

Responses to Fire in Selected Tropical Dry Forest Trees¹

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ABSTRACT

Fire is a frequent disturbance in the tropical dry forests of Central America, yet very little is known about how native species respond to such events. We conducted an experimental burn in a tropical dry forest of western Nicaragua to evaluate plant responses to fire with respect to survivorship and recruitment. Measurements of woody vegetation of all size classes were carried out prior to the prescribed burn and three successive years post fire. We selected the 15 most abundant species <10 cm DBH to assess percent survivorship and sprouting responses post fire. Changes in seedling densities for these 15 most abundant species and the 15 least abundant species were analyzed using a repeated measure ANOVA. We also assessed changes in seedling densities for three species of international conservation concern. We found three major fire-coping strategies among common dry forest plants: resisters (low fire-induced mortality), resprouters (vigorous sprouting), and recruiters (increased seeding post-fire). While survivorship was generally high relative to tropical moist forest species, those species with lower survivorship used either seeding or sprouting as an alternative strategy for persisting in the forest community. Seed dispersal mechanisms, particularly wind dispersal, appear to be an important factor in recruitment success post-fire. Burn treatment led to a significant increase in the density of seedlings for two species of conservation concern: *Guaiacum sanctum* and *Swietenia humilis*. Results of this study suggest that common dry forest species in western Nicaragua are fire tolerant. Further study of individual species and their fire responses is merited.

RESUMEN

El incendio forestal causa perturbación frecuente en los bosques secos tropicales de Centroamérica, sin embargo se conoce poco del comportamiento de las especies nativas a ésta perturbación. Nosotros llevamos a cabo una quema experimental en un bosque seco tropical de Nicaragua occidental para evaluar el comportamiento de la flora con respecto a la sobrevivencia y reclutamiento de las especies después de la quema. Se midió todas las clases diamétricas de la vegetación leñosa antes de la quema controlada y durante 3 años consecutivos después de la quema. Seleccionamos las 15 especies más abundantes en la clase diamétrica <10 dap para evaluar el porcentaje de sobrevivencia y la actividad de rebrote después de la quema. Cambios en la densidad de plántulas para las 15 especies más abundantes y para las 15 especies menos abundantes fueron analizadas utilizando el análisis de varianza de medición repetido (ANOVA). También, evaluamos cambios en la densidad de plántulas para tres especies de interés a nivel internacional con respecto a su conservación. En la flora común del bosque seco se encontró tres estrategias principales utilizadas por las especies para contender con los incendios forestales, estas fueron: resistentes (baja mortalidad por el incendio), rebrotadores (rebrotamiento vigoroso), y reclutores (reclutamiento elevado pos-incendio). Mientras la sobrevivencia de especies en el bosque seco en general fue relativamente alta a la de especies de bosque húmedo tropical, las especies con menor sobrevivencia utilizaron el reclutamiento ó rebrotamiento como estrategia para persistir en la comunidad boscosa. El mecanismo de dispersión de semilla, particularmente la dispersión eólica, parece ser un factor importante en el éxito de reclutamiento después de la quema. Las quemas controladas produjeron un aumento significativo en la densidad de plántulas para dos de las especies de interés para la conservación: *Guaiacum sanctum* L. (Zygophyllaceae) y *Swietenia humilis* Zucc. (Meliaceae). Resultados de esta investigación sugieren que las especies comunes del bosque seco de Nicaragua son tolerantes al fuego. Por lo tanto, es merecido hacer más estudios de estas especies y su comportamiento ante la perturbación del fuego.

Key words: Central American dry forest; fire life histories; *Guaiacum sanctum*; life history traits; Nicaragua; sprouting; tropical dry forest; tropical fire ecology.

THE HIGHLY FRAGMENTED CENTRAL AMERICAN DRY FOREST (CADF) is a global priority for conservation (Janzen 1988a, Lerdau *et al.* 1991). Fire is a prominent disturbance throughout this ecosystem (Koonce & González-Cabán 1990, Janzen 2002), occurring at high frequencies and burning with a low-to-moderate intensity. Although known to be crucial in maintaining other tropical dry ecosystems such as savannas (Kellman 1984, Trollope 1984), the extent to which fire regulates plant communities in the Neotropical dry forest is unknown. In this paper we seek to characterize species responses to fire in a CADF.

The CADF is prone to fire due its strong seasonality. During dry season months, leaf litter and woody debris accumulate along the forest floor as a result of deciduous trees and strong easterly trade winds. Most wildfires in dry forests are linked to fires set intentionally by farmers who are preparing agricultural fields or maintaining pasture. Such human activities lead to frequent ignitions and fire return intervals are often less than 20 yr in CADFs. Since wildfires are primarily anthropogenic, they are not generally considered part of any “natural” disturbance regime (Janzen 1988b). However, “natural” ignitions do occur and have been recently observed in the region as the result of lightning (Middleton *et al.* 1997) and volcanic activity (S. Otterstrom pers. obs.). Also, anthropogenic ignition is not always undesirable; human activities provide the primary ignition for many fire-dependent ecosystems. In Central America,

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anthropogenic fires shaped ecosystems throughout the Holocene (Horn & Sanford 1992), and although these fires likely did not occur over a period sufficient for fire-adaptive traits to evolve, they could have selected for a dry forest composition favoring fire-adapted plants.

