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Fire-dependent pine forests in the Caribbean Basin cover extensive areas in the coastal plain of the Caribbean Sea and Gulf of Mexico and on several islands in the Bahamas Archipelago, Cuba, Hispaniola, and the Honduran Bay islands. These forests are high in conservation value but, unfortunately, remain mostly unprotected. Moreover, even though they are fire dependent, the use of fire for forest management often suffers from poor public perception and is prohibited by law in several countries. In this paper, we describe the fundamental links among fire, forest regeneration, and forest persistence in these ecosystems. We identify two general strategies based on the presence or absence of pine seedling adaptations for fire survival and describe management implications of these two strategies. We also introduce conceptual models describing fire, forest structure, and regeneration strategy linkages.

INTRODUCTION

The Caribbean Basin is home to a number of highly diverse forest types. Forest disturbances are a salient feature of the region, as many areas are subject to frequent hurricanes and wildland fires. Interactions among disturbances are also common; for example, the behavior and intensity of wildland fires can be influenced by heavy fuel loading resulting from storms (1, 2). Extensive stands of fire-dependent native *Pinus* spp. grow across the greater Caribbean Basin, here defined broadly to include the coastal plains of the Caribbean Sea and Gulf of Mexico as well as the islands. These native pines occur in parts of the Central American and southern US Gulf coastal plains, the Bahamas Archipelago, Cuba, Hispaniola, and the islands of Guanaja and Roatan. In these ecosystems, fire arrests succession and can determine forest community type (3). Many Caribbean Basin endemic plant species have fire-dependent life-history strategies and do not persist in ecosystems where fire is excluded (4, 5). In these fire-dependent forests, there is a synergy between fire and vegetation wherein morphological and ecological adaptations protect plants from fire and simultaneously promote conditions conducive to frequent fire incidence. Although each locale has a characteristic suite of plant species, the ecosystems appear remarkably similar structurally, with a tall monospecific pine overstory, a low-stature shrub/palm layer, and a species-rich herbaceous ground stratum. Pine forests of the Caribbean are an underappreciated element of the region's biodiversity, and they have received less attention than other forest types in terms of conservation, protection, and research. One critical aspect of their conservation is that, although they are dependent on fire, the use of fire for management of these forests is prohibited by law in many countries, including the Bahamas, Dominican Republic, and Honduras.

PREHUMAN FIRE HISTORY

Fire and terrestrial vegetation are inextricably linked (6); fossil evidence of wildfire dates back as far the Silurian Period, 420 million years ago, when land was first colonized by plants (7). Wildland fire has been present in the Caribbean Basin at least since the Pleistocene and likely much longer. Direct paleoecological evidence of fires in the Caribbean Basin dates back more than 13 000 y in Hispaniola (8, 9) and >40 000 y in Florida (10). The presence of endemic fire-dependant plant species provides strong indirect evidence that repetitive fires have likely occurred over millennia. Fire regimes in most pine-dominated areas in the Caribbean region have short return interval, low-intensity surface fires (11–13). In fact, fire return interval can be extremely short, as in the US Gulf coastal plain, where fires can occur annually. Forests in other areas, such as the Bahamas and Dominican Republic, typically burn less often, on the order of 3–10 y (8, 9; H. Grissino-Mayer pers. comm.). Lightning was the primary ignition source until humans colonized the region, and it remains a major source of wildland fire ignition.

HUMAN FIRE USE

Human cultures have used fire across the globe for various purposes for many millennia (14). In fact, evidence of fire use by *Homo erectus* predates the evolution of *Homo sapiens* (15). This early use of fire certainly extended into the realm of what contemporary practitioners would recognize as active management of ecosystems. There is ample evidence of ancient American cultures using fire for the purpose of habitat alteration to favor the abundance of useful plants and animals. Indeed, some authors have interpreted fire use by indigenous peoples in the Americans as having the objective of maintaining a diverse mosaic of habitats for resource diversity and security (16).

