

INTERACTIONS OF LARGE-SCALE DISTURBANCES: PRIOR FIRE REGIMES AND HURRICANE MORTALITY OF SAVANNA PINES

WILLIAM J. PLATT,^{1,5} BRIAN BECKAGE,^{1,3} ROBERT F. DOREN,² AND HAROLD H. SLATER^{1,4}

¹Department of Biological Sciences, Louisiana State University, Baton Rouge, Louisiana 70803 USA

²Southeast Environmental Research Program, Florida International University, Miami, Florida 33199 USA

Abstract. Differences in initial large-scale disturbances might change effects of subsequent large-scale disturbances. We explored possible effects of prior fire regimes on subsequent hurricane-related mortality of south Florida slash pine (*Pinus elliottii* var. *densa*) in remnant Everglades pine savannas that were unburned, burned during the wet (lightning fire) season, or burned during the dry (anthropogenic fire) season in the decade before Hurricane Andrew (1992). We measured direct mortality during Andrew (snapped trees) and extended mortality over the subsequent 24–30 mo (mainly insect attacks on damaged trees). We used Bayesian model averaging to obtain probabilities of different models of survival based on fire regime and site characteristics (remnant area, distance to the Atlantic Ocean, depth to water table in the dry season, sustained wind speeds, tree sizes). Most likely models for direct and extended mortality included large negative effects of tree size and dry-season fire regime, and positive effects of stand area (direct mortality) and wet-season fire regime (extended mortality). Depth to water table and distance to the ocean had less certain effects. Our results, not predicted from fires or hurricanes alone, suggest that anthropogenic changes to dry-season fires strongly influence the effects of subsequent hurricanes on the mortality of pines in subtropical savannas.

Key words: direct and extended mortality; dry-season fires; fire regimes; hurricanes; multiple disturbances; pine savannas; *Pinus elliottii* var. *densa*; south Florida slash pine; wet-season fires.

INTRODUCTION

Large-scale disturbances influence most ecological systems (Turner and Dale 1998). If such disturbances are juxtaposed, effects may not be predictable based on each disturbance in isolation (Paine et al. 1998). A prior disturbance might change effects of later disturbances, with the nature of interactive effects dependent on the order of the disturbances (Robertson and Platt 2001). Moreover, alterations of initial disturbances by humans might exacerbate the effects of a subsequent natural disturbance (Paine et al. 1998).

Fires and hurricanes are large-scale disturbances that frequently affect trees in coastal savannas of the southeastern United States. Lightning-initiated fires historically occurred in pine savannas more than once a decade (Platt 1999). Humans have shifted fires outside the lightning season (Platt 1999), but neither anthropogenic nor natural fires cause substantial pine mortality (Taylor 1981). Hurricanes affect most southeastern coastal regions every 1–2 decades (Batista and Platt 1997). In old-growth stands, hurricanes kill 10–20% of overstory pines and elevate mortality levels during

subsequent years (Platt and Rathbun 1993, Platt et al. 2000).

In this study, we examined effects of fire–hurricane interactions on pines. Interactions have been proposed on the basis that post-hurricane fuels increase the likelihood and intensity of fires and, thus, the mortality of trees (e.g., Myers and Van Lear 1998). We explored a different possibility: differences in prior fire regimes might influence mortality of pines during and after hurricanes. We examined mortality of south Florida slash pine (*Pinus elliottii* Engelm. var. *densa* Little & Dor.) directly caused by Hurricane Andrew in 1992 and over the subsequent 24–30 mo in sites that differed in the seasonal timing of fires during the prior decade.

METHODS

Study sites and data collection

Historically, subtropical pine savannas occurred on consolidated oolitic limestone outcroppings 1–4 m above mean sea level (a.s.l.) along the Atlantic Coastal Ridge in southeast Florida, USA (Hoffmeister et al. 1967). The overstory was south Florida slash pine; the ground cover was a diverse mixture of grasses, forbs, and shrubs (Schmitz et al., *in press*). Of the original 75 000 ha, <10% remains (Snyder et al. 1990). Some Metro-Dade County remnants are 50–100 ha, but most are small (2–5 ha). All remaining large remnants are on outcroppings of several hundreds to thousands of hectares separated by almost treeless transverse glades in Everglades National Park (Olmsted et al. 1983). In

Manuscript received 11 May 2001; revised 20 November 2001; accepted 28 November 2001.

³ Present address: Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996-1610 USA.

⁴ Present address: 1034 Gibraltar Road, Key Largo, Florida 33037 USA.

