkill than savanna species, for a given stem diameter ($\chi^2 = 64.62$, $P < 0.0001$; Fig. 2). The autoregressive term was highly significant ($\chi^2 = 42.24$, $P < 0.0001$), indicating that there was considerable spatial autocorrelation in topkill probability. Nevertheless, when the autoregressive term was included in the model, there were still significant effects of char height ($\chi^2 = 8.53$, $P = 0.0035$), stem diameter ($\chi^2 = 102.78$, $P < 0.0001$), and species type ($\chi^2 = 44.00$, $P < 0.0001$) on topkill. The higher rates of topkill among forest species may have resulted largely from the tendency of forest species to have thinner bark. When bark thickness,

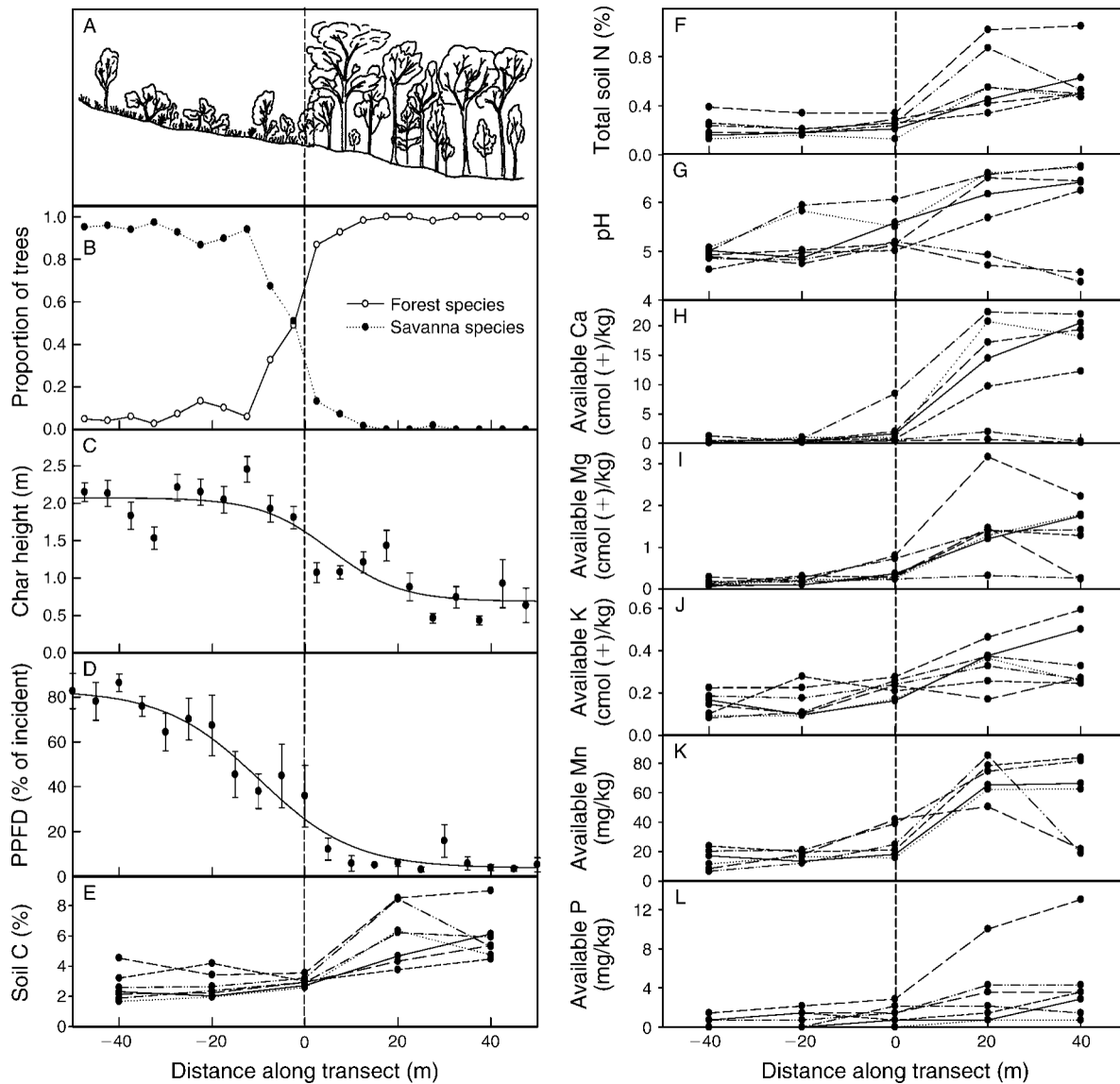


FIG. 1. Characteristics of seven transects in savanna-forest boundaries in central Brazil. (A) Schematic of the transect (not to scale). (B) Fraction of species in each 5×5 m segment that are species typical of forest and savanna environments. (C) Height (mean \pm SE) of charring following the wildfire. (D) Canopy transmission of photosynthetically active radiation (mean \pm SE), as measured at 1 m height. (E-L) Characteristics of surface soils (0–10 cm depth) across the savanna-forest boundary. (H–J) Cation exchange capacity is measured as centimoles of charge. For soil characteristics, each line represents one transect. The dashed vertical line represents the location of savanna-forest boundary as determined by the distribution of savanna grasses. All variables shown were significantly correlated with distance along the transects ($P < 0.05$).

rather than stem diameter, was used as a covariate, savanna species had higher probabilities of topkill than forest species ($\chi^2 = 7.92$, $P = 0.0049$; Fig. 2). This effect appears to result from the higher fire intensities in savanna; when char height is included in the autologistic model, there was no difference in topkill between savanna and forest species ($\chi^2 < 0.01$, $P = 0.99$). Based on a simple logistic regression equation including all species, 50% topkill is predicted for trees with a bark thickness of 6.2 mm.

Overall, forest species exhibited 52% topkill, compared to 41% for savanna species, despite the fact that, relative to savanna species, forest tree species had larger mean stem diameter (10.4 vs. 7.6 cm) and lower mean char height (1.0 vs. 2.1 m). If we account for these differences, the differences in rate of topkill are greater. Taking, for example, the overall mean stem diameter (9 cm) and mean char height (1.5 m), the multiple logistic regression predicts that topkill would be 15% among savanna species, but 47% among forest species.