Archeological evidence indicates the Caribbean islands were first colonized by humans at least 6000 y ago (17) and possibly more than 40 000 y ago in Mexico, though pre-Clovis sites are controversial (18). With the first arrival of humans in the region, fire frequency seems to have increased, though data are scanty (19; H. Grissino-Mayer pers. comm.). After the collapse of indigenous populations following European contact, fires may have become less frequent, and then increased again after European recolonization (19). Humans continue to have direct and indirect effects on fire in these forests by altering patterns of ignition and the arrangement of fuels in the landscape. Human fire use still occurs throughout the region for hunting, pest management, to ease foot travel, and, in some areas, it is used extensively by forestry and conservation land managers. Nonetheless, forest fragmentation, agriculture, and other human-induced changes in landscapes have profound impacts on fire ecology, including direct manipulation of stands resulting in changes to fire behavior and thus forest regeneration. Here, we describe conceptual models of interactions between fire and vegetation structure, and we provide two case studies to demonstrate how overstory structure, canopy gaps, fuels, fire, and pine regeneration are linked. We also discuss how interactions among gap size, release of fire-sensitive broadleaf species, and differences in pine seedling life-history strategies can critically determine the regeneration of pines in different forest types.

Table 1. Taxa of pine native to the wider Caribbean Basin. Y indicates presence of a fire-resistant seedling grass stage.

Taxon	Map symbol	Grass stage
Pinus caribaea Morelet var. *bahamensis* (Grisebach) W.H. Barrett & Golfari	Pcb	
Pinus caribaea Morelet var. *caribaea*	Pcc	
Pinus caribaea Morelet var. *hondurensis* (Sénéclauze) W.H. Barrett & Golfari	Pch	
Pinus elliottii Engelmann var. *elliottii*	Pee	
Pinus elliottii Engelmann var. *densa* Little & K.W. Dorman	Ped	
Pinus occidentalis Swartz	Po	
Pinus palustris P. Mill.	Pp	Y
Pinus tropicalis Morelet	Pt	Y

PLANT ADAPTATIONS IN A DISTURBANCE-PRONE FOREST

Interactions among fire, fuels, stand structure, and vegetation are complex and are just beginning to be understood (2, 20). Nevertheless, sustainable management of Caribbean Basin pine forests hinges on this knowledge and will be critical to achieving goals ranging from conservation of inherent biological and cultural resources, to silvicultural uses, to mitigation of risks associated with wildfires. The short fire return intervals typical of Caribbean Basin pine forests make pine litter a critical fuel because litter carries fire across nonvegetated space and through less flammable vegetation. These forests, like most pine forests, are fire dependent; that is, without repetitive fires, succession to other vegetation types occurs. Alteration of the disturbance regime can lead to the establishment of an alternative ecological stable state (21–23), where less flammable fire-sensitive vegetation dominates and persists. In some cases, the replacement of pines by broadleaved species can occur in as little as 25 y (4).

Studies of how overstory gaps in forests influence the dynamics of plant species distributions have traditionally focused on understory plants. These studies have emphasized the importance of changes in resource availability when gaps form, usually manifested as seedling release from competition for light, water, or nutrients (24). Studies of gap dynamics have been useful in understanding patterns of forest regeneration and informing forest management activities. Fire, however, adds another layer of complexity to gap dynamics in forests with frequent fire regimes (20). In these forests, gaps can alter both resource availability and fire behavior. Canopy gaps increase the availability of light and other resources to understory plants and seedlings (25), while at the same time reducing fine fuel loads. The decrease in fine fuels leads to lower fire intensity and frequency, and, thus, fire sensitive plants in the gaps are released from overstory competition and from fire-associated mortality. Competition plays out depending on how plant species allocate resources to growth, storage, and fire-resistant morphology. There are tradeoffs associated with different strategies. If resource allocation to fire defenses causes lower competitive ability, then gaps can be the locus of a shift to another plant community in an alternative stable (fire-free) state. Fire fulfills a critical role in determining the outcome of the competition for resources and, therefore, determines the type of ecosystem found on a given piece of ground.