⁵ E-mail: btplat@unix1.sncc.lsu.edu

TABLE 1. Characteristics of savanna pine sites used in study.

Site	Site number on map [†]	Area [‡] (ha)	No. plots	Density (no. pine stems/ha)	Mean pine stem diameter (cm)	Fire season prior to Andrew [§]	Distance from Atlantic Ocean (km)	Estimated sustained 1-min wind speeds (m/s)	Dry-season depth to groundwater (m)
Biscayne Drive	1	5	5	519	17.0	unburned	11.3	55–60	2.7
Coast Guard Station	2	110	5	823	9.3	unburned	7.7	60–65	2.7
Florida City	3	50	5	603	9.6	unburned	15.3	55–60	1.8
Moody Drive	4	15	5	632	10.8	unburned	5.0	55–60	2.0
Owaissa Bauer Park	5	24	5	568	14.0	unburned	12.6	55–60	2.5
Palm Drive	6	10	5	603	19.2	unburned	19.0	55–60	1.8
East Long Pine Key	7	300	10	294	20.2	wet	32.0	55–60	1.9
Moody Drive	4	15	5	539	12.0	wet	5.0	55–60	2.0
Pine Island	8	50	5	372	21.8	wet	27.0	55–60	1.0
Pines West	9	150	8	863	12.3	wet	44.0	50–55	0.6
West Long Pine Key	10	400	11	808	13.5	wet	36.0	55–60	1.5
Biscayne Drive	1	5	5	730	16.0	dry	11.3	55–60	2.7
Deering Estate	11	47	5	975	16.0	dry	1.3	60–65	2.2
Moody Drive	4	25	5	338	19.5	dry	5.0	55–60	2.0
Navy Wells	12	101	10	394	16.8	dry	12.0	55–60	2.1
Tamiami Pineland	13	49	5	211	22.6	dry	12.3	55–60	2.3
Thompson Park	14	89	5	255	21.7	dry	9.2	60–65	2.7

[†] Numbers correspond to those in the Fig. 1 map; some sites had distinct areas with different fire management regimes, and these are separated in the table.

[‡] The size of remnant pine forests (metro-Dade County) or pine islands (Everglades National Park) in which plots were located.

[§] Sites are grouped according to fire regime during the decade prior to Hurricane Andrew.

these remnants, pine stands, most of which resulted from regeneration after logging in the early 1900s, are second growth and even aged (Doren et al. 1993).

Subtropical pine savannas historically experienced lightning-initiated surface fires 2–3 times a decade (Harper 1927, Taylor 1981). Such fires maintained an incomplete canopy cover and a high-diversity ground cover (Schmitz et al., *in press*). Most fires were ignited by thunderstorms during the wet/lightning season, June–October (Doren et al. 1993). Fire management practices have often differed from historical patterns. We used fire records and information from land managers to assign one of three fire regimes to each site for the decade prior to Hurricane Andrew (Table 1). First, some Metro-Dade County remnants had not burned for ~10 yr before Andrew. Second, pine savannas managed by the National Park Service had burned 2–3 times during the wet season under prescribed fires (Doren et al. 1993). One remnant outside the park also had been burned in the wet season by arson fires. Third, some Metro-Dade remnants had been burned 2–3 times in the dry season by Florida Division of Forestry prescribed fires. Some nonmanaged remnants also were burned in the dry season by arson fires.

Hurricane Andrew made landfall along the southeast coast of Florida on 24 August 1992 (Armentano et al. 1995). The eye wall crossed the region (Fig. 1) with estimated sustained 1-min wind speeds of 50–65 m/s (180–240 km/h; 115–150 mph; Powell and Houston 1996). Higher peak winds occurred in the eye wall; local 3-s gusts were estimated as high as 80 m/s (290 km/h; 180 mph; Powell and Houston 1996).

We used 17 savanna remnants (hereafter, sites) in the

path of the eyewall (Fig. 1). Site characteristics that might have influenced pine mortality associated with the hurricane are presented in Table 1. More wind damage might have occurred in smaller stands; we used the sizes of sites or of local “habitat” islands of slash pines if they occurred within Everglades National Park. Ocean salt spray might have affected mortality; we used distance to the ocean as a proxy for this potential effect. Sustained 1-min wind speeds at sites were estimated from pressure models of Powell and Houston (1996). Depth to the water table during the dry season might have influenced site hydrology and potential differences in pine stress (Oberbauer et al. 1997). We averaged monthly groundwater depths (October 1989–September 1994) for three hydrological wells in Everglades National Park and 17 wells in southern Metro Dade County. Depths to groundwater for each site were estimated from data at nearby wells.