There was no significant difference in community-wide whole-plant mortality rates between savanna and forest species (6.6% vs. 7.5%, $\chi^2 = 0.68$, $P = 0.41$; Fig. 2), nor was there a significant effect of stem diameter on mortality ($\chi^2 = 2.15$, $P = 0.14$; Fig. 2). The lack of a difference appears to be unrelated to the lower fire intensity in forest; even when comparing savanna and forest species occurring within savanna, there was no significant difference in mortality rates (6.0% vs. 2.9%; $\chi^2 = 1.03$, $P = 0.31$), though small sample size for forest species results in low power for detecting differences. A community-wide comparison utilizing these transect data did not reveal a significant difference between the savanna and forest environments in size of resprouts of topkilled trees, using preburn size as a covariate ($F_{1,205} = 1.70$, $P = 0.19$; not shown).

Comparative studies on congeneric species pairs

On average, bark thickness of savanna species was more than double that of forest species (paired $t_{20} = 8.50$, $P < 0.0001$; Fig. 3). Overall, bark accounted for 31.5% of the total stem diameter of savanna species, but only 13.5% for that of forest species. When we tested each congeneric pair, the savanna species had significantly thicker bark than the forest species in 18 of 21 genera, while in no genus did the forest species have thicker bark. When examined over all species, the gallery forest species studied here had considerably thicker bark than was observed by Uhl and Kauffman (1990) in an Amazonian forest (Fig. 4).

For genera in which both species could be found growing within savanna, there was no consistent tendency for savanna species to resprout more vigorously than forest species when tested over all genera (Fig. 5). When we tested each congeneric pair, savanna species did have greater resprout sizes than forest species for *Aegiphila*, *Schefflera*, and *Myrsine*; however the opposite was true for *Aspidosperma*, *Byrsonima*, *Machaerium*, and *Piptocarpha* (Fig. 5). For the remaining six congeneric pairs, there was no significant difference in resprout size between savanna and forest species (Fig. 5). When tested for all genera combined, there was no overall difference in resprout vigor between savanna and forest species ($F_{1,14} = 0.19$, $P = 0.67$). These trends were largely unchanged by the second year after burning, except that the forest *Qualea* had greater mean resprout size than its savanna congener, after accounting for preburn size ($F_{1,21} = 5.17$, $P = 0.033$; data not shown).