Fires in the CADF are widely considered destructive and some scientists argue that they pose the largest threat to dry forest conservation (Janzen 1988a). Such concerns are justified in view of the nonnative pyrophytic grasses (*i.e.*, *Hyperannia rufā*) present throughout many of the region's abandoned pastures and disturbed forest fragments. Exotic grasses interacting with fire can lead to a grass-fire cycle that inhibits forest regeneration (Mueller-Dombois 1978, D'Antonio & Vitousek 1992, Kramer 1997). Although this dynamic is well established, we hypothesize that it is premature to generalize its destructive effects to intact dry forests where exotics are absent, particularly because the fire responses of native species have not been thoroughly explored.

Ultimately, fire's role within the CADF depends on the life history characteristics of individual species as they respond to fire disturbance. Adaptations to fire generally revolve around a plant's ability to (a) survive fire or to (b) regenerate post fire (Gill 1981, Keeley 1986, Bond & van Wilgen 1996). Survival is often greatest in species with protective features such as thick bark (Uhl & Kauffman 1990, Pinard & Huffman 1997, van Mantgem & Schwartz 2003). Postfire regeneration is enabled by species traits such as wind-dispersed seeds (Janzen 1988b), fire-stimulated germination (Sweeney 1956), and serotinous cones with wind-dispersed seeds (Gill 1975). Sprouting is a particularly advantageous trait because it can allow for both the survival of the main stem and postfire regeneration through vegetative recruitment (Bond & Midgely 2001). Among CADF tree species sprouting (Snook 1993), wind dispersal (Augspurger 1986, Janzen 1988b, Gentry 1995), and thick bark (Snook 1993) are all traits commonly observed. In Neotropical rain forests, sprouting is also a common trait (Kauffman 1991). However, bark thickness is greater and wind dispersal is more frequent in Neotropical dry forests than in rain forests (Gentry 1982, Pinard & Huffman 1997, Barlow *et al.* 2003a).

If the CADF were composed of species poorly adapted to fire, then one would not expect its common plants to exhibit life histories consistent with fire-prone environments. Bond and van Wilgen (1996) classified plant life histories according to responses to fire as: fire-recruiting species, nonfire-recruiting species, sprouters, non-sprouters. Fire recruiters regenerate after fire from a seedbank and can have an increase in fire-stimulated flowering or a seed release from serotinous cones. Sprouters can be categorized as obligate sprouters (genets rarely killed, recruitment consists primarily of resprouting) and facultative sprouters (genet mortality variable, recruitment from both seeds and sprouts; Keeley & Zedler 1978, Christensen 1985, Keeley 1986).

In this study, we examine the hypothesis that CADF woody plants are fire sensitive. This hypothesis predicts that these species will exhibit sensitivity to fire through high mortality and low post-fire recruitment. Our alternative hypothesis is that dominant CADF woody species are fire tolerant. This hypothesis predicts fire tolerance via high survivorship or other strategies adaptive to fire.

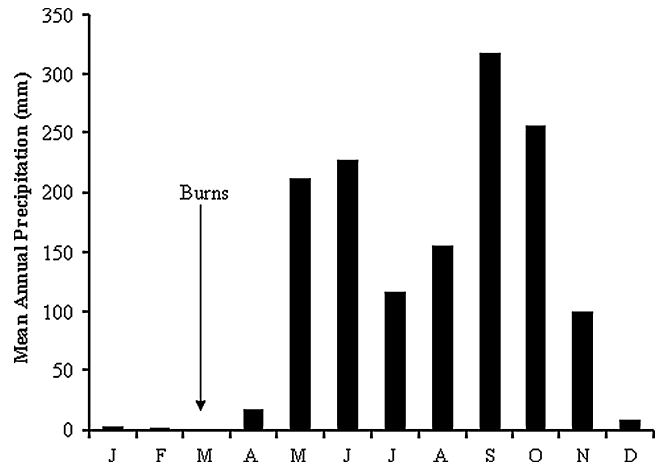


FIGURE 1. Mean annual precipitation for El Terrero/Río Escalante Station, $11^{\circ}35'N$, $86^{\circ}07'W$ during years 1983–1999. x-axis = months of calendar year, y-axis = mean annual precipitation in millimeters. Arrow indicates month when the three experimental burn treatments were conducted.

METHODS

We carried out field research in an upland dry forest at the Río Escalante-Chacocente Wildlife Refuge, Nicaragua ($11^{\circ}30'N$, $86^{\circ}08'W$) where mean annual temperature and precipitation are $26^{\circ}C$ and 1407 mm, respectively (INETER 2001). Rainfall at this site is highly seasonal and is concentrated between the months of May and November (Fig. 1). We selected the forest stand used for experimental burns based on site accessibility, level topography, willingness of landowners to permit burns, and the maturity of the forest. Local farmers reported that the study area had not burned for over 20 yr.