We established 5–11 plots within each study site 24–30 mo after Hurricane Andrew. We randomly located plots (11.4 m radius) in sites, avoiding edges and human disturbances. For each tree, we recorded diameter at breast height (dbh) and whether it died in the hurricane (direct mortality), following the hurricane (extended mortality), or was still alive. We were able to distinguish direct and extended mortality based on study of damage in plots in two Everglades National Park sites sampled 4–6 and 24–30 mo after the hurricane. Trees directly killed were tipped up or snapped off; standing trees retained green needles for ≥6 mo (Platt et al. 2000). Hurricane-snapped trees had jagged breaks, with large, long splinters and strips of bark that had been torn loose when snapped in high winds. Pines

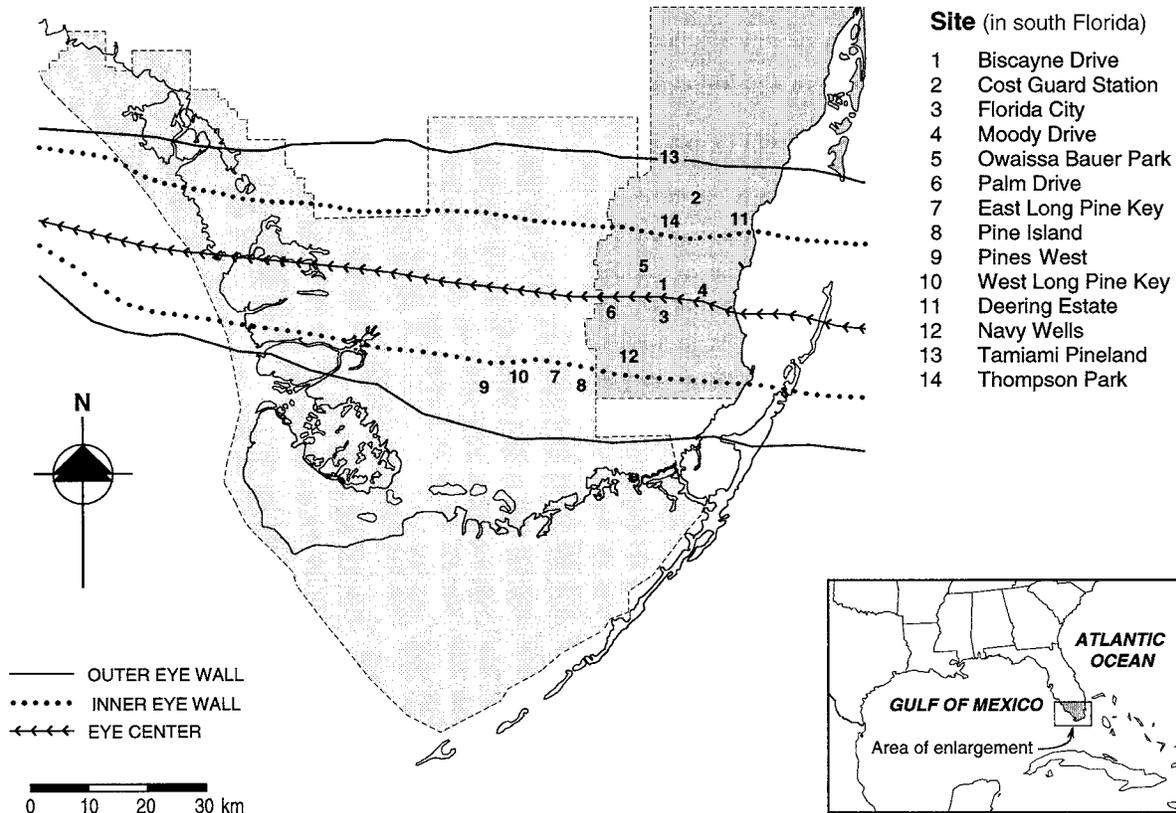


FIG. 1. The path of the eyewalls of Hurricane Andrew across the southern tip of the Florida peninsula on 24 August 1992 (adapted from Armentano et al. 1995). Solid and dotted lines indicate outer and inner edges, respectively, of the north and south eye walls. A solid line with arrows indicates the direction of movement of the center of the eye. Everglades National Park and metropolitan Dade County are indicated by light and dark shading, respectively. Numbers indicate locations of remnant pine savannas sampled (Table 1).

that survived but died over the next 24–30 mo were still standing or had snapped. The latter trees had breaks in the trunk that were perpendicular to the length of the bole. There were no long splinters, and the bark remained intact at the snap.