PINES OF THE CARIBBEAN BASIN

There are eight pine taxa that dominate in fire-dependent forests across the Caribbean Basin (26) (Table 1, Fig. 1). Mature trees in all the taxa have morphological adaptations for fire tolerance, such as self-pruning limbs, thick bark, and the ability to reflush scorched crowns. A few taxa have additional adaptations that confer fire tolerance even in very young seedlings. After germination, these seedlings spend up to a decade growing in a "grass stage," which allocates resources almost entirely to root system development, stem thickening, and belowground energy storage. The shoot apical bud is protected from fires by a dense sheath of long needles resembling a clump of grass. Upon leaving the grass stage, seedlings bolt, quickly reaching a stature sufficient to survive a surface fire. A true, genetically programmed grass stage is exhibited by *Pinus palustris* and *Pinus tropicalis*, whereas a third species, *Pinus elliottii* var. *densa*, exhibits some characteristics of a grass stage (27). In *P. elliottii* var. *densa*, seedlings have diminished height growth for a few years, but this does not seem to confer fire tolerance, and it is possibly related to site conditions or due to introgression from *P. palustris* or *P. tropicalis* (27). The remaining Caribbean taxa have seedlings and small saplings that are vulnerable to fire and require a fire-free period to reach a height and girth sufficient to escape fire mortality. Data from southern Florida suggest that up to 10 y are required for *P. elliottii* var. *densa* to survive a surface fire (M. S. Ross pers. comm.). Given the observation that different pine species in the Caribbean region have seedlings that are either fire-tolerant or fire-sensitive, we suggest that divergent strategies have developed for pine-regeneration responses to overstory gaps following disturbance. We summarize two strategies of pine seedling persistence next.

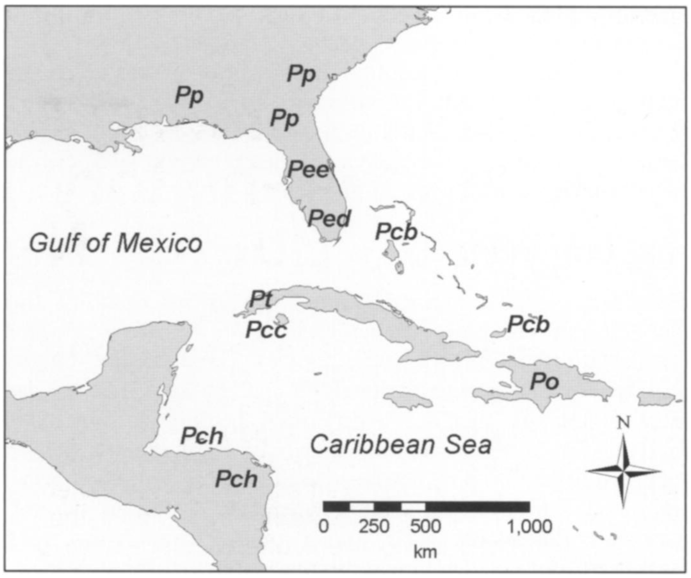

Figure 1. Distribution of canopy-dominant pine taxa in the coastal plain and insular Caribbean Basin. Abbreviations are the first letters of the genus, species, and variety of the pines listed in Table 1.

Fire-tolerant Seedlings

Fire-tolerant seedlings have adaptations to survive fire. These seedlings establish in the understory of low to moderate basal area stands, survive repetitive fires, and are released from resource competition upon gap formation, but they still require fire to suppress fire-sensitive competitors in the gap.

Fire-sensitive Seedlings

These seedlings are fire-sensitive for several years. Annual seed production allows seedling establishment upon gap formation. Lower fire frequency/severity in these gaps allows seedlings to recruit to a fire-tolerant sapling size. Fast growth allows competitive advantage over released fire-sensitive broadleaved species. Fine fuel production is quickly restored, allowing reestablishment of fires that then suppress slower-growing or fire-sensitive competitors.

In the following conceptual models and case studies, we envision that the method a particular forest type uses for pine regeneration, via strategies of fire-tolerant seedlings or fire-sensitive seedlings, is largely dependent upon two critical variables: fuel continuity and gap size.

FUEL CONTINUITY

There is a complex interaction among overstory structure, fine fuel distribution, pine regeneration, and fire effects in pine forests with frequent surface-fire regimes. The overstory supplies dead needles that create a critical fine fuel; because they are rich in flammable oils, pine needles are often the only fuel capable of carrying fire across vegetation-free patches of mineral soil or rock. Additionally, pine needles can increase fire intensity when combined with other vegetation where fallen needles "drape" over less flammable fuels and promote combustion (28). Harvested gaps in the pine overstory interrupt the continuity of fine "needle" fuel, lower the fire intensity inside gaps, and simultaneously reduce competition with the overstory. Gaps caused by wind throw increase fine fuel loads until the first fire consumes the elevated fuel load, after which, wind-throw gaps experience a reduction in fuel loads similar to harvested gaps. Release of both fire-sensitive broadleaved species and pines can occur in these gaps. The combined effects of lowered fire intensity, release from belowground competition, and higher light levels likely act synergistically to increase growth rates in both pine and fire-sensitive broadleaved species (20).