For these trees growing within savanna, where light availability is high and presumably not limiting to plant growth, several soil variables were significantly correlated with the size of resprouts after both the first and second growing seasons. In both years, soil pH, available Ca, and available Mg were each positively correlated with resprout size after accounting for the effects of preburn size ($F > 5.98$, $P < 0.015$; see Appendix). In the first year, resprout size was significantly correlated with total N ($F_{1,516} = 3.94$, $P = 0.048$

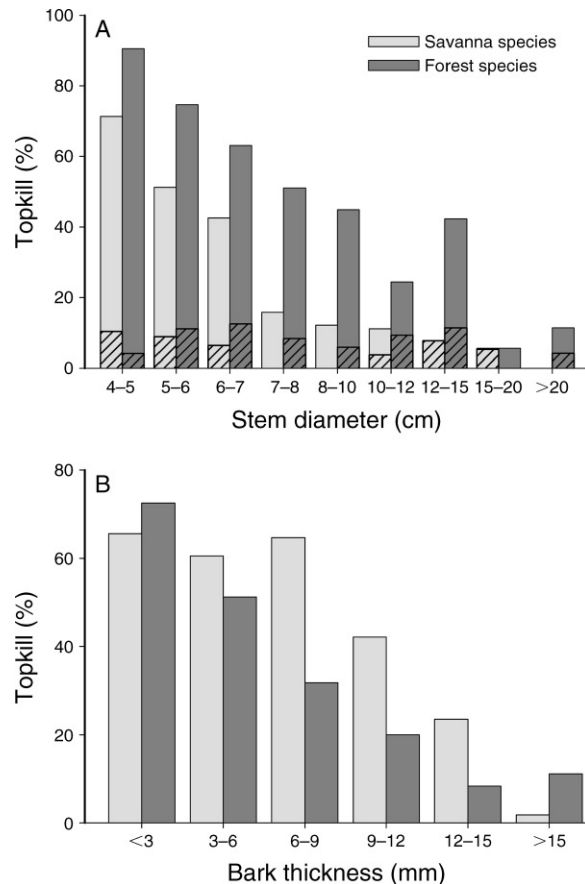


FIG. 2. Topkill of savanna and forest tree species over a range of (A) stem diameters and (B) bark thicknesses following wildfire at three savanna-forest boundaries. Stem diameter, bark thickness, and species type all had significant effects ($P < 0.0001$) on topkill rates. The hatched bars in the top graph represent whole-plant mortality, which was not significantly affected by stem diameter or species type. Individuals that underwent whole-plant mortality were also considered to have experienced topkill.

and available P ($F_{1,516} = 5.55$, $P = 0.019$), while there was a significant correlation with Mn only in the second year ($F_{1,467} = 6.58$, $P = 0.011$; see Appendix).

Of all soil variables, Ca^{2+} and Mg^{2+} concentrations had the strongest correlations with resprout size within species. Based on soil Ca^{2+} concentrations, we predict mean resprout sizes in forest soils to be 256% of those on savanna soils. When based on soil Mg^{2+} concentrations, the expected effect on size is 281% (Appendix). These estimates, however, may only be valid for plants growing in high light environments, such as the savanna habitats where these congeneric pairs were studied.

Literature survey of fire effects

When pooled with published data, tree mortality in tropical forests was significantly higher than that of tropical savanna (35.1% vs. 9.4%, $t_{14} = 3.50$, $P = 0.002$). However, there was a strong relationship between mean