Statistical analyses

Our goal was to determine if prior fire regimes were associated with survival of pines during or after Hurricane Andrew. We adopted the philosophy that, although observational relationships may suggest hypotheses, they do not establish causal relationships (James and McCulloch 1990). When covariates are collinear, as in our study, demonstrating an association between a response variable and a covariate is problematic. Selecting the “best” model is uncertain and often depends on the selection method (Raftery 1995). We address this problem by Bayesian model averaging, in which probabilities of models being the “best” are calculated instead of selecting a single “best” model. Estimated magnitudes of individual covariates and their probabilities of having a value other than zero are computed by marginalizing over all likely models, giv-

en the covariates. This may be more reliable in gauging the relative importance of covariates.

Bayesian analyses follow from Bayes’ rule, which states that the distribution of a quantity of interest, θ , after observing the data is given by:

$$\Pr(\theta | \text{Data}) = \frac{\Pr(\text{Data} | \theta)\Pr(\theta)}{\int \Pr(\text{Data} | \theta)\Pr(\theta) d\theta} \quad (1)$$

where $\Pr(\theta | \text{Data})$ is the posterior probability of θ (i.e., after having observed the data); $\Pr(\text{Data} | \theta)$ is the likelihood of the data given θ ; and $\Pr(\theta)$ is the prior probability of θ (prior to seeing the data) (Gelman et al. 1997). The prior probability of θ may be based on previous research or subjective experience and may be chosen to exert little influence on the posterior probability. We use Bayes’ rule (1) to calculate the posterior probability of model M_j given the data:

$$\Pr(M_j | \text{Data}) = \frac{\Pr(\text{Data} | M_j)\Pr(M_j)}{\sum \Pr(\text{Data} | M_j)\Pr(M_j)} \quad (2)$$

where $\Pr(M_j)$ is the prior probability of model M_j and

the summation is over all j models. When the prior probabilities for all models are the same, the priors exert no influence on the posterior model probabilities. $\Pr(\text{Data} | M_j)$ is the integrated likelihood of the data given model j , where θ is the vector of model parameters:

$$\Pr(\text{Data} | M_j) = \int \Pr(\text{Data} | \theta) \Pr(\theta | M_j) d\theta. \quad (3)$$

We use the resulting posterior probabilities of the models to calculate the posterior distribution of each covariate “averaged” across models where it is nonzero:

$$\Pr(B_i | \text{Data}) = \sum_{A_j} \frac{\Pr(B_i | \text{Data}, M_j) \Pr(M_j | \text{Data})}{\Pr[B_i \neq 0 | \text{Data}]}. \quad (4)$$

B_i is a parameter estimated from data on the effects of covariates on θ , and $A_j = \{M_j: j = 1, \dots, J: B_i \neq 0\}$. Similarly, we can calculate the probability, averaged across j models, that an estimated parameter B_i is different from 0:

$$\Pr(B_i \neq 0 | \text{Data}) = \sum_{A_j} \Pr(M_j | \text{Data}). \quad (5)$$

We used this model-averaging approach. The response was the status of each tree (alive or dead), modeled as a Bernoulli trial. Potential variables were tree dbh, fire regime, remnant area, sustained hurricane wind speeds, distance from the ocean, and depth to ground water in the dry season. We did not include interactions between variables. We used bic.logit, an Splus function written by Adrian Raftery and Chris T. Volinsky at the University of Washington for model fitting and averaging.⁶ Eq. 3 is calculated using the Bayesian Information Criterion (BIC) approximation to $\Pr(\text{Data} | M_j)$, assuming a standard multivariate normal prior for $\Pr(\theta | M_j)$ (Raftery 1995). Each model had equal prior weight. The algorithm selects a subset of models by excluding those 20 times less likely than the most likely model, using the leaps and bounds algorithm of Furnival and Wilson (1974).

We further investigated the adequacy of our model fitting, as well as the potential for residual spatial autocorrelation, by adding a random-effects term for sites to the most probable models for direct and extended survival. The random-effects term absorbs variability not accounted for by fixed effects. A large variance associated with the random effects would suggest that we did not measure important covariates. Similar random effects (e.g., similar sign and magnitude) in adjacent sites might indicate residual autocorrelation.