Within the selected forest stand, we established a total of 60 5×15 m plots. The total size of the experimental burn area was limited by both logistical constraints and by ministry of environment officials. Plots were spatially arranged in four groups of 15 plots each, with each group forming a total area of 15×75 m. This elongated spatial arrangement, commonly used for prescribed burns, enabled fire spread and consistent burning. However, as with other fire studies, these plots lack spatial independence within each burn treatment (van Mantgem *et al.* 2001). Therefore, with this study design the interpretation of any treatment effects is limited to this particular dry forest site. The orientation and location of the plot groups were assigned randomly.

Within each plot we identified all woody species >1.5 m height, measuring the height and diameter of each individual and mapping its location for continued monitoring. We conducted species counts for all species <1.5 m height in each plot. Sampling took place in December at the end of the rainy season. Basal area for trees >2.5 cm DBH was $21\text{m}^2/\text{ha}$ and there were 36 trees >10 cm DBH per 0.1 ha. This forest structure is consistent with other upland CADF stands (Gentry 1995, Gillespie *et al.* 2000). Nonnative pyrophytic grasses such as *H. rufā* were absent in the area. During

the dry season following initial sampling we conducted three separate experimental burns in 45 of the plots (Fig. 1), leaving 15 plots as controls.

Wildfire events are common during March when the experimental burns were conducted. Experimental burns were likely less intense than most CADF wildfires because plots were located on a relatively low slope (3–7%) and burns were conducted in the late afternoon (between 1500 h and 1800 h) when relative humidity (RH) and temperature begin to fall. Temperatures at the time of burns were between 34°C and 35°C and RH was between 46 and 51 percent with winds at 2–6 km/h. Fires were low intensity surface fires with average flame heights of 1.4 m and rate of spread varied between 30 and 60 m/hr. Fires did not consume 100 percent of the study plots; therefore, immediately following the fire we recorded char heights on all woody vegetation and mapped the burn. Mean char height was 16 cm and maximum char height was 1.5 m.

Following the burn, we repeated prefire measurements exactly 1, 2, and 3 yr from the time of prefire sampling. In addition to prefire measurements, we recorded mortality (dead or die-back) and the presence and type of sprouting behavior (basal, root, or stem) during each year post fire. All plants within the study were collected and identified at Nicaragua's National Herbarium. Within study plots, there were 60 species of adult or juvenile trees and 74 species of woody seedlings (excluding lianas).

Fire's effect on adult trees was limited, with less than 12 percent mortality observed in burned trees >10 cm DBH. This low mortality, combined with a relatively small sample size, restricted our ability to further analyze fire's effects on species of this larger size class. Therefore, saplings—defined as trees and shrubs <10 cm DBH and >1.5 m height—were the only woody plants considered for our analysis.

We analyzed fire responses among saplings by selecting the 15 most abundant sapling species affected by the experimental burns. Our analysis only considers vegetation within burned portions of the plots. Therefore, all saplings assessed exhibited fire injury in the form of charring. Fire responses considered include: percent survivorship (No. of post fire/No. of pre fire), frequency (proportion of burned trees sprouting), number of sprouts per individual plant, and the type of sprouts (root sprouts, basal sprouts, or stem). Root and stem sprouts are epicormic sprouts from dormant meristematic tissues (Kauffman 1991), and those classified as basal sprouts are sprouting from subterranean tissue. We tested the relationship between sprouting and survivorship by applying a linear regression model. Postfire changes in seedling densities were also calculated for each species, but resprouts were not considered as seedlings in the analysis.

The effect of burn treatment on postfire seedling recruitment (seeding) was analyzed for the 15 most abundant species by applying a one-way repeated measure ANOVA on seedling data pre fire and 3 yr post fire. This approach, along with making before and after comparisons, is recommended as a method to increase the confidence in the results of fire studies where there has been pseudoreplication (van Mantgem *et al.* 2001). To assess the position of each species on the fire-tolerance continuum, we rank ordered each of the 15 most abundant species according to the three primary fire-response

categories: survivorship, sprouting, and seeding. We calculated the change in population (λ) as the proportion of burned individuals resprouting plus the mean change in seedling densities relative to preburn densities.

We evaluated the treatment effect on postfire recruitment for two species of international conservation concern located within experimental plots using a one-way repeated measure ANOVA for each of the selected species. These species were: *Guaiacum sanctum* (CITES Appendix II, IUCN endangered C2), and *Swietenia humilis*—Pacific Mahogany (CITES Appendix II, IUCN vulnerable).

RESULTS

Mean survivorship was 46.5 percent for the 15 most abundant saplings. This mean survivorship was not significantly different from the survivorship observed in the remaining saplings species not ranked among the 15 most abundant species ($\chi^2 = 0.002$, $df = 1$, $P = 0.96$). Table 1 provides a list of the selected 15 woody species representing ten families and their postfire survivorship, seedling recruitment, and sprouting characteristics. The three species with highest survival were *Acacia colinsii* (67.5%), *Casearia corymbosa* (62.5%), and *Diospyros salicifolia* (62.5%). The species with the lowest survivorship were *Randia aculeata* (35.29%), *Jacquinia nervosa* (23.07%), and *Semialarium mexicanum* (33.3%). The understory shrub species *J. nervosa* experienced the lowest survivorship and also presented the most vigorous sprouting behavior.