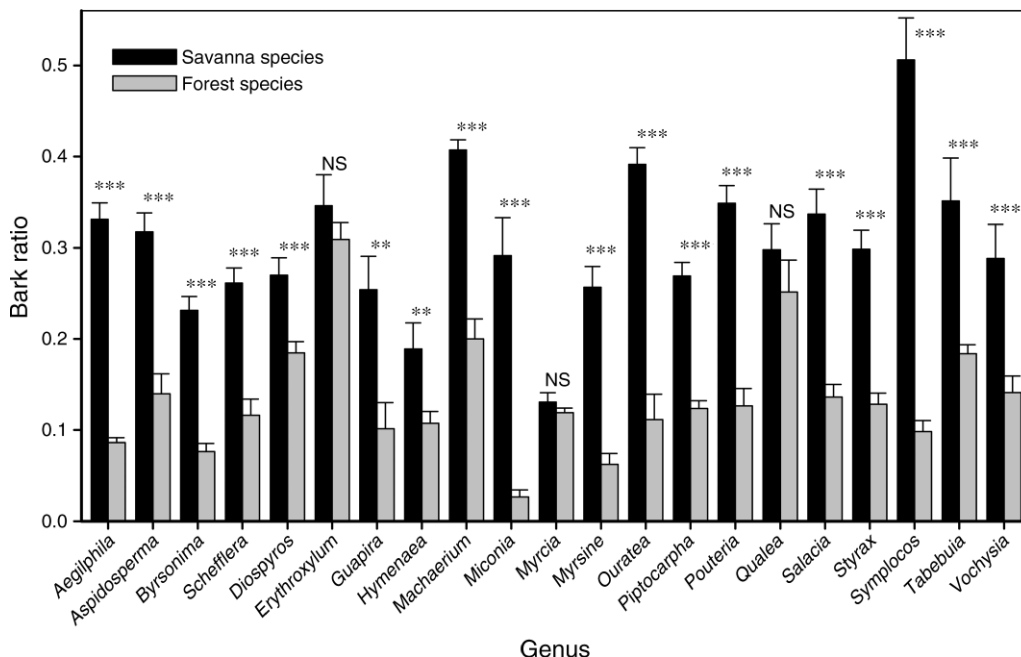


FIG. 3. Ratio of bark thickness to stem radius (mean + SE) for 21 congeneric species pairs from savanna vs. forest. Based on *t* tests, significant differences between species within each genus are indicated as asterisks (NS, not significant). * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

annual precipitation and whole-plant mortality following fire ($r^2 = 0.69$, $P < 0.0001$; Fig. 6), which largely accounts for the higher mortality rates in forest. There was little overlap in precipitation values between savanna and forest sites in the compiled data set, which precluded the use of ANCOVA for testing for a difference in tree mortality between savanna and forest after accounting for precipitation effects.

DISCUSSION

Contrary to predictions, savanna trees did not exhibit higher survival rates or greater growth rates of resprouts

than did forest tree species. At the three savanna–forest boundaries studied here, fire caused a mean mortality rate of 6.6% among savanna tree species, compared to 7.5% for forest species. Postfire mortality in these gallery forests was much lower than observed in other Neotropical forests. The high survival of gallery forest trees might best be explained by the occasional exposure to fire, either due to natural selection or by eliminating fire-sensitive species from the community. Trees in these forests tend to have thicker bark than those measured in an Amazonian forest (Fig. 4), providing support for a role of fire in shaping the tree community. Greater bark

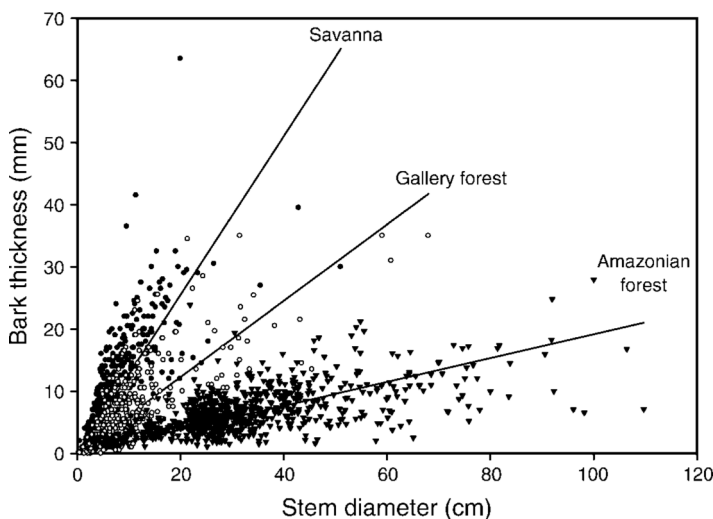


FIG. 4. Relationship between bark thickness and stem diameter in savanna and gallery forest (this study) compared to Amazonian forest (Uhl and Kauffman 1990). Regression lines were fit through the origin, with slopes of 1.28, 0.61, and 0.19 for savanna, gallery forest, and Amazon forest, respectively. Symbols are: solid circles, savanna; open circles, gallery forest; solid triangles, Amazon forest.