RESULTS

Mortality was associated with prior fire regime (Fig. 2). Less than 30% of the trees in unburned or wet-

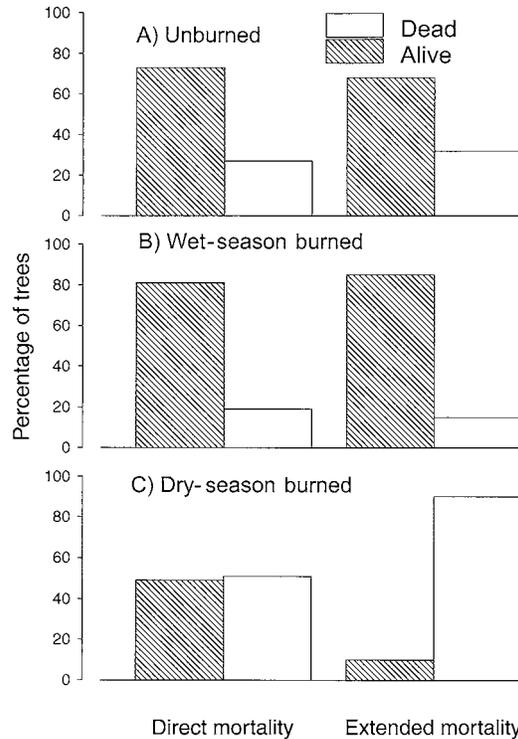


FIG. 2. The effect of prior fire regime (unburned, wet-season burned, dry-season burned) on hurricane-related mortality of south Florida slash pine (all sizes and sites combined). Data are expressed as the percentage of trees alive and dead after Hurricane Andrew (direct mortality) and the percentage surviving the hurricane that were alive and dead after 24–30 mo (extended mortality).

season burned sites, but >50% in dry-season burned sites were directly killed during the hurricane. During the next 24–30 mo, <35% of the trees that survived the hurricane subsequently died in unburned and wet-season burned sites, but >90% died in dry-season burned sites. Such differences occurred even in adjacent sites that shared other covariates. Direct and extended mortality at the Moody Drive site were, respectively, 23% and 31% for unburned portions, 25% and 16% for wet-season burned portions, and 35% and 78% for dry-season burned portions, despite being separated by only several hundred meters. These values are not very different from the overall percentages (Fig. 2).

Sources of mortality differed for direct and extended mortality. Direct mortality was associated with the ability to withstand wind stress; >80% of trees that died during the hurricane snapped 1–6 m above ground (Platt et al. 2000). Extended mortality was associated with lowered resistance to attacks by wood-boring beetles. Collections from insect traps indicated that turpentine beetles (*Dendroctonus terebrans*), pine engravers (*Ips* sp.), and regeneration weevils (*Pachylobius picivorus*, *Hylobius pales*) increased in abundance

⁶ URL: (http://lib.stat.cmu.edu)

TABLE 2. Model-averaging results for probabilities that individual slash pines would survive during Hurricane Andrew (left) and for the next 28–30 mo (right). The posterior mean and standard deviation indicate the effect of each variable in the first column on survival.

Variable	Survival during hurricane (direct mortality)				Model ^{††}		
	Mean	1 SD	Odds ratio [¶]	Pr($B^1 \neq 0$) [#]	1	2	3
Dbh	-0.097	0.007	0.91	>0.99	*	*	*
Dry-season burn [‡]	-0.793	0.124	0.45	>0.99	*	*	*
Wet-season burn [‡]	0.000	0.000	1.00				
Area [‡]	0.197	0.049	1.22	>0.99	*	*	*
Wind speed [§] 55–60 m/s	0.000	0.000	1.00	<0.01			
Wind speed [§] 60–65 m/s	0.000	0.000	1.00	<0.01			
Ocean distance	-0.001	0.004	1.00	0.05			*
Depth to water	-0.174	0.161	0.84	0.62	*		*
Model probability					0.57	0.38	0.05

[†] Effects of dry and wet fire seasons are expressed relative to effects in unburned sites.

[‡] Changes in area are expressed per 100 ha.

[§] Wind speed effects are expressed relative to effects at wind speeds of 50–55 m/s.

^{||} For continuous variables, the mean expresses the effects of unit increase in the variable within the range of values observed in the data.

[¶] For fire season and wind speeds, the odds ratio describes the relative expected differences in probabilities of survival that result from including the variable in column 1. For continuous variables, the odds ratio describes the differences in probabilities of effects on survival of a unit increase in the variable.

[#] The probability that effects of each variable are not equal to zero, based on model-averaging results.

^{††} Component variables of models with significant probabilities ($Pr \geq 0.05$) are denoted by asterisks.

at all sites during the post-hurricane period (R. Snow and J. Meeker, unpublished data).