Sprouting was observed in all but two species: *Randia monantha* and *Gyrocarpus americanus*. Six species exhibited sprouting while simultaneously maintaining their central stem alive. All sprouting species produced basal sprouts, but root sprouts were also observed in nine species and stem sprouting in four species. Some species were more vigorous sprouters, both in terms of the percent of burned individuals sprouting and the number of sprouts per individual. There was no relationship between proportion of sprouting individuals and survivorship ($R^2 = 0.06$, $N = 15$; $P = 0.37$). However, there was a strong relationship between the two indicators of sprouting ability: percent of individuals sprouting and the mean number of sprouts per individual (Fig. 2). One-year post fire, sprouts from resprouting saplings were abundant. The total number of sprouts were only slightly less (15%) than the total number of new seedlings during the first two years post fire. By year three post fire, the total number of living resprouts decreased by a third.

Fire-response strategies varied according to species with many of the species ranking high in one or two fire responses, while receiving a medium-to-low rank in other categories (Table 1). Eleven of the 15 species were ranked among the top five in at least one of the fire-response categories. Four species were ranked within the top five in at least two of the fire-response categories. Two species, *R. monantha* and *Erythroxylum sp.*, ranked relatively low across all three of the fire responses.

Based on the range of observed fire responses, we established a framework for qualifying fire life histories in the tropical dry forest. The primary three strategies are resisters, recruiters, or resprouters

TABLE 1. The 15 most abundant woody species affected by fire (<10 cm DBH, >1.5 m height). Indicators of survivorship are: percent survivorship, percent sprouting, and mean change in seedling densities {Mean change = (Δ mean treatment plots – Δ mean control plots) / mean prefire density}.

	No. of individuals observed	Survivor-ship (%)	Sprouting (%)	Δ Seedling densities	Sprout type	Rank survivorship	Rank sprouting	Rank seedling	λ	
<i>Acacia collinsii</i> Saff.	40	67.5	17.5	0.125	b, r	1	13	6	67.63	
<i>Diospyros salicifolia</i> Humb. & Bonpl.	8	62.5	62.5	1.85*	b, r	2	5	1	64.35	
<i>Casearia corymbosa</i> H.B.K	11	62.5	75	–0.95**	b	2	3	14	61.55	
<i>Stemmadenia obovata</i> (Hook. & Arn.)	143	56.64	50.35	–0.15**	b, r, s	4	7	7	56.49	
<i>Randia monantha</i> Benth.	9	55.56	0	–0.75	–	5	14	13	54.81	
<i>Gyrocarpus americanus</i> Jacq.	9	50	0	0.19	–	6	14	3	50.19	
<i>Erythroxylum havanense</i> Jacq.	92	50	27.17	–0.38	b, r, s	6	11	8	49.62	
<i>Casearia tremula</i> (Griseb) Griseb. ex W. Wright	27	45.23	45.73	–0.6**	b, r	8	8	10	44.63	
<i>Croton niveus</i> Jacq.	33	42.42	84.85	0.179	b, r, s	9	1	4	42.59	
<i>Erythroxylum</i> sp.	66	39.39	43.94	–0.97	b, r	10	9	15	38.42	
<i>Albizia adinocephala</i> (Donn. Sm.)	8	37.5	62.5	–0.699	b	11	5	12	36.8	
<i>Trichilia martiana</i> C. DC.	11	36.36	72.73	–0.39	b, r	12	4	9	35.97	
<i>Randia aculeata</i> L.	34	35.29	32.35	–0.612*	b, s	13	10	11	35.22	
<i>Semialarium mexicanum</i> (Miers)	9	33.33	22.22	0.329	b	14	12	2	33.66	
<i>Jacquinia nervosa</i> C. Presl.	13	23.07	76.92	0.17	b, r	15	2	5	23.24	

Statistically significant treatment effects on seedling densities are shown by: * = $P < 0.05$, ** = $P < 0.005$. Sprout types are: b = basal, r = root, s = stem. Species are assigned a number based on their rank order for fire responses in terms of survivorship, sprouting, and seedling changes. Lambda- λ is the proportion of saplings surviving + change in seedling densities.

(Table 2). Species not strongly displaying any of the three mechanisms for coping with fire were identified as vulnerable.

Postfire seedling varied among species, but in general seedling densities in rare species increased while seedling densities of common species decreased. The repeated measure ANOVA carried out for each of the 15 most abundant species demonstrated that burn treatment had a negative effect on seedling densities for *Stemmadenia obovata* ($F = 6.96$, $df = 2$, $P < 0.005$), *Randia aculeata* ($F = 4.22$, $df = 2$, $P < 0.05$), *Casearia tremula* ($F = 19.69$, $df = 2$, $P < 0.001$), *C. corymbosa* ($F = 19.04$, $df = 2$, $P < 0.001$), and a positive effect on seedling densities for *D. salicifolia* ($F = 7.59$, $df = 2$, $P < 0.05$). Meanwhile, seedling densities increased for nearly all of the species that were among the 15 least abundant woody species. No

species, rare or abundant, had their seedling populations completely eliminated post fire. In the year following the fire, 18 completely new species of seedlings were found; these were not present during prefire sampling. These results are consistent with a significant increase in seedling diversity following burn treatment (Otterstrom 2004).