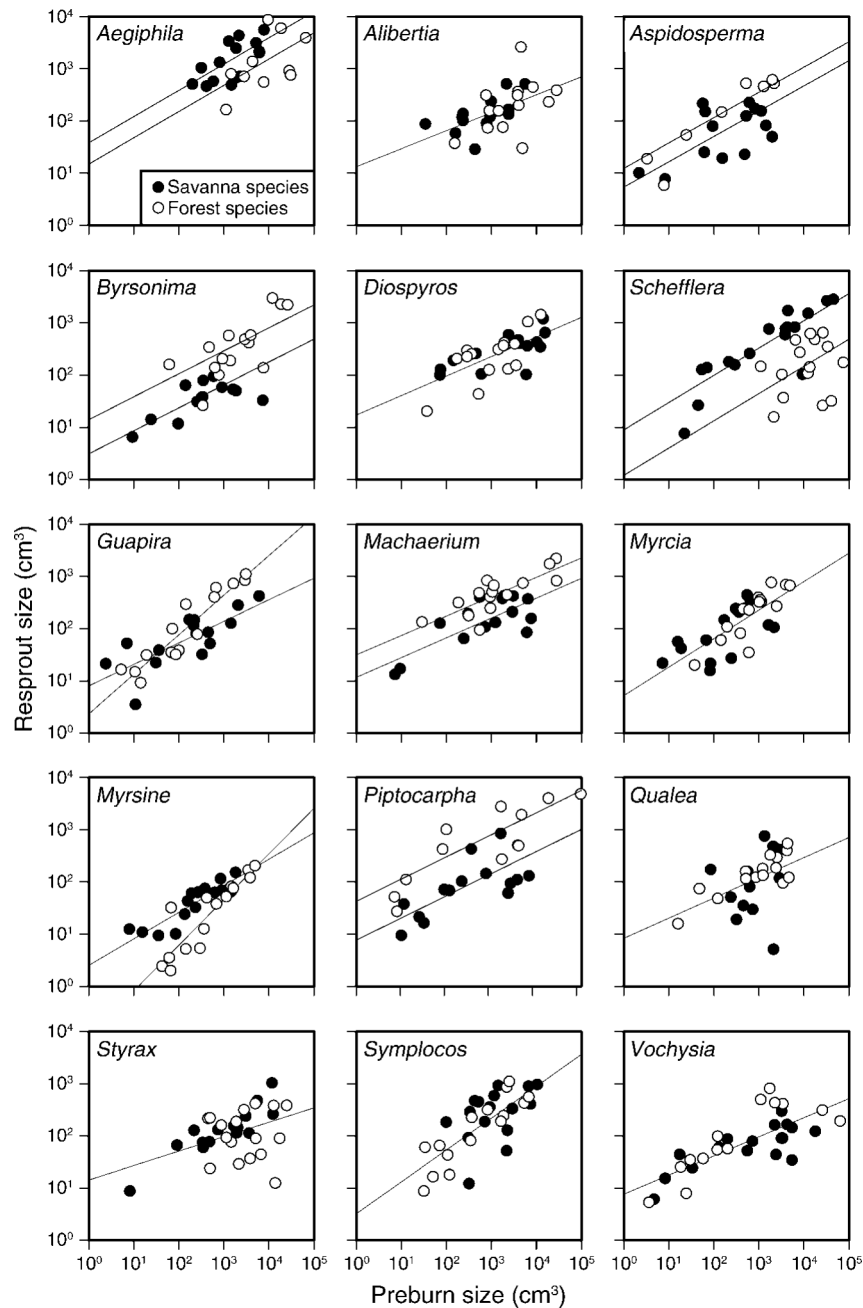


FIG. 5. Allometric relationships between resprout (postburn) size and preburn size in 2006, one year after burning. Size is defined as $\pi r^2 h$, where r and h are stem radius and height. In graphs where two parallel lines are plotted, there was a significant difference in intercept between the savanna and forest species ($P < 0.05$). Two nonparallel lines indicate there were significant differences in the slope of the allometric relationship. Where a single line is plotted, neither intercept nor slope differed between savanna and forest species.