Model-averaging results are presented in Table 2. All most likely models for survival, during and after the hurricane, included large estimated effects of tree size; probabilities of nonzero effects [$Pr(B \neq 0)$] were >0.99. A 1-cm increase in dbh was estimated to result in 9% and 10% reductions in the probability of survival during and after the hurricane. Such mortality resulted in decreased average tree size; few large trees survived in any site (Platt et al. 2000).

The effects of fire regime on survival during and after Hurricane Andrew were expressed relative to effects in unburned sites (Table 2). Dry-season burning reduced the probability of a tree surviving during and after the hurricane by 55% and 94% compared to unburned sites, with probabilities of nonzero effects >0.99. In contrast, the probability of survival in wet-season burned sites (compared to unburned sites) was not reduced during the hurricane, and increased by 281% after the hurricane, with a probability of a nonzero effect of 0.97. Trees in wet-season burned plots were estimated to be twice as likely to survive the hurricane as trees in dry-season burned plots, and to be nearly 47 times more likely to survive the 24–30 mo after the hurricane. All models for survival during and after Andrew included effects of dry-season fires, whereas only the most likely models for survival after Andrew included effects of wet-season fires.

Model-averaging results indicated less certain effects of site characteristics other than tree size and fire regime on survival during and after the hurricane (Table 2). The exception was remnant area. An increase in area from 1 to 100 ha, for example, was estimated to

increase the probability of survival during the hurricane by 22%; the chances of this effect being nonzero were >0.99. Increased remnant size may have resulted in reduced wind damage during Andrew, but did not affect the likelihood of post-hurricane insect outbreaks. The association between mortality and depth to the water table during the dry season, estimated as a 16% decrease in the probability of survival during the hurricane in sites with a 1-m increase in depth, had a probability of only 0.62 of being nonzero. No significant effect of depth to the water table was estimated after the hurricane. Distance to the ocean was estimated to be associated with survival only after the hurricane; the probability of survival was estimated to increase by 1% with each kilometer of distance from a site to the ocean, but the probability that this effect differed from zero was only 0.51. The small differences among sites in sustained wind speeds during the hurricane were estimated not to have affected the odds of survival, during or after the hurricane.

The most likely models suggested that different combinations of variables influenced survival during and after the hurricane (Table 2). All three most likely models for survival during the hurricane contained tree diameter, dry-season fire regimes, and area; addition of depth to groundwater during the dry season resulted in the most likely model ($P = 0.57$), with a probability 1.5 times that of the other most likely model. All three most likely models for survival after the hurricane included tree diameter, dry-season fire regimes, and wet-season fire regimes. The most likely model ($P = 0.51$) also included distance to the ocean.

The standard deviation associated with the random effects models was 0.48 for direct survival and 0.35

TABLE 2. Extended.

Survival after hurricane (extended mortality)						
Mean	1 SD	Odds ratio¶	Pr($B^1 \neq 0$)#	Model††		
				1	2	3
-0.105	0.009	0.90	>0.99	*	*	*
-2.751	0.220	0.06	>0.99	*	*	*
1.035	0.365	2.81	0.97	*	*	*
0.009	0.050	1.01	0.03			
0.007	0.050	0.99	0.03			
0.000	0.000	1.00	>0.01			
0.012	0.013	1.01	0.51	*		
-0.041	0.146	0.96	0.09			*
				0.51	0.36	0.06

for extended survival, indicating that the random effects were of the same order of magnitude or smaller than the fixed effects for both direct and extended survival. The magnitude and sign of the random effects did not show any obvious spatial pattern, suggesting that no residual spatial autocorrelation was present.

DISCUSSION

Prior fire regime, along with tree size and remnant area, was strongly associated with hurricane-related mortality of south Florida slash pine. Frequent fires typically result in low mortality in Everglades pine savannas, regardless of season (Taylor 1981, Doren et al. 1993). Our analyses suggest that natural fires, historically wet-season fires ignited by lightning (Platt 1999), do not increase mortality during hurricanes. They also suggest that wet-season fires increase post-hurricane survival relative to long-unburned sites, and that anthropogenic dry-season fires result in increased mortality during and especially after hurricanes. Pines were essentially eliminated from many savanna remnants by such anthropogenic changes in fire regimes.

The most likely models included depth to water table during the dry season (direct mortality) and distance to the Atlantic Ocean (extended mortality). Depth to the water table might have influenced the ability of trees to withstand high winds, but did not appear to affect post-hurricane insect attacks. Increased distance to the ocean, which could have resulted in less salt spray, might have affected survival after the hurricane, possibly as a result of lowered stress. Nonetheless, our analyses indicated that tree size, area, and fire regime were the variables most strongly associated with hurricane-related mortality.