Seedling densities for the two species of conservation concern increased one-year post fire, while seedling densities for all woody species in treatment plots decreased immediately following fire (Fig. 3). One-way repeated ANOVA demonstrated a significant effect of fire treatment on seedling densities for *S. humilis* ($F = 9.14$, $df = 2$, $P \leq 0.005$) and *G. sanctum* ($F = 5.12$, $df = 2$, $P = 0.025$).

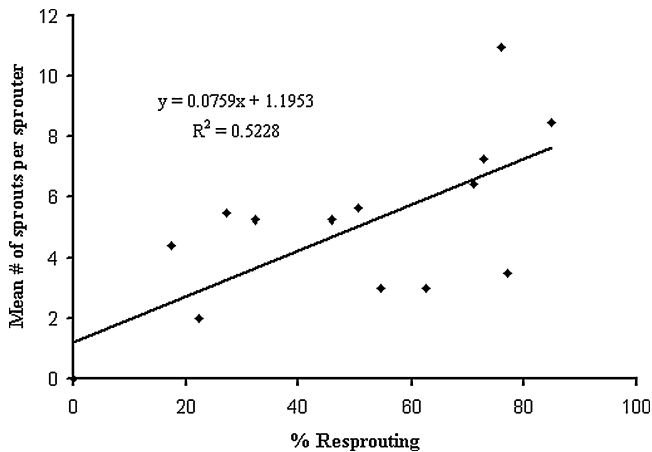


FIGURE 2. Significant relationship between portion of population sprouting and the mean number of sprouts per individual plant ($P < 0.005$). x -axis = percent of population of given species sprouting, y -axis = mean number of sprouts per sprouting individual for given species. Species further from zero have a greater sprouting ability.

DISCUSSION

Our results indicate that common species in this Nicaraguan CADF were not especially susceptible to the prescribed fire treatment. Mortality among larger-diameter trees (>10 cm DBH) was very low (12% mortality) and was consistent with mortality observed after wildfires near the same site (Otterstrom 2004). Saplings (<10 cm DBH) were also surprisingly resilient to fires, with nearly half of both rare and abundant species surviving the fire. Most woody species in this study exhibited a strategy to either survive the fire or persist in the forest community through new seeding or resprouting.

Postfire survivorship of woody plants <10 cm DBH was far higher than that observed in tropical rain forests ($<25\%$; Woods 1989, Barlow *et al.* 2003b) and in subhumid tropical forests (26–50%; Pinard *et al.* 1999). This ability to resist fire’s damaging heat may be attributed to bark thickness. Given the small size class of the saplings analyzed, few, if any, had conspicuously thick bark. Bark thickness varies greatly among dry forest species, and many dry forest trees at low size classes do not have the bark thickness necessary to avoid cambial injury (Pinard *et al.* 1999). Furthermore, when

TABLE 2. Using a conceptual framework adapted from Bond and van Wilgen (1996), we describe fire life histories in a Nicaraguan tropical dry forest species as classified by fire response.

Fire response category	Survivorship	Sprouting	Recruiting
Resisters	high	high	variable
Recruiters	medium-to-low	variable	high
Resprouters	low	high	variable
Vulnerable	low-to-medium	low	low

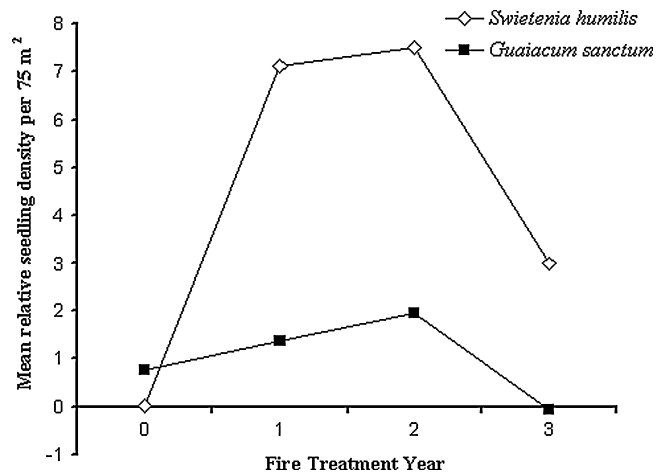


FIGURE 3. Mean relative seedling densities for two endangered dry forest species: *Swietenia humilis* and *Guaiacum sanctum*. Mean relative seedling density per 75 m^2 is the seedling density relative to the control and preburn densities. Mean relative density = (mean treatment density - mean control density) / mean prefire density. x -axis = year 0 is prefire and years 1, 2, and 3 are successive postfire years. y -axis = Mean relative seedling density per 75 m^2 . Treatment had a significant positive effect on *S. humilis* ($SE = 0.142$) and *G. sanctum* ($SE = 3$) seedling densities ($P < 0.05$).