thickness in these forests should result in considerably lower rates of topkill (i.e., total loss of aerial stem), relative to humid tropical forest. However, this alone cannot account for the greater ability to survive fire because even top-killed individuals exhibited high rates of survival in the gallery forests studied here.

Upon topkill, root carbohydrate reserves are essential for sustaining resprouting until sufficient leaf area has developed to sustain net plant growth. Previous work failed to find significant differences in nonstructural carbohydrate concentrations between savanna and forest congeners (Hoffmann et al. 2003), though greater

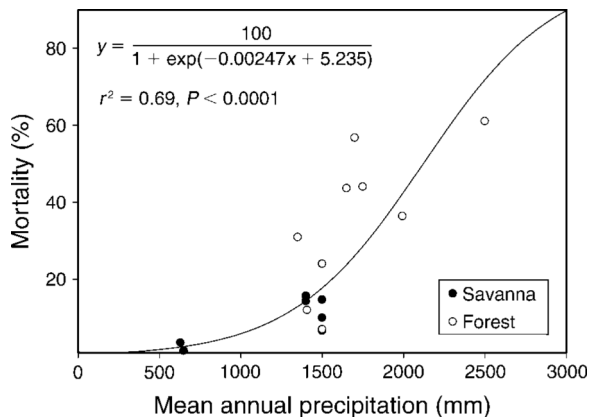


FIG. 6. Literature values of postfire tree mortality in tropical savanna and forest in relation to precipitation. Each point represents community-wide mortality for a single site or study. Data are from this study and published literature, with each study being represented by no more than a single point per vegetation type (Rutherford 1981, Woods 1989, Kauffman 1991, Lonsdale and Braithwaite 1991, Holdsworth and Uhl 1997, Cochrane and Schulze 1999, Pinard et al. 1999, Williams et al. 1999, Miranda et al. 2002, Ivanauskas et al. 2003, Holdo 2005, Marrinan et al. 2005, Otterstrom et al. 2006).

total investment in root biomass may nevertheless provide savanna species with more total nonstructural carbohydrates per unit of aboveground biomass. If this is the case, it did not result in greater resprout sizes for savanna species after one or two years following the fire.

Combining our data with observations from other tropical savannas and forests revealed a strong positive relationship between precipitation and postburn mortality (Fig. 6), which may partially account for previously reported differences in mean tree mortality between savanna and forest trees (Hoffmann and Moreira 2002). Among forest environments, the correlation with precipitation might be explained by historical exposure to higher fire frequencies in drier climates, but in savanna, fire intensity and frequency tend to be positively correlated with mean annual precipitation (Russell-Smith et al. 2007). Perhaps more importantly, species from dry environments may be preadapted to fire due to high investment in roots and carbohydrate reserves.

Regardless of the historical cause of high postburn survival in these ecotonal forests, this trend suggests that the dynamics of natural savanna–forest boundaries are very different than forest boundaries created by deforestation. In humid tropical forest remnants, postburn mortality can exceed 50%, with severe impacts on forest structure (Woods 1989, Kauffman 1991, Cochrane and Schulze 1999). Repeated burning is common in these degraded forests, often with intervals of only a few years between fires, resulting in rapid conversion to anthropogenic savanna dominated by exotic pasture grasses (Cochrane et al. 1999). In contrast, natural savanna–forest boundaries should be

considerably more stable than anthropogenic boundaries where forests have not been historically exposed to fire.

Compared to many other tropical evergreen forests, the low rates of whole-plant mortality in these ecotonal forests should greatly slow the rate of forest retreat under frequent exposure to fire. Even if successive burning causes thinning of the forest canopy and colonization by savanna grasses, high densities of resprouting individuals are likely to persist. These could allow for fairly rapid recovery of forest cover if fire is suppressed. This, however, is somewhat speculative because we do not know how repeated burning will affect tree survival and resprout vigor in these forests.