Proposed mechanisms for fire-hurricane interactions should explain direct and extended mortality and, hence, the ability to withstand both wind damage and insect attacks. Dry-season fires (possibly in conjunction with water levels) might influence wood structure. If dry-season fire regimes affect wood structure, what effects might result in an increased likelihood that trees will snap and that they will be attacked and killed by

insects? Menges and Deyrup (2001), working in the sandy central ridge region of central Florida, suggested that fires (especially those of higher intensity) may damage the vascular cambium and rupture resin ducts of south Florida slash pine. Path analysis in that study suggested that fire intensity was higher in dry-season fires and that insect attacks were greatest after such fires (Menges and Deyrup 2001).

We propose a different effect of dry-season fires in the Everglades region. Dry-season fires on metro-Dade remnants prior to Hurricane Andrew were typically backing and flanking fires of low intensity, unlikely to cause sublethal cambium damage (maximum fire temperatures typically <500°C; Taylor 1981; Joy Kline, *personal communication*). Such low-intensity fires might have resulted in increased diameter growth compared to that on unburned and wet-season burned sites, especially where greater distance to the water table leads to reduced water stress compared to low-lying sites subject to flooding during the growing season (Oberbauer et al. 1997, Foster and Brooks 2001). Greater growth was documented by Oberbauer et al. (1997) in remnants that were dry-season burned and had greater depths to the water table than in Everglades National Park, where fires occurred during the wet season and depths to the water table were lower. Faster growing trees in dry-season burned sites might have had weaker wood, making them more susceptible to wind damage during the hurricane. Similar suggestions regarding greater mortality in faster growing trees have emerged from studies in other systems (e.g., Jenkins and Palardy 1995). In addition, surviving trees might have had more extensive wind damage, including ruptured resin ducts. They might have been unable to mobilize pitch reserves in their crowns when attacked by insects, resulting in elevated extended mortality. We noticed that resin exuded from damaged, but surviving trees was infrequent in dry-season burned plots, but was common in wet-season burned plots.

In addition, extended mortality was higher in unburned than in wet-season burned sites. Dense woody

vegetation, 4–5 m tall and dominated by the exotic shrub *Schinus terebenthifolius*, occurred in all unburned sites. Pines may have been stressed by competing woody vegetation, which may have reduced the growth of trees (lowering the susceptibility to wind damage), but also reduced the ability of damaged trees to mobilize pitch reserves (increasing susceptibility to insect attacks). Both dry-season and unburned fire regimes, possibly in conjunction with effects of salt spray, might have reduced the ability of wind-damaged trees to withstand insect attacks.

Our study supports the hypothesis that disturbances can interact in ways not foreseen from the study of individual disturbances (Paine et al. 1998). We extend this idea: variation in characteristics of initial disturbances may influence not only direct, but also more long-term extended effects of a subsequent disturbance. In our study, dry-season fires were associated with increased hurricane-related mortality of pines. Such mortality should increase fuels and thus the intensity of post-hurricane fires (Platt and Rathbun 1993, Myers and van Lear 1998, Platt et al. 2000). Hot spots from crowns and downed wood should affect the mortality of both pines and the local ground cover, producing cascading effects and changing the ecosystem. What might appear to be innocuous alterations of ecological processes by humans thus may produce very large effects during, and for some time after, subsequent large-scale disturbances.

ACKNOWLEDGMENTS

The National Park Service and Everglades National Park funded this study (CA 5280-4-9004 & 9005 to W. J. Platt, PI). Tom Armentano, Dave Baker, Chris Casado, Cathy Dull, Deborah Feichtinger, Josh Gallamore, John Goedken, Hester Johnson, David Jones, Joy Kline, Charlie Kwit, Jim Mabrey, Billy Platt, Germaine Ploos, Jed Redwine, Sarah Riley, Kevin and Wendy Robertson, Martin Schmitz, Jason St. Martin, Don Waller, and Andy Woolwine helped with fieldwork. Joy Kline and Joe Maguire provided locations and fire regimes of MDC remnants. Skip Snow and Jim Meeker provided information about pine beetles. Jean Huffman, Kerry Woods, and two reviewers made comments on prior drafts. Brian Beckage was supported by the National Parks Foundation and Andrew W. Mellon Foundation as a National Parks Foundation Fellow.

