Posthurricane Seedling Structure in a Multi-aged Tropical Dry Forest: Implications for Community Succession

Mary E. Carrington[1,4], **Michael S. Ross**[2,3], and **Alia F. Basit**[1]

[1] Division of Chemistry and Biological Sciences, Governors State University, University Park, Illinois, 60484, U.S.A.

[2] Southeast Environmental Research Center, Florida International University, University Park, Miami, Florida, 33199, U.S.A.

[3] Department of Earth and Environment, Florida International University, University Park, Miami, Florida, 33199, U.S.A.

ABSTRACT

Hurricane-caused tree mortality in tropical dry forests occurs predominantly in early successional species. Consequently, hurricanes may accelerate succession in these forests. Forest regeneration, however, must be measured over an extended posthurricane time period to demonstrate this pattern. In this study, we recorded tree seedlings in 19 Florida Keys forests during May–August 1995, 3 years after Hurricane Andrew. For these forests—spanning a chronosequence from 14 to over 100 years since the most recent clearing—we used weighted averaging regression on relative abundances of pre-hurricane trees to calculate a successional age optimum for each species; and used weighted averaging calibration to calculate inferred successional ages for stands based on pre-hurricane trees and on posthurricane seedlings. To test the hypothesis that successional stage of seedlings exceeded successional stage of pre-hurricane trees, we compared inferred stand ages based on posthurricane seedlings with those based on pre-hurricane trees. Across the study area, inferred stand ages based on posthurricane seedlings were greater than those based on pre-hurricane trees ($P < 0.005$); however, more seedlings in the youngest stands were early successional than in older stands. Of 29 species present both as pre-hurricane trees and posthurricane seedlings, 23 had animal-dispersed seeds. These results provide evidence that: (1) hurricanes do not 'reset' succession, and may accelerate succession; and (2) a strong legacy of stand successional age influences seedling assemblages in these forests.

Key words: Caribbean forests; chronosequence; disturbance; Florida.

ALTHOUGH SHORT-TERM EFFECTS OF HURRICANES RESEMBLE THOSE OF OTHER NATURAL disturbances (*i.e.*, changed community or ecosystem structure, altered resource availability, and physical environment; Pickett & White 1985), longer term effects on ecological succession may differ from those of other types of disturbance. While most natural disturbances reverse successional trajectories, studies suggest that hurricanes in some instances reinforce or accelerate pre-disturbance trajectories (Fu *et al.* 1996, Ross *et al.* 2001, Zhao *et al.* 2006). Hurricane impacts on succession are influenced by: (1) pattern and extent of tree mortality and canopy gap formation; (2) primary mode of canopy re-establishment (*i.e.*, resprouting of surviving trees, new seedling establishment or release of suppressed stems; Everham & Brokaw 1996, Zhao *et al.* 2006); and (3) species-specific syndromes of response to disturbance (*sensu* Bellingham *et al.* 1995). In addition, successional legacies from pre-hurricane land use history may affect posthurricane vegetation dynamics (Zimmerman *et al.* 1995, Thompson *et al.* 2002, Flynn *et al.* 2010, Heartsill Scalley *et al.* 2010).

Dry broadleaf forests comprising species of tropical origin occur on well-drained, limestone-based sites in southern peninsular Florida and the Florida Keys (Snyder *et al.* 1990). Like dry tropical forests at lower latitudes, Florida dry broadleaf forests are threatened with extirpation due to several causes (*e.g.*, land development, sea level rise). Dominated by West Indian tree species near the northern extent of their ranges (Tomlinson 1986), these forests have experienced major hurricanes at about 27-yr intervals, on average (Ross *et al.* 2001).

The last major hurricane to impact dry broadleaf forests in the Florida Keys was Hurricane Andrew in 1992. Studies of forests affected by Hurricane Andrew on the Miami rock ridge at the southern tip of the mainland showed that: (1) mortality was higher for trees with larger diameter stems (Slater *et al.* 1995); (2) up to 30 mo after the event, forest regeneration included pioneer native species, later successional native tree species and non-native species (Horvitz *et al.* 1998, Kwit *et al.* 2000); and (3) non-native vine species inhibited further regeneration of native species (Horvitz *et al.* 1998). A study conducted in Key Largo across a chronosequence of 23 forests ranging from 14 to 100 yr since clearing (the only study of which we are aware of hurricane effects on dry broadleaf forests in the Florida Keys) found that mortality of early successional trees following Hurricane Andrew was higher than their late successional counterparts (Ross *et al.* 2001). Although this pattern of mortality suggests that the hurricane may have accelerated succession in these forests, data on forest regeneration patterns and species composition changes over longer time periods is needed to demonstrate accelerated succession.