comparing forest trees to their savanna congeners, bark in savanna trees is nearly three times as thick (Hoffman *et al.* 2003). However, we do not discount bark as a potential factor in survivorship. Some CADFs exhibit thick bark, and small differences in thickness can greatly increase a tree’s ability to withstand the heat of fire (van Mantgem & Schwartz 2003). High survivorship might also be explained by the low intensity of the fire. However, the mean char height (16 cm) in our study was higher than surface fires observed in rain forest environments (Cochrane 2003). Finally, high survivorship might be a result of reduced fire residence time attributable to rapidly burning fine litter (rate of spread as fast as 1 m/min). Low mortality may also be linked to the limited buttressing found in upland dry forest trees (Smith 1972), since buttressing is known to increase the vulnerability of tropical trees to fire (Barlow *et al.* 2003a).

Species with relatively low survivorship were effective at alternative strategies for persisting after fire, namely sprouting or seeding. Sprouting was the most widely observed fire response. Although sprouting is in no way limited to fire environments, sprouters are favored by frequent, low intensity disturbance regimes (Bond & Midgley 2001). A total of nine out of the 15 selected species were root sprouters, a trait understood to be indicative of fire environments (Saha & Howe 2003). According to Keeley and Zedler (1978), fire return intervals of <25 yr would favor a sprouting over a seeding strategy. Dry forest species may be called “facultative sprouters” in that their expansion or recruitment is not limited to fire events. Many of the saplings that died as a result of fire, were only top-killed and remained in the plant community through multiple basal and root sprouts. In many other individuals, they were able to

both survive the fire and also put out new sprouts, thus creating an advantageous opportunity for persistence and expansion (Bond & Midgley 2001).

Seed dispersal mechanisms appeared to be an important consideration in those species with no sprouting ability. The non-sprouting tree *G. americanus* was particularly effective at seedling recruitment post fire via its wind-dispersed seed. Meanwhile, the understory tree *R. monantha* was also a nonsprouter, yet it had low postfire recruitment apparently due to a low number of large globulous fruit that do not disperse easily. It is not uncommon to find nonsprouters within fire-prone vegetation (Bond & van Wilgen 1996). In this small-scale burn experiment, the surrounding forest likely contributed to postfire seedling recruitment. However, our results may have been different after a large landscape-scale fire where there would likely be a decrease in seed sources.

None of the top 15 sapling species characterized in this study is considered threatened. Nevertheless, they all form part of the native vegetation in the dry forest biome and thereby are important for conservation purposes. Four of the species are described as being part of secondary forest vegetation (Stevens *et al.* 2001), but they are also naturally occurring components of the dry forest understory.

One might argue that an abundance of fire-tolerant species at this particular study site does not demonstrate adaptation to fire; rather, it is evidence that the forest is highly disturbed. The forest structure is consistent with other CADFs (Gentry 1995). Woody vegetation under 10 cm DBH (excluding lianas) was composed primarily of understory shrubs and trees, not pioneer vegetation. However, fire has undoubtedly been a selective factor at this site during the past century (Sabogal 1992; Gillespie & Walter 2001). Its selective forces were likely even greater when Amerindians used frequent fire to maintain grasslands and savannas prior to European contact (Dull 2004).

Although some species did experience a decrease in seedling densities post fire, no common species was devastated by fire's impact and many new species were introduced as a result of the fire. The majority of these new species were relatively rare, including 18 species that were new observations within the plots post fire. This increase in seedling richness and abundance has some positive implications for dry forest conservation. Although many of the newly introduced seedlings may be considered early colonizers (*e.g.*, *Malvaviscus arboreus* Cav.; *Senna pallida* var. *pallida*; *Cordia collococca* L.), at least eight species are overstory trees consistent with a healthy dry forest (*i.e.*, *Pterocarpus rohrii* Vahl; *Lonchocarpus costaricensis* (Pittier); *Zanthoxylum* sp.). No nonnative plants emerged following these low-intensity fires of small spatial extent.

Fire treatment increased recruitment for two internationally threatened hardwood trees. Our results do not demonstrate whether fire works as a germination mechanism, but they do provide some valuable questions as to why there was an increase in recruitment. One possible explanation is that fire creates suitable space for germination—in terms of light and soil conditions—in forests with otherwise limited germination sites. For example, mahogany trees (*S. humilis*) have wind-dispersed seeds that are known to disperse up to several hundred meters (Snook 1993). Further, mahogany

seedlings require high-light environments and bare soil to establish (Wolffsohn 1961 in Snook 1993), and would therefore be favored by a more open postfire environment. *Guaiacum sanctum* was one of the more conspicuous species observed post fire in locations that had burned as hotspots. Seeds of this avian-dispersed plant are hard, black ellipsoids (Wendelken and Martin 1987) and fire scarification may be a mechanism facilitating germination. In a Costa Rican dry forest, *G. sanctum* populations have reduced regeneration (Jimenez 1999). At this Costa Rican site, fire has been excluded during the past 15 yr. For the two species of conservation concern, fire did not have an adverse effect on any adult and juvenile stems within study plots, thus possibly indicating a resistance to fire. *Swietenia humilis* trees near the study area had obvious thick bark and deciduous leaves. At other sites, mahogany stems have shown elevated fire survival due to thick bark (Snook 1993).