Despite similar mortality rates for savanna and forest species, differences in susceptibility to topkill have important implications for vegetation dynamics. Topkill causes a large and immediate reduction in individual size. The stem of a resprouting tree will be even more susceptible to topkill in subsequent fires until it has exceeded its preburn size (Hoffmann and Solbrig 2003). If fire-return intervals are shorter than the time required for resprouts to reach a fire-resistant size, these will be maintained in a suppressed and, typically, nonreproductive state. Even low mortality rates, combined with reduced reproduction and lack of recruitment into mature size classes, should result in gradual attrition of tree populations under frequent fire (Hoffmann 1999). For a given fire regime, this should be less of a constraint for savanna species, which tend to reach maturity at smaller sizes (Hoffmann et al. 2003) and are less prone to topkill for a given size (Fig. 2). As a result, savanna tree populations can persist under decades of frequent burning, but with a predominance of individuals in small size classes (Higgins et al. 2007).

The tendency for frequent fires to maintain trees in a reduced, often nonreproductive stage has been referred to as a fire trap (Gambiza et al. 2000). The importance of the fire trap in determining savanna tree density has been previously recognized, but here we build on this by revealing its particular importance in governing the balance between tropical savanna and forest, resulting from the greater susceptibility of forest trees to topkill. Once caught in the fire trap, recruitment of a sapling into large size classes will depend on the time between fires, the rate of growth following resprouting, and by the stem diameter at which fire resistance is attained. Because of thinner bark, a typical gallery forest tree attains fire resistance at stem diameters of more than twice those required for a savanna species. Because growth rates of sprouts are similar for the two species types, a typical forest tree should require a fire-free interval more than twice as long as is required for savanna species to escape the fire trap. This should greatly reduce or eliminate adult recruitment of forest species in savannas subject to frequent fire.

Even under fire suppression, forest expansion into savanna is often quite slow (Bowman 1993, Fensham

and Butler 2003). At our study site, fire suppression has resulted in an increase in tree density in the savanna, but forest species still account for little of this increase. At distances >15 m from the forest edge, forest species comprised only 7% of stems with stem diameter <4 cm, despite three decades of fire suppression. Elsewhere in the Cerrado, succession from savanna to closed woodland (cerradão) has been observed (Durigan and Ratter 2006). Cerradão is probably best characterized as forest, rather than savanna (Ribeiro and Walter 2001), but tends to be shorter and more open than other forest types in the region. This vegetation type is composed of a mixture of savanna and forest tree species (Pinheiro and Monteiro 2006), but it is not clear whether these coexist indefinitely in the absence of fire. In Australia, savanna species were observed to persist for some time following forest expansion (Banfai and Bowman 2007), but it is likely that savanna species are eventually eliminated, due to their shorter stature (Hoffmann et al. 2003) and shade intolerance. There appears to be little, if any, recruitment of savanna tree species within the gallery forests studied here, and only one individual of a savanna tree species was encountered >15 m into the forest. Savanna grasses appear similar to savanna trees in their response to the gradient in light availability across the savanna–forest boundary, being absent in the forest, a pattern which contributes considerably to the lower flammability there (Biddulph and Kellman 1998, Hennenberg et al. 2006).

Fire is not the only abiotic factor that differs between savanna and forest. At landscape and regional scales, forest tends to occupy soils with higher water or nutrient availability than savanna (Tinley 1982, Furley 1992, Hopkins 1992, Ruggiero et al. 2002). We hypothesize that forest tends to be restricted to sites of high resource availability because the resulting higher growth rates reduce the time needed to reach fire-resistant sizes. This mechanism is similar to the one hypothesized by Bond and Midgley (2000) to explain woody plant encroachment under elevated CO₂. In the savanna soils studied here, Ca²⁺, and Mg²⁺ concentrations were particularly strongly correlated with resprout size. Based on observed differences in Ca²⁺ and Mg²⁺ concentrations in forest, we predict that resprouts in forest soils should be 250–280% the size of those in savanna soils (based on an index of stem volume), assuming similar light environments. Where these elements are scarce, the long times required for forest trees to reach a fire-resistant size should virtually eliminate any possibility of succession to forest between fire events. In contrast, where abundant soil resources promote rapid tree growth, a fire-resistant size will be attained more quickly. Given the stochastic nature of fire regimes, occasional fire-free intervals of sufficient length should eventually allow high-resource sites to succeed to forest.