GAP SIZE

Regardless of seedling-regeneration strategy, newly germinated seedlings of all species are fire-sensitive. Even in pines with a grass stage, a short fire-free period is necessary to survive the first fire postgermination. Gaps are required for the establishment of seedlings with either strategy. In the case of pine species with a grass stage, small openings increase resource availability, resulting in higher growth rates and seedlings reaching a fire-tolerant size more quickly than outside of gaps. These grass-stage seedlings are then able to persist until subsequent canopy disturbances release them (23). For pines with fire-sensitive seedlings, gap size must be sufficient to diminish fine fuels and lower fire intensity and frequency, allowing seedling survival.

In species with a grass stage, gap size must fall into a narrow window for successful pine regeneration. Dense pine overstory eliminates seedling establishment through competition and fire intensity,. However, competition and fire also reduce the presence and vigor of fire-sensitive broadleaf species. Small disturbances to the overstory (i.e., lightning) create small gaps sufficient to allow for the establishment and accumulation of advanced regeneration of grass-stage seedlings, even in the presence of frequent fire. Subsequent disturbances enlarging the gap release the grass stage to quickly bolt through a fire-sensitive height while frequent fire continues uninterrupted to suppress fire-sensitive broadleaved species. In this case, gaps must be large enough to release the young pines from competition with the overstory for light and nutrient resources, but small enough that fine fuel inputs are sufficient to carry low-intensity fire through the gap. If the gap becomes too large, and there is insufficient fuel to carry fires, fire-sensitive vegetation can outcompete the pines (Fig. 2) (24). Moreover, once broadleaved species are released, subsequent changes in fuels and microclimate make fires less likely to carry into the interior of the gap (29). These changes in competition and fire intensity increase the probability of fire-sensitive broadleaved species dominating the gaps and providing a locus for conversion to broadleaved forest (20).

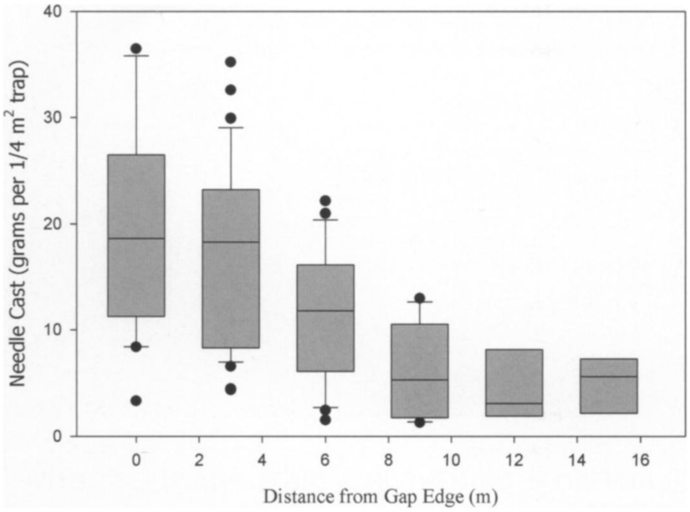

Figure 2. Box plots of decline in pine litterfall from forest edge into canopy gap in the *P. palustris* forest described in case study 1. Boxes indicate means (horizontal lines) and standard deviations, with 95% confidence intervals (whiskers) and outliers (points). The data were collected from thirty-three 0.25 m^2 traps located in nine gaps of 0.13–0.25 ha from September to December 2006.

In pines without a grass stage, when released from competition and fire, seedlings rapidly grow in height (30), and, as these seedlings mature, other adaptations for surviving fire are expressed (e.g., thick bark develops) while simultaneously producing the needle cast that will return fire to the gap. Once fires are reestablished, fire-sensitive broadleaved vegetation becomes suppressed. Thus, while gap size must exceed a minimum area, there is effectively no maximum gap size as long as seed dispersal limitations are not exceeded. This may represent an adaptation to large-scale disturbances such as hurricanes or insect outbreaks. Forests dominated by *P. caribaea*, *P. elliottii*, and *P. occidentalis* appear to fit this model as abundant natural regeneration occurred after extensive clear-cutting in the mid-twentieth century. Figures 3a,b outline the scenarios described here for how gap size and regeneration strategy interact. Next, we apply these conceptual models to two case studies.