The goals of the present study, conducted in 19 of the original 23 stands (Ross *et al.* 2001), were to characterize seedling

recruitment 3 yr after Hurricane Andrew and compare seedling species assemblages with pre-hurricane tree species assemblages reported in the earlier study. We expected most posthurricane recruitment to come from seed rain from (local surviving trees and dispersed in from other hurricane-damaged stands) and release of suppressed seedlings. Because surviving trees were predominately late successional species, we hypothesized that the successional stage of posthurricane seedling assemblages would exceed that of pre-hurricane tree assemblages. We also expected patterns of seedling recruitment to vary with the successional status of stands, due to local effects on seed rain, seedling microsites, and habitat for seed dispersers. We tested our hypotheses by: (1) comparing the successional status of posthurricane seedlings and pre-hurricane trees; and (2) examining variation in the successional status of seedlings across the chronosequence of Key Largo stands.

STUDY AREA.—We conducted the study in 19 dry broadleaf forests in Crocodile Lakes National Wildlife Refuge and Key Largo Hammocks State Botanical Area on Key Largo. The upland forests in this region occur on thin organic soil overlaying fossil coral reef limestone, at elevations not normally subject to flooding by sea water except during storm tides associated with some tropical storms or hurricanes. Canopy height is low (8–13 m; Hilsenbeck 1976, Ross et al. 1992), but relatively high basal area (15–40 m²/ha; Ross et al. 2003) results in a closed canopy with a sparse to absent herbaceous layer.

Even though these forests are located north of the Tropic of Cancer, their maritime location results in a tropical climate (mean annual temperature = 25.1°C; mean annual precipitation = 1178 mm; Ross et al. 2001), and classification within the Tropical Dry Forest Life Zone (Holdridge 1967). Tree species are primarily West Indian in origin, and approximately two-thirds have animal-dispersed fruits. Primary animal seed dispersers include white-crowned pigeons (Patagioenas leucocephala), Neotropical migrant bird species, and raccoons (Procyon lotor).

Ross et al. (2001) described a tree species replacement sequence for Florida Keys dry broadleaf forests (including the 19 forests in this study) varying from 14 to 100 yr or more since most recent clearing. Deciduous species dominated forests for 40 to 50 yr following clearing. Although these early successional species remained in older forests, they gradually were replaced by evergreen species that were not present in younger forests.

These forests are subject to several kinds of natural and anthropogenic disturbance. Although hurricanes are the most frequent natural disturbances, fires also occur infrequently. Unlike the relatively low rates of stem mortality from hurricanes, fires may kill most vegetation, while incinerating the shallow soil layer (Olmsted et al. 1980, Craighead 1981). Anthropogenic disturbance includes forest clearing for agriculture during the first half of the 20th century. Subsequently, land clearing has occurred in anticipation of residential development, and for oil exploration and military uses (Ross et al. 2001).

In August 1992, Hurricane Andrew made landfall on the southeast coast of Florida, with the southern eye wall passing over the northern portion of our Key Largo study area. In 23 forests visited in 1994, tree stem mortality from the hurricane averaged 7.5 percent of pre-hurricane basal area and 4.9 percent of pre-hurricane density. Stem mortality was higher for large, early successional trees than for smaller trees associated with late successional stages (Ross et al. 2001).