Once established, the low flammability of evergreen forest contributes to its subsequent persistence. Savanna fires commonly fail to spread into adjacent forest

(Biddulph and Kellman 1998, Hennenberg et al. 2006), but in particularly long dry seasons, such as in 2005, these forests eventually become flammable. Even then, fire intensities (measured as height of stem charring) were considerably lower in the forest than in the adjacent savanna from which the fire had spread. As a result, rates of topkill in the forest were substantially lower than the same trees would have experienced in savanna or at the forest edge. The lower frequency and intensity of burning in forest, together with the ability of large forest trees to avoid topkill, should allow forest to stably persist in the same landscapes where forest expansion is prevented by frequent fire. The result would be a hysteresis in the dynamics of savanna–forest boundaries, whereby higher frequency of savanna burning should be necessary to drive forest retreat than is required to prevent forest expansion. Sternberg (2001) hypothesized that there should exist a hysteresis in the response of savanna–forest boundaries to climate, due to a positive feedback between vegetation and climate. However, such vegetation–climate feedbacks require vegetation changes over regional scales, whereas vegetation–fire feedbacks operate at scales of tens of meters, allowing savanna and forest to coexist as alternate stable states within close proximity to each other.

Sharp savanna–forest boundaries resulting from vegetation–fire feedbacks may be reinforced by feedbacks between vegetation and soil. Although the observed gradients in soil nutrients are likely to have played a role in determining the distribution of savanna and forest, the converse also may be true. Forest may be able to capture larger quantities of nutrients from groundwater (Jobbagy 2004) and dry deposition (DeLonge et al. 2008), while experiencing reduced nutrient loss from burning (Cook 1994) and leaching, due to greater cation exchange capacity provided by higher soil organic carbon. Such a vegetation–soil feedback would likely reinforce feedbacks driven by fire. Vegetation effects are likely to explain the differences in C and N, which ultimately come from atmospheric sources and are volatilized by burning. It is unlikely, however, that forest vegetation alone is responsible for the presence of the more basic, calcium-rich soils along five of the transects. Patches of calcareous soils have been previously noted in these same three gallery forests (Silva and Haridasan 1997), and appear to have a geologic origin, though transport by litterfall may expand these patches. Along the two remaining transects, the soil nutrient concentrations are more typical for gallery forests in the region, (Furley 1992, Silva 2005), being only moderately higher than in savanna. In such cases, there is evidence suggesting that past forest expansion may have resulted in increased soil nutrient pools. A carbon isotope study at two forest edges on the same reserve as the present study revealed that forest has expanded into savanna, yet soil nutrient gradients reflect the current vegetation distribution (Silva et al. 2008). Though not unequivocal evidence for vegetation effects on soils, such observa-

tions do point to the dynamic nature of these savanna–forest boundaries.

CONCLUSION

In contrast to humid tropical forests, the transitional forests studied here exhibited high postfire resilience due to low tree mortality and high growth rates of resprouting trees. Fire nevertheless represents a considerable constraint to the recruitment of forest tree species, in comparison to savanna species, because of the thinner bark and higher rates of topkill among forest species. Longer fire-free intervals are therefore required for forest species to reach a fire-resistant size not prone to topkill. Long fire-free intervals are typically rare events under natural fire regimes in tropical savannas, so succession to forest is most likely to have occurred preferentially where high soil resource availability permits more rapid tree growth, and hence reduces the time needed for trees to reach a fire-resistant size. Once forest is established, however, the tendency to suppress fire, combined with high resilience in the event of a fire, should allow these forests to persist despite frequent burning in adjacent savanna.

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APPENDIX

Summary of nutrient differences between savanna and forest soils and the predicted effects on resprout growth (*Ecological Archives* E090-087-A1).