CONCLUSIONS.—The results of this study strongly suggest that this particular dry tropical forest is dominated by species able to survive in the face of infrequent, low-intensity fires of small spatial extent. The interpretation of our results apply specifically to the study site; however, if one is to accept the forest site as representative of other CADFs, then it is reasonable to expect similar fire effects in other such forests. Consistent with our alternative hypothesis, common CADF species exhibited fire tolerance through either high survivorship or a combination of vegetative responses adaptive to fire. This is similar to other fire-adapted ecosystems where varying strategies coexist due to spatial and temporal stochasticity in fire events (Keeley 1986). From this study we can conclude that local populations of two endangered dry forest species are not immediately threatened by a single fire event, and, in fact, they may benefit from increased recruitment following fire. Further study is necessary to determine if fire may be a useful tool for restoring populations of these species. Our results suggest that, similar to the situation in other tropical dry forests (Maxwell 2004), fire may be a useful management tool because it reduces fuels and thereby the risk of more destructive high-intensity fires. As we develop a better understanding of disturbance dynamics in the tropical dry forest we will be better able to conserve this unique and threatened ecosystem.

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LITERATURE CITED

- AUGSPURGER, C. K. 1986. Morphology and dispersal potential of wind-dispersed diaspores of Neotropical trees. *Am. J. Bot.* 73: 353–363.
- BARLOW, J., B. O. LAGAN, AND C. A. PERES. 2003a. Morphological correlates of fire-induced tree mortality in a central Amazonian forest. *J. Trop. Ecol.* 19: 291–299.
- , C. A. PERES, B. O. LAGAON, AND T. HAUGAASEN. 2003b. Large tree mortality and the decline of forest biomass following Amazonian wildfires. *Ecol. Lett.* 6: 6–8.
- BOND, W. J., AND J. J. MIDGLEY. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends Ecol. Evol.* 16: 45–61.
- , AND B. VAN WILGEN. 1996. *Fire and plants*, pp. 34–50. Chapman and Hall, London, UK.
- CHRISTENSEN, N. M. 1985. Shrubland fire regimes and their evolutionary consequences. *In* S. T. A. Pickett and P. S. White (Eds.). *The ecology of natural disturbance and patch dynamics*, pp. 93–94. P.S. Academic Press, Inc., San Diego.
- COCHRANE, M. A. 2003. Fire science for rain forests. *Nature* 421: 913–919.
- D'ANTONIO, C. M., AND P. M. VITOUSEK. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 1992: 63–87.
- DULL, R. A. 2004. A Holocene record of Neotropical savanna dynamics from El Salvador. *J. Paleolimnol.* 32: 219–231.
- GENTRY, A. H. 1982. Patterns of Neotropical plant species diversity. *Evol. Biol.* 15: 1–84.
- . 1995. Diversity and floristic composition of Neotropical dry forests. *In* S. H. Bullock, H. A. Mooney, and E. Medina (Eds.). *Seasonally dry tropical forests*, pp. 47–194. Cambridge University Press, Cambridge, UK.
- GILL, A. M. 1975. Fire and the Australian flora. *Aust. For.* 38: 4–25.
- . 1981. Fire adaptive traits of vascular plants. *In* H. A. Mooney, T. M. Bonnicksen, N. L. Christensen, J. E. Lotan, and W. A. Reiners (Eds.). *Fire regimes and ecosystem properties*, pp. 208–230. Gen. Tech. Rep. WO – U.S. Forest Service, GTR-WO-26.
- GILLESPIE, T. W., AND H. WALTER. 2001. The distribution of bird species richness at a regional scale in tropical dry forest of Central America. *J. Biogeogr.* 28: 651–662.
- , A. GRIJALVA, AND C. N. FARRIS. 2000. Diversity, composition and structure of tropical dry forests in Central America. *Plant Ecol.* 147: 37–47.
- HOFFMAN, W. A., B. ORTHEN, P. KIELSE, AND V. D. NASCIMENTO. 2003. Comparative fire ecology of tropical savanna and forest trees. *Funct. Ecol.* 17: 720–726.
- HORN, S. P., AND R. L. SANFORD. 1992. Holocene fires in Costa Rica. *Biotropica* 24: 354–361.
- JANZEN, D. H. 1988a. Tropical dry forests: The most endangered major tropical ecosystem. *In* E. O. Wilson (Ed.). *Biodiversity*, pp. 24–36. National Academic Press, Washington, D.C.
- . 1988b. Management of habitat fragments in a tropical dry forest: Growth. *Ann. Mo. Bot. Gard.* 75: 105–116.