METHODS

We collected data on tree species composition, abundance, and hurricane-caused mortality during May and June 1994 (Ross et al. 2001). For this study, we used pre-hurricane tree data from 19 of the original 23 stands, along with successional ages of stands identified as time since last clearing and determined from historical aerial photos. Time since clearing ranged from 14 to at least 100 yr for stands with well-developed canopies dating back through the earliest (1928) photographs; these old stands were assigned a successional age of 100 yr (Ross et al. 2001). We recorded tree species and dbh (diameter at breast height, 1.45 m height) for all live and hurricane-killed trees rooted within 1 m (1.0–9.9 cm dbh) and 2 m (10.0–24.9 cm dbh) of the center line of a 60–100 m transect in each site. In addition, we recorded trees ≥ 25 cm dbh within 5 m and 10 m of the center line for live and hurricane-killed trees, respectively. For this study, we summarized pre-hurricane tree species as basal area of live and hurricane-killed trees combined.

In May–August 1995, we quantified seedling species abundances along the same transects used for sampling trees. We counted seedlings rooted within 0.5 m of the center line in each transect within two size classes: small (<10 cm height) and large (≥10 cm height and <1 cm dbh). Although many plants no longer had cotyledons and thus were not true seedlings, here we refer to all potential new recruits into the forest subcanopy or canopy as 'seedlings'. We summarized seedling data as seedling density in small and large categories. Nomenclature for species follows Wunderlin and Hansen (2003).

DATA ANALYSIS.—To determine if extent of hurricane damage varied with stand age or stand location, we conducted Pearson correlation coefficients for percent tree mortality versus stand age, and percent tree mortality versus distance north (distance in km from the south end of the study area; the further north, the closer to the hurricane eye wall). Percent tree mortality values were arcsine square-root transformed before analysis.

We used weighted averaging (WA) regression and calibration (C2 v. 1.7.3; Juggins 2007) of pre-hurricane tree species relative abundances (species occurring in at least three stands) in the 19 stands of known age since last disturbance (i.e., successional age) to characterize a species–successional age relationship. Weighted averaging regression was used to calculate species successional age optima through abundance-weighted averaging in the calibration dataset with known successional ages (Ross et al. 2001). As in Ross et al. (2001), we calculated each species' successional age optimum ($\widehat{SAO}_k$) as

$$\widehat{SAO}_k = \frac{\sum\limits_{i=1}^{n} y_{ik} x_i}{\sum\limits_{i=1}^{n} y_{ik}}$$

and its tolerance (weighted standard deviation; $\hat{t}_k$) as

$$\hat{t}_k = \left[\frac{\sum\limits_{i=1}^{n} y_{ik} (x_i - \widehat{SAO}_k)^2}{\sum\limits_{i=1}^{n} y_{ik}} \right]^{1/2},$$

where x_i is time since disturbance in stand i and y_{ik} is relative abundance of species k in stand i ($i = 1, \ldots\ n$ stands and $k = 1, \ldots\ m$ species).

We used classical deshrinking during WA calibration to construct WA models for inferring stand successional ages based on both pre-hurricane tree and posthurricane seedling assemblages. During WA calibration, the successional age of each stand in the calibration dataset was inferred from abundance-weighted species successional age optima, and the regression of these values on observed successional ages was used to 'deshrink' successional age estimates for both calibration and test (i.e., posthurricane seedlings from 19 stands) datasets (ter Braak 1988). Deshrinking corrects for a contraction in the range of estimated values (i.e., overestimates at the low end of the range and underestimates at the high end of the range) that is a result of double-averaging during WA regression and calibration (i.e., first weighted averaging to obtain species successional age optima, and second weighted averaging to infer stand successional ages; ter Braak & van Damm 1989).

To compare successional status of all posthurricane recruiting seedlings with pre-hurricane trees across all stands, we used a WA model without downweighting by species tolerances (Ross et al. 2001) to infer stand successional ages based on both pre-hurricane trees and posthurricane seedlings. Each seedling species occurred in at least three stands and was present in the tree layer of the study area. We calculated the two inferred stand ages (ISA) for each site as

$$ISA_i = \frac{\sum\limits_{k=1}^{m} y_{ik} \widehat{SAO}_k / \hat{t}_k^2}{\sum\limits_{k=1}^{m} y_{ik}},$$

where y_{ik} is relative abundance of either pre-hurricane tree species i or posthurricane seedling species i in stand k. We calculated the difference between ISA based on posthurricane seedlings and ISA based on pre-hurricane trees for each stand; the mean and 95% confidence interval of differences; and conducted a paired t-test to determine if the mean difference in ISA was >0.