CASE STUDY, FIRE-TOLERANT SEEDLING STRATEGY: US GULF COASTAL PLAIN LONGLEAF PINE FORESTS

To determine the influence of fine fuel loading on seedling survival, we manipulated fuel loads on plots established in a 17 ha burn unit. This site, at the Joseph W. Jones Ecological Research Center, southwestern Georgia, USA, has been frequently burned with return intervals of 1–3 y for >70 y. Plots were located in naturally regenerated, mature (70+ y), upland longleaf pine (*Pinus palustris*) forests with intact native groundcover vegetation (predominantly wiregrass; *Aristida beyrichiana* Trin. & Rupr.). The plots were located in canopy openings where natural advanced regeneration was abundant. Seedlings and saplings were counted and measured in the plots.

We established three 7 × 14 m plots in each of three blocks (n = 9 plots) with advanced regeneration. Within these plots, three litter treatments were applied: *i)* a reduced litter treatment with complete removal of pine litter from the forest floor; *ii)* an ambient litter treatment; and *iii)* a litter-addition treatment where litter from the removal plots was added to the forest floor, effectively doubling pine needle loading. In the litter-addition plots, needles were applied in such a way as to simulate

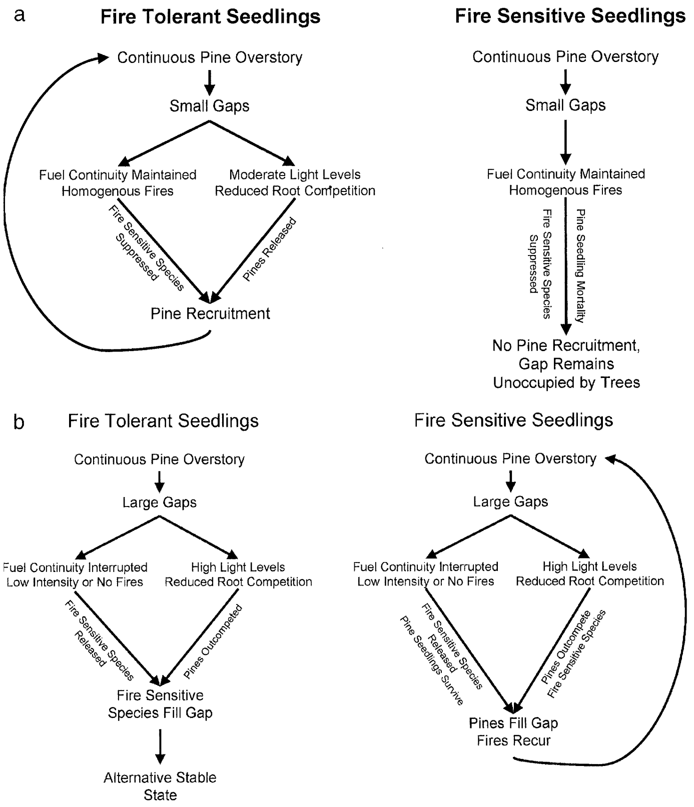

Figure 3. a. Conceptual model of the effect of small gaps on pine regeneration. b. Conceptual model of the effect of large gaps on pine regeneration.

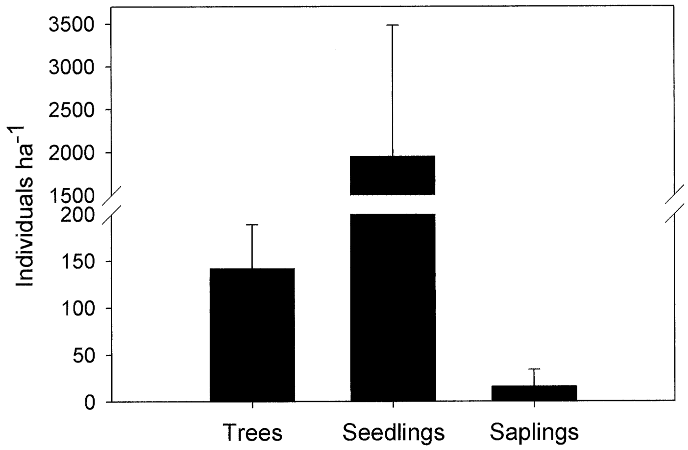

Figure 4. Density of various size classes (described in case study 2) of pines in Abaco National Park. Whiskers indicate standard errors.

natural needle fall. Fire temperatures were estimated at three heights (0 m, 1 m, and 2 m above the soil surface) at two locations within each plot. The entire experimental area was burned by prescription in June 2004.