LITERATURE CITED

- Armentano, T., R. F. Doren, W. J. Platt, and T. Mullins. 1995. Effects of Hurricane Andrew on coastal and interior forests of southern Florida: overview and synthesis. *Journal of Coastal Research* **SI 21**:111–114.
- Batista, W. B., and W. J. Platt. 1997. An old-growth definition for southern mixed hardwood forests. United States Department of Agriculture Forest Service, Southern Research Station General Technical Report **SRS-10**.
- Doren, R. F., W. J. Platt, and L. D. Whiteaker. 1993. Density and size structure of slash pine stands in the everglades region of south Florida. *Forest Ecology and Management* **59**:295–311.
- Foster, T. E., and J. R. Brooks. 2001. Long-term trends in growth of *Pinus palustris* and *Pinus elliottii* along a hydrological gradient in central Florida. *Canadian Journal of Forest Research* **31**:1661–1670.
- Furnival, G. M., and R. W. Wilson, Jr. 1974. Regression by leaps and bounds. *Technometrics* **16**:499–511.
- Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 1997. Bayesian data analysis. Second edition. Chapman and Hall, New York, New York, USA.
- Harper, R. M. 1927. Natural resources of southern Florida. Eighteenth Annual Report of the Florida Geological Survey: 27–206.
- Hoffmeister, J. E., K. W. Stockman, and H. G. Multer. 1967. Miami limestone of Florida and its recent Bahamian counterpart. *Bulletin of the Geological Society of America* **78**:175–190.
- James, F. C., and C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics* **21**:129–166.
- Jenkins, M. A., and S. G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. *Canadian Journal of Forest Research* **25**:1119–1127.
- Menges, E. S., and M. A. Deyrup. 2001. Postfire survival in south Florida slash pine: interacting effects of fire intensity, fire season, vegetation, burn size, and bark beetles. *International Journal of Wildland Fire* **10**:53–63.
- Myers, R. K., and D. H. van Lear. 1998. Hurricane–fire interactions in coastal forests of the south: a review and hypothesis. *Forest Ecology and Management* **103**:265–276.
- Oberbauer, S. B., P. S. Kariyawasam, and J. N. Burch. 1997. Comparative analysis of growth, nutrition, carbon isotope ratios, and hurricane-related mortality of slash pines in south Florida. *Florida Scientist* **60**:210–222.
- Olmsted, I. C., W. B. Robertson, Jr., J. Johnston, and O. L. Bass, Jr. 1983. The vegetation of Long Pine Key, Everglades National Park. South Florida Research Center, **SFRC-83/05**.
- Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* **1**:535–545.
- Platt, W. J. 1999. Southeastern pine savannas. Pages 23–51 in R. C. Anderson, J. S. Fralish, and J. Baskin, editors. The savanna, barren, and rock outcrop communities of North America. Cambridge University Press, Cambridge, UK.
- Platt, W. J., and S. L. Rathbun. 1993. Dynamics of an old-growth longleaf pine population. *Proceedings of the Tall Timbers Fire Ecology Conference* **18**:275–297.
- Platt, W. J., R. F. Doren, and T. Armentano. 2000. Effects of Hurricane Andrew on stands of slash pine (*Pinus elliottii* var. *densa*) in the Everglades region of south Florida (USA). *Plant Ecology* **146**:43–60.
- Powell, M. D., and S. H. Houston. 1996. Hurricane Andrew's landfall in south Florida. Part II. Surface wind fields and potential real-time applications. *Weather and Forecasting* **11**:329–349.
- Raftery, A. E. 1995. Bayesian model selection in social research. Pages 111–163 in P. V. Marsden, editor. *Sociological methodology*. Blackwell, Cambridge, Massachusetts, USA.
- Robertson, K. M., and W. J. Platt. 2001. Effects of multiple disturbances (fire, hurricane) on epiphyte–host tree associations in a subtropical forest, Florida, USA. *Biotropica* **33**:573–582.
- Schmitz, M., W. J. Platt, and J. DeCoster. *In press*. Substrate heterogeneity and number of plant species in everglades savannas (Florida, U.S.A.). *Plant Ecology*.
- Snyder, J. R., A. Herndon, and W. B. Robertson. 1990. South Florida rockland ecosystems: tropical hammocks and pine-lands. Pages 230–274 in R. Myers and J. Ewel, editors. *Ecosystems of Florida*. University of Florida Press, Gainesville, Florida, USA.
- Taylor, D. L. 1981. Fire history and fire records for Everglades National Park, 1948–1979. South Florida Research Center **T-619**.
- Turner, M. G., and V. H. Dale. 1998. Comparing large, infrequent disturbances: what have we learned? *Ecosystems* **1**:493–496.