We examined trends in seedling establishment across the stand chronosequence by first conducting a Pearson correlation test for total seedling density versus stand age. Total seedling density values were log-transformed before analysis. Second, we examined the trend in ISAs based on posthurricane seedlings ($ISA_{seedlings}$) versus pre-hurricane trees (ISA_{trees}) across the chronosequence by conducting a linear regression of $ISA_{seedlings}$ on ISA_{trees}, and used a t-test to compare the slope of the regression line with a 1:1 relationship (i.e., slope = 1.0). To determine if either total seedling density or seedling successional stage varied with extent of hurricane damage, we calculated Pearson correlation coefficients for total seedling density versus percent tree mortality, and $ISA_{seedlings}$ versus percent tree mortality.

To identify any difference in seedling survival or timing of establishment associated with successional status, we again used a WA model to infer stand successional ages based on small and large posthurricane seedlings. We calculated the difference between ISA based on small seedlings and ISA based on large seedlings for each stand; and the mean and 95% confidence interval of differences. To detect evidence of seed dispersal into stands from external sources, we calculated proportion of species present only as seedlings for each stand.

RESULTS

We calculated successional age optima for this study from data collected in 1994 for a total of 3439 pre-hurricane trees of 29 species. Three species—*Guettarda scabra, Guettarda elliptica* and *Lysiloma latisiliquum*—had highest abundances as trees early in succession; i.e., in stands less than 50 yr old. Seventeen species had highest abundances as trees in mid-successional stands between 50 and 75 yr old, and ten species were most abundant as trees in late successional stands over 75 yr old. Seeds of 23 of the 29 species were animal-dispersed. Of the six species with other seed dispersal mechanisms, *Lysiloma latisiliquum* and *Gymnanthes lucida* were gravity-dispersed and were most abundant in early and late successional stands, respectively. *Colubrina elliptica* had dispersal through explosive dehiscence and was abundant in late successional stands. The remaining three species had wind-dispersed seeds and were most abundant in mid-successional stands (Table 1).

In 1995, we recorded a total of 19,348 posthurricane seedlings (comprising the same 29 species as pre-hurricane trees) across the chronosequence of 19 stands, with seedlings of each species occurring in at least three stands. Hurricane-caused percent tree mortality among stands tended to increase northward ($r = 0.33$, $t_{17} = 1.44$, $P = 0.084$ for percent mortality vs. distance north), but was not correlated with stand age ($r = 0.26$, $t_{17} = 1.11$, $P = 0.141$ for percent mortality vs. stand age). Neither total seedling density nor ISA based on seedlings was correlated with percent tree mortality ($r = 0.11$, $t_{17} = 0.46$, $P > 0.1$ for seedling density vs. percent mortality; $r = 0.28$, $t_{17} = 1.20$, $P > 0.1$ for $ISA_{seedlings}$ vs. percent mortality). Total seedling density, however, tended to be higher in older stands ($r = 0.32$, $t_{17} = 1.39$, $P = 0.091$ for seedling density vs. stand age).

ISAs based on assemblages of all posthurricane seedlings were greater than ISAs based on pre-hurricane trees for 18 of 19 stands (Fig. 1; mean difference $\pm$ 95% CI = 24.3 $\pm$ 9.7 yr; $t_{18} = 5.27$, $P < 0.005$). Differences between ISAs based on

TABLE 1. *Successional age optima and tolerances, and seed dispersal mode for 29 Key Largo tree species recorded in 19 Key Largo forests. Species with successional age optima <50 yr, ≥50 yr and ≤75 yr, and >75 yr are defined as early successional, mid-successional, and late successional, respectively. Sample size indicates number of stands in which trees >1 cm DBH of a species occurred.*