An initial survival survey was conducted 2 wk after burning. In October 2004, all seedlings were monitored for survival, and growth variables were remeasured. Individuals from four age/height classes were evaluated. These classes included: 1 = small grass stage (<0.2 m); 2 = grass stage (<1 m); 3 = bolting stage (in active height growth, <2m); and 4 = sapling (>2 m tall with root collar diameter $<$ 15 cm). Data were analyzed using analysis of covariance procedures, except for categorical data (residence time and mortality), which were analyzed using the chi-square test for independence. The critical value of α for all tests was 0.05. Initial growth measurements were used as covariates.

Seedling mortality in all classes 2 wk after the prescribed fire was greatest in the litter-addition treatment (11% *vs.* 2% control and 0.5% low litter). Four months later, mortality was significantly higher in the litter-addition treatment relative to the control and removal treatments (30% *vs.* 4% and 1%, respectively). Postfire mortality was highest for seedlings in the small grass stage for all treatments (21% *vs.* 7% grass stage and 3% bolting stage), but particularly so in the litter-addition treatment (48% *vs.* 10% in control and 4% in removal). Only the litter-addition treatment had a significant effect on bolting-stage seedling mortality. Sapling mortality was not affected by prescribed fire for any litter level. Finally, seedlings were significantly taller in the litter-removal treatment, suggesting that growing-season fires may negatively impact seedling growth, likely due to scorching of photosynthetically active leaves in these fires. In the context of our pine-regeneration conceptual models, we suggest that these data support the concept that small gaps are adequate for the regeneration of pines with seedlings adapted to withstand low-intensity fires. Moreover, when seedlings achieved sufficient size in the grass stage, seedling survival was still relatively high, regardless of loading.

CASE STUDY, FIRE-SENSITIVE SEEDLING STRATEGY: BAHAMIAN PINEYARDS

In an effort to understand and inform fire management in Abaco National Park, a study of pine mortality after prescribed fire was undertaken in 2004. The area is a relatively dense, naturally regenerated, even-aged stand. Nearly the entire island had been clear-cut in the mid-twentieth century, with ~4 trees ha^{-1} left as seed sources. In October–November 2004, plots were sampled within three ~20 ha blocks demarcated by old logging roads. These were designated as the treatment blocks to be ignited by prescription. Within each plot, 20 randomly located points and nested circular plots were established to sample vegetation (trees and saplings: 5 m radius; seedlings: 2 m radius). Fuel loads indicated that the area appeared to have burned approximately 3 y prior. Pines were classified as follows: trees = 10 cm or greater diameter at 1.2 m height, saplings = >1 m tall, <10 cm diameter at 1.2 m, seedlings = <1 m tall. For the study, 143 trees, 41 saplings, and 31 seedlings were tagged prior to the fire. The area studied had a continuous canopy, with a high density of trees, abundant seedlings, and few saplings (Fig. 4). On 30 and 31 October 2004, the blocks were burned. Wind speed during all fires was low, never exceeding 2.6 m s^{-1}, and both relative humidity and fuel moisture were high. Even though a variety of ignition techniques was employed, fire behavior was very moderate due to the moist conditions. The fires crept slowly and with small flame lengths of ~0.5 m. All trees and all saplings survived with only sporadic crown scorching. Even with the low-intensity fire, none of the tagged seedlings survived. A subsequent recensus in October 2005 found zero tree mortality. The low sapling recruitment (Fig. 2) indicates that for at least the last decade or so, fires have been burning frequently enough in this are to effectively eliminate seedling regeneration. Our observations of 100% seedling mortality in relatively low-intensity fires, combined with our observations of single-age stands of *P. caribaea* var. *bahamensis* following clear-cutting in the 1940s and 1950s, and single-age stands in large-scale hurricane blow-downs, lend support to our concept that these species have adaptations and life-history traits that suit them to occupy sites where large gaps are routinely created by major disturbances, and that small-gap dynamics may not be adequate to protect seedlings from fire mortality.