- . 2002. Tropical dry forest: Area de Conservación Guanacaste, Northwestern Costa Rica. *In* M. R. Perrow and A. J. Davy (Eds.). *Handbook of ecological restoration, volume 2, restoration in practice*, pp. 559–583. Cambridge University Press, Cambridge, UK.
- JIMENEZ, Q. 1999. Consideraciones sobre el manejo y conservación de 18 especies forestales vedadas en Costa Rica. Tesis de Maestría. Universidad Internacional de Andalucía. España.
- KAUFFMAN, J. B. 1991. Survival by sprouting following fire in tropical forests of the Eastern Amazon. *Biotropica* 23: 219–224.
- KEELEY, J. E. 1986. Resilience of Mediterranean shrub communities to fires. *In* B. Dell, A. J. Hopkins, and B. B. Lamont (Eds.). *Resilience in Mediterranean-type ecosystems*, pp. 95–112. Junk, Dordrecht.
- , AND P. H. ZEDLER. 1978. Reproduction of chaparral shrubs after fire: A comparison of sprouting and seeding strategies. *Am. Midl. Nat.* 99: 142–161.
- KELLMAN, M. 1984. Synergistic relationships between fire and low soil fertility in Neotropical savannas: A hypothesis. *Biotropica* 16: 158–160.
- KOONCE, A. L., AND A. GONZÁLEZ-CABÁN. 1990. Social and ecological aspects of fire in Central America. *In* J. Goldammer (Ed.): *Fire in the tropical biota—ecosystem processes and global challenges*, pp. 106–116. J. J.G.Springer, Berlin.
- KRAMER, E. A. 1997. Measuring landscape changes in remnant tropical dry forests. *In* W. F. Laurance and R. O. Bierregaard, Jr. (Eds.). *Tropical forest remnants: Ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago, Illinois.
- LERDAU, M., WITHBECK, J., AND HOLBROOK, N. M. 1991. Tropical deciduous forest: Death of a biome. *Trends Ecol. Evol.* 6: 201–202.
- MAXWELL, A. L. 2004. Fire regimes in northeastern Cambodian monsoonal forests, with a 9300-year sediment charcoal record. *J. Biogeogr.* 31: 225–239.
- MIDDLETON, B. A., E. SANCHEZ-ROJAS, B. SUEDEMEYER, AND A. MICHELS. 1997. Fire in a tropical dry forest of Central America: A natural part of the disturbance regime? *Biotropica* 29: 515–517.
- MUELLER-DOMBOIS, D. 1978. Fire in tropical ecosystems. *In* Proceedings of the conference: Fire Regimes and Ecosystem Properties. Honolulu, Hawaii.
- OTTERSTROM, S. M. 2004. Fire in a Neotropical dry forest: Cultural uses and ecological effects. Doctoral Dissertation. University of California, Davis.
- PINARD, M. A., AND J. HUFFMAN. 1997. Fire resistance and bark properties of trees in a seasonally dry forest in Eastern Bolivia. *J. Trop. Biol.* 13: 727–740.
- , F. E. PUTZ, AND J. C. LICONA. 1999. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *For. Ecol. Manage.* 166: 247–252.
- SABOGAL, C. 1992. Regeneration of tropical dry in Central America, with examples from Nicaragua. *J. Veg. Sci.* 3: 407–416.
- SAHA, S., AND H. F. HOWE. 2003. Species composition and fire in a dry deciduous forest. *Ecology* 84: 3118–3123.
- SMITH, A. P. 1972. Buttressing of tropical trees: A descriptive model and new hypotheses. *Am. Nat.* 106: 33–45.
- SNOOK, L. K. 1993. Stand dynamics of mahogany (*Swietenia macrophylla* King) and associated species after fire and hurricane in the tropical forests of the Yucatan Peninsula, Mexico. Doctoral Dissertation. Yale School of Forestry and Environmental Studies. pp. 64.
- STEVENS, W. D., C. ULLOA, A. POOL, AND O. M. MONTIEL. 2001. *Flora of Nicaragua, Volumes 1–3*. Missouri Botanical Garden Press, Saint Louis, Missouri.
- SWEENEY, J. R. 1956. Responses of vegetation to fire. *Univ. Calif. Pub. Bot.* 28: 141–216.
- TROLLOPE, W. S. W. 1984. Fire savanna. *In* P. de V. Booyend, and N. M. Tainton (Eds.). *Ecological effects of fire in South African ecosystems*, pp. 149–175. Springer-Verlag, New York, New York.
- UHL, C., AND J. B. KAUFFMAN. 1990. Deforestation, fire susceptibility, and potential tree responses to fire in the eastern Amazon. *Ecology* 71: 437–449.
- VAN MANTGEM, P., AND M. W. SCHWARTZ. 2001. Monitoring fire effects for managed burns and wildfires: Coming to terms with pseudoreplication. *Nat. Areas J.* 21: 266–273
- , AND ———. 2003. Bark heat resistance of small trees in Californian mixed conifer forests: Testing some model assumptions. *For. Ecol. Manage.* 178: 341–352.
- WENDELKEN, P. W., AND R. F. MARTIN. 1987. Avian consumption of *Guaiaacum sanctum* fruit in the arid interior of Guatemala. *Biotropica* 19: 116–121.
- WOODS, P. 1989. Effects of logging, drought, and fire on structure and composition of tropical forests in Sabah, Malaysia. *Biotropica* 21: 290–298.