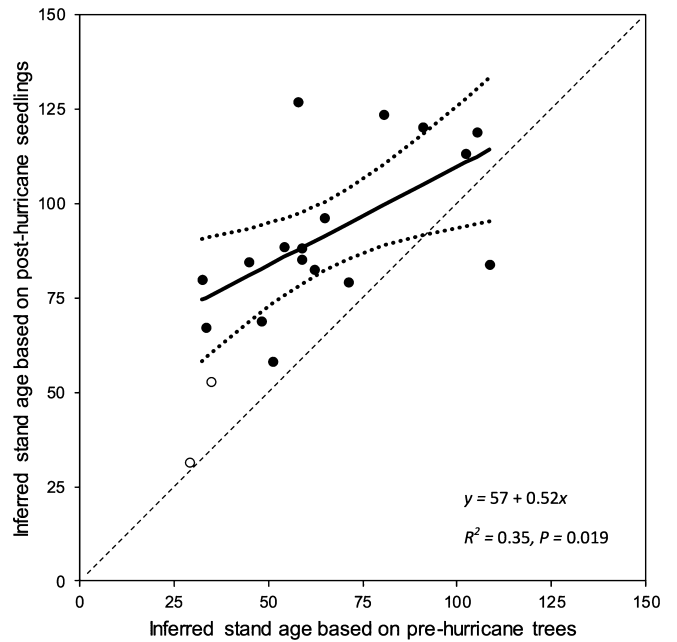| Species	N	Optimum (yr)	Tolerance (yr)	Seed dispersal mode
Guettarda scabra	7	32.6	28.3	Animal
Guettarda elliptica	12	41.0	41.9	Animal
Lysiloma latisiliquum	9	48.0	22.9	Gravity
Bourreria succulenta	7	52.0	36.9	Animal
Ficus citrifolia	10	58.2	26.8	Animal
Zanthoxylum fagara	8	59.6	31.7	Animal
Pithecellobium unguis-cati	8	59.7	14.6	Animal
Sideroxylon salicifolium	17	60.0	22.9	Animal
Metopium toxiferum	19	61.3	19.1	Animal
Bursera simaruba	18	61.7	30.2	Animal
Swietenia mahagoni	13	62.4	17.1	Wind
Piscidia piscipula	17	63.4	21.4	Wind
Eugenia axillaris	19	65.3	29.7	Animal
Guapira discolor	5	66.8	29.1	Animal
Reynosia septentrionalis	4	67.0	6.9	Animal
Canella winterana	5	67.1	20.5	Animal
Eugenia foetida	7	69.0	10.3	Animal
Exostema caribaeum	3	73.5	14.2	Wind
Coccoloba diversifolia	19	74.4	25.9	Animal
Eugenia confusa	3	78.6	25.0	Animal
Gymnanthes lucida	17	83.9	25.4	Gravity
Krugiodendron ferreum	13	87.4	17.9	Animal
Ocotea coriacea	6	88.1	31.4	Animal
Exothea paniculata	3	91.8	27.6	Animal
Colubrina elliptica	4	92.3	25.7	Explosive dehiscence
Drypetes diversifolia	7	96.4	14.6	Animal
Amyris elemifera	9	98.2	9.6	Animal
Calyptranthes pallens	8	98.3	11.1	Animal
Simarouba glauca	4	99.8	5.0	Animal

FIGURE 1. Inferred stand ages (ISAs) based on pre-hurricane tree assemblages and posthurricane seedling assemblages in 19 Key Largo forests. The diagonal dashed line represents points for which ISAs based on pre-hurricane trees and posthurricane seedlings are equal. Solid and dashed lines represent least squares regression and 95% confidence limits for relationship between seedling- and tree-based ISAs, excluding 14-yr-old stands. Unfilled points are 14-yr-old stands.

the abundance-weighted mean successional age optimum of the eight most abundant seedling species in stands ≥40 yr old was 90.0 yr, it was only 40.5 yr in 14-yr-old stands. When small and large seedlings were analyzed separately, ISAs based on assemblages of large seedlings were less than ISAs based on small seedlings for 14 of 19 stands (Fig. 3; mean difference ± 95% CI = 12.5 ± 6.1 yr; $t_{18} = 2.90$, $P < 0.005$), indicating that large seedlings were earlier successional species than small seedlings.

The late successional seedling assemblages across most of the chronosequence likely resulted from one of (or some combination of) two mechanisms: (1) preferential dispersal of late successional species into stands; or (2) more successful seedling establishment of late successional species. To roughly quantify the prevalence of dispersal of species into stands (and acknowledging that results are scale-dependent, based on width of transects sampled for seedlings and trees), we calculated proportions of species present only as seedlings in stands. Across the chronosequence, the proportion of species present only as seedlings was 0.24 ± 0.02 (mean ± S.E., $N = 19$), with no discernable trend with stand age.