CONCLUSION

We have outlined two pine-regeneration strategies and their interactions with differences in fire regime and different scales of overstory disturbance. Interactions between frequency and scale of canopy disturbance and the subsequent loading of fine fuels appear to have been a selective force driving seedling adaptations. We suggest that this could be a result of differences in frequency of wind-driven overstory disturbance in the region. Data from the US National Hurricane Center indicate that over the period 1850–2006, 48 major storms (Saffir-Simpson Hurricane Scale category 3 or greater), including seven category 5 storms, passed within 120 km of the Abaco study area, where pine seedlings are fire sensitive and require large gaps to reach fire-tolerant size, whereas only two category 3 storms impacted the Georgia study site, where pines have fire-tolerant seedlings. In western Cuba, where the other pine species with fire-tolerant seedlings occurs, 22 major storms passed, but only two were category 4, and none was a category 5 storm. In most of the Caribbean, especially in areas prone to large-scale overstory disturbances and less frequent fires, pines with fire-sensitive seedlings are dominant. These pines grow rapidly and produce seeds annually that are capable of long-range dispersal, which ensures timely colonization of canopy openings where fine fuel loads are diminished. We have observed this phenomenon in the posthurricane environment on Great Abaco, where hurricane disturbances are frequent. After any initial poststorm fires, large gaps remain fire free until the canopy develops sufficient needle cast to carry fire. By this time, regenerating pines are large enough to survive fires that suppress competing fire-sensitive broadleaved species. In these areas, there is a minimum gap size in order for pine seedlings to establish, but the maximum gap size would only be limited by seed dispersal. The alternate fire-tolerant seedling strategy relies on banking of fire-resistant advanced regeneration. Such a strategy requires a narrower range of gap sizes to maintain frequent fire and suppress competition from fire-sensitive species. These areas also experience shorter fire return intervals that are more continuous in time and space. In these ecosystems, canopy openings are more frequently created by individual tree mortality or small groups (e.g., 4 adults) (31). When large disturbances do occur, some overstory trees (10–20%) are usually retained and provide some continuity of fuels (31). The practical implications of our observations are that land managers must be aware of the regeneration strategy that is operative in their particular forest in order to effectively manage the pine species with fire. For example, forestry practices in *P. caribaea* stands could be more flexible, with gap sizes determined by desired management goals, and less constrained by the need to prevent the establishment of broadleaved competitors. In *P. tropicalis* or *P. palustris* stands, care must be taken not to disrupt the continuity of fuels through canopy removal, or a shift in vegetation will likely occur.

The presence of other fine fuel sources such as fire-tolerant native or exotic graminoids capable of forming swards presents another pathway to an alternative ecological stable state where pines with fire-sensitive seedlings could be converted to grasslands. Examples of native grasslands replacing stands of *P. caribaea* var. *hondurensis* stands in the Honduran coastal plain, where fires occurred annually, provide evidence of this pathway (J. O'Brien pers. observ.). Invasions by exotic grasses such as *Imperata cylindrical* (L.) Raeuschel or *Neyraudia renaudiana* (Kunth) Keng ex A.S. Hitchc. have the potential to replace pines and associated biodiversity in the region. These species also have the potential to increase adult pine mortality due to increased fire intensity (32).

Understanding the nexus among canopy structure, fuel distribution, fire behavior, and pine regeneration is critical for forest mangers, regardless of management objectives. Although clearly a critical element of these ecosystems, use of fire for forest management has been questioned and criticized by parties concerned with whether or not human fire ignition is "natural" (33). We view "natural" as a value-laden and diffuse term, making it difficult to objectively apply it to the success or failure of management actions. Furthermore, there is beginning to be much discussion on the utility of using historical targets for management objectives (34), in the case of the Caribbean Basin, prehuman settlement. There are two obvious criticisms of using this historical target as an objective: The composition of the vegetation of the region thousands of years ago is poorly understood, and the climate regime that existed prior to human settlement no longer exists. Humans (ancient and contemporary) have clearly had a tremendous impact on the present environment, so much so that some argue that Earth has entered a new geological epoch, the Anthropocene (35). Rather than argue about what is or is not natural, we believe our approach allows the identification of a concrete target, in this case, promoting pine regeneration and persistence, and gives managers and researchers tools to assess whether their activities are moving the resource toward those targets.

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