DISCUSSION

Approximately 3 yr after a major hurricane, seedling assemblages across the chronosequence of stands were primarily late successional. In conjunction with disproportionately high hurricane-caused mortality of early successional trees reported from the same sites (Ross *et al.* 2001), these results provide further evi-
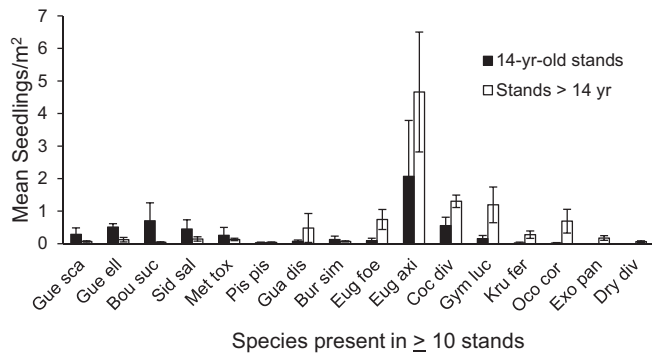
posthurricane seedlings and ISAs based on pre-hurricane trees decreased with increasing stand age, with the exception of the youngest, 14-yr-old stands. A linear regression of ISA_seedlings on ISA_trees yielded a best-fit line with slope not different from 1.0 ($t_{17} = -1.62$, $P = 0.123$). When the 14-yr-old stands were excluded, however, the slope of the best-fit line was different from 1.0 ($t_{17} = -2.59$, $P = 0.019$; Fig. 1). Instead of having the largest ISA differences (as would be predicted from the regression line), the two 14-yr-old stands had among the smallest differences in ISAs between seedlings and trees, due to higher densities of early successional seedlings (Figs. 1 and 2). Although

FIGURE 2. Mean seedling densities in 14-yr-old stands (N = 2) and stands >14 yr old (N = 17), of species present in at least 10 of 19 Key Largo forests. Species are in order of increasing successional age optima from left to right; error bars represent standard errors. Species codes consist of the first three letters of the genus followed by the first three letters of the specific epithet.
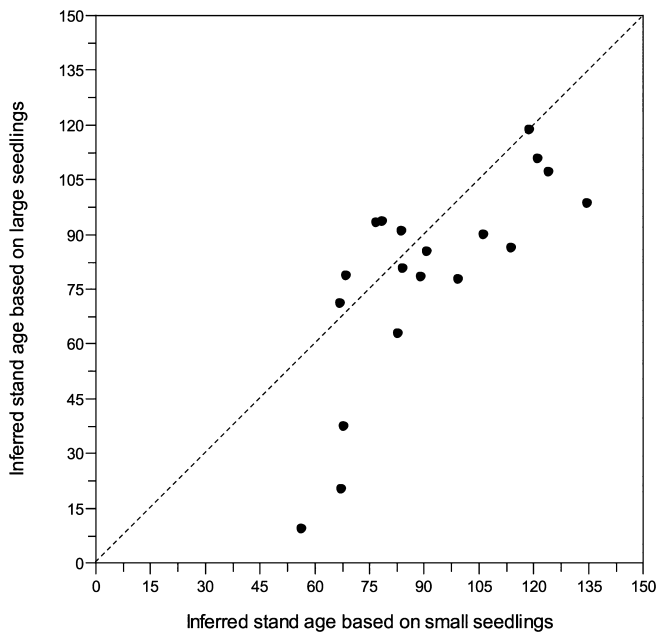

FIGURE 3. Inferred stand ages (ISAs) based on small (<10 cm height) and large (>10 cm height and <1 cm dbh) seedling assemblages in 19 Key Largo forests. The dashed line represents points for which ISAs based on small and large seedlings are equal.

dence that succession is accelerated following a hurricane. With predominantly animal-dispersed fruits, these late successional species either are preferentially dispersed into stands, or they are more readily established in stands than earlier successional species. Preferential seed dispersal of late successional species into stands likely plays a role in accelerated succession, as most seedlings were late successional and a relatively high, constant proportion of species was present only as seedlings in stands across the chronosequence.

Additional results from this study, however, suggest that two qualifications be placed on the interpretation of accelerated suc-

cession. First, seedling assemblages in the youngest stands in the chronosequence were largely early successional, in contrast to the remainder of the chronosequence. Due perhaps to fundamental differences from older stands in seed dispersal dynamics or seedling establishment conditions, stands younger than 40 yr old may represent an initial stand initiation/canopy closure stage in succession, followed by an accelerated successional trajectory in stands ≥40 yr old. The 14-yr-old stands, generally with more open canopy, may function as habitat and food sources for different seed dispersers than ≥40-yr-old stands, with more closed canopy. As a result, seed dispersers visiting young stands may visit older stands relatively rarely, and *vice versa*.

The second qualification to accelerated succession is our finding that large seedlings were earlier successional than small seedlings. Although entire seedling assemblages of stands were late successional, they also were predominantly small seedlings. Higher survival rates to large seedling size by early successional species would slow down any forward successional trajectory.

The relatively large size of early successional seedlings may result from: (1) higher survival rates; (2) higher growth rates; or (3) earlier establishment of early successional species compared to late successional species. Earlier successional species might survive at higher rates or grow faster in response to canopy gaps produced during the hurricane. Because hurricane-caused mortality was disproportionately high among earlier successional tree species (Ross *et al.* 2001), we expected that canopy gaps would be more prevalent in younger stands. Contrary to our expectation, however, percent tree mortality did not vary with stand age, but instead increased northward (*i.e.*, closer to the hurricane eye wall). In addition, ISA based on seedlings did not decrease with increasing percent tree mortality, as would be expected if early successional seedlings established at higher rates in canopy gaps.

It is possible that seedling establishment in these forests is not light-limited, and thus is not driven by canopy gap formation in the same way as documented in other forests (*e.g.,* Brokaw 1985, Whitmore 1989). Recent research conducted in the same sites that we studied found no difference in light availability (inferred from canopy density) with canopy gap size, and recorded later successional species of saplings in canopy gaps compared to intact forest (Diamond 2014). Results from the study suggest that due to the short stature of these forests, treefalls fail to generate canopy gaps large enough to substantially increase light availability. Alternatively, seedling establishment may be limited by another resource such as soil moisture as shown in other tropical dry forests (Ray & Brown 1995, Gerhardt 1996).

We were unable to compare our posthurricane seedling assemblages with those from non-hurricane impacted forests, and so cannot definitively identify our posthurricane seedlings as advance regeneration (*i.e.*, from seeds germinating before the hurricane) or as originating from seed rain or dispersal after the hurricane. Regardless of seedling origin or timing of establishment, however, results of this study show that the hurricane did not reverse or 'reset' succession *via* seedling establishment. Rather, results demonstrated a strong legacy of stand successional age on seedling assemblages.

We propose the following successional model for testing in future studies in which aboveground canopy structure influences seed dispersal and is related to belowground competition for soil water. Early successional stands (somewhat less than 40 yr old) have a relatively open forest canopy, and function as habitat and food sources for a suite of seed dispersers that frequent shrubby, relatively short stature sites with open canopy. These seed dispersers continue to disperse early successional species within and among the stands. Under conditions of high light and soil moisture levels, early successional species continue to recruit into the canopy. Between 14 and 40 yr of age, growth of early successional trees causes the forest canopy to close. Stands then begin to function as habitat and food sources for a suite of seed dispersers that frequent closed canopy forests. These seed dispersers transport seeds of later successional species from older forests into the relatively young stands. Seedling recruitment into large size classes and eventually into the subcanopy and canopy, however, is regulated by soil moisture availability, which declines due to more intense belowground competition. As a result of periodic hurricane damage to earlier successional trees, canopy gaps are formed that allow recruitment into the canopy primarily by later successional species that are better competitors for soil water. Recruitment by earlier successional species into the canopy in stands ≥40 yrs old is extremely rare, because canopy gaps rarely are large enough to result in increased light availability needed for these shade-intolerant species, or the earlier successional species are poor competitors for water.

ACKNOWLEDGMENTS

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