Journal of the Torrey Botanical Society 135(3), 2008, pp. 367–376

The impact of Hurricane Frances (2004) on the invasive Australian pine (*Casuarina equisetifolia* L.) on San Salvador Island, The Bahamas

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RODGERS, J. C. III (Department of Geosciences, Mississippi State, MS 39762) AND D. W. GAMBLE (Department of Geography and Geology, University of North Carolina, Wilmington, Wilmington, NC 28403). The impact of Hurricane Frances (2004) on the invasive Australian pine (*Casuarina equisetifolia* L.) on San Salvador Island, The Bahamas. J. Torrey Bot. Soc. 135: 367–376. 2008.—On September 2, 2004 Hurricane Frances (Category 3) passed directly over San Salvador Island, The Bahamas. This event offered the opportunity to gather baseline data regarding the impact of hurricanes on populations of the invasive Australian pine (*Casuarina equisettifolia* L.) in the Bahamas. Results of vegetation surveys within both forest stands and beach environments suggest that the overall impact of this hurricane was minimal. Less than 13% of forest individuals and 17% of beach individuals surveyed were damaged, and the majority of damage was restricted to just one location for both the forest and beach study sites. The most common damage type within the forest sites was "snapped" trees (8%) and this primarily occurred within trees ranging in size from 7–12 cm in diameter. Browning of the entire foliage was the most common damage type within the beach sites (9.3%) but this damage type only occurred within tree sizes less than or equal to 90 cm in height. Thus it appears that Hurricane Frances had a negligible effect on Australian pine populations as a whole on San Salvador Island and that this disturbance event will probably not limit future population expansion. It is suggested that more powerful or more frequent hurricanes would be needed to significantly affect Australian pine populations on San Salvador Island. Similar patterns in damage should be expected with comparable hurricane events on other islands in the Bahamas and for other tropical beaches in which this species has invaded.

Key words: Australian pine, *Casuarina equisetifolia*, hurricane impact, The Bahamas.

The Australian pine (*Casuarina equisetifolia* L.) is an invasive plant that was introduced in the Bahamas and throughout the Caribbean (Hammerton 2001). The native range includes Southeast Asia, Indonesia, Australia, New Guinea, and the South Pacific (Parrotta 1993, Hammerton 2001), but it has been introduced in many tropical beaches around the world, such as in southern Florida, Hawaii, the Caribbean, China, and coastal Africa (Parrotta 1993). It was initially established in the Bahamas during the late Nineteenth Century and early Twentieth Century for multiple reasons, including to plant as ornamentals, to stabilize beaches, to be used as hedgerows and windbreaks, and to plant areas damaged from tropical cyclones or from strip mining (Hammerton 2001). Since its introduction, though, it has rapidly extended its range and it currently has become pervasive across much of the Bahamian archipelago. Australian pines have several characteristics that contributed to its rapid dispersal in the Bahamas. For one, it is well suited to beach environments due to its preference for sandy soils and to its ability to tolerate saline conditions (Parrotta 1993). Because it thrives in beach environments it has been widely planted around resorts and hotels to provide shade and privacy (Hammerton 2001). Additionally, this species produces hundreds of wind-dispersed seeds per year, fixes nitrogen, has a leave litter that may be allelopathic, and

[1] The authors would like to thank the Department of Geosciences and the North Mississippi Daily Journal Undergraduate Research Award for providing financial support for this research and the Bahamas Department of Agriculture for granting the research permit to conduct the study. We also thank Vince Vogeli and the Gerace Research Center for providing both logistical support and local expertise. Our deepest appreciation goes to Drs. Mike Brown and Paul Grady Dixon for help with hurricane interpretations and to our field assistants Erik Mylroie, Robika Modak, Tonya Neaves, Joan Mylroie, Lars Mylroie, Leif Mylroie, Kevin Toepke, Jared Allen, Liza Colucci, Corinne Wong, and Julia Johnston.

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Received for publication February 4, 2008, and in revised form May 27, 2008.

has a rapid growth rate (Elfers 1988, Parrotta 1993, Hammerton 2001, Swearingen 2008). Furthermore, because they are abundant within human disturbed habitats (Hammerton 2001, Rodgers 2005), there are perhaps more available areas for the Australian pine to invade due to increasing levels of disturbance. Regardless of these dispersal methods, the rapid expansion of Australian pine has created a plethora of environmental problems, including contribution to beach erosion and disruption of native ecosystems (Elfers 1988, Hammerton 2001, Patil et al. 2002, Sealey 2006, Swearingen 2008). Nevertheless, it is surprising that there is very little research on its population dynamics, dispersal capabilities, or interactions with native biota.

One important research question regarding Australian pines in the Bahamas is how will hurricanes affect their distribution? Based upon previous research of hurricane impact on Caribbean vegetation (Tanner et al. 1991), there are at least two possible outcomes. The first is that strong winds and storm surge may injure or kill individual trees, or reduce the abundance of existing Australian pine populations. In this case, tropical cyclones might benefit native species by removing existing Australian pines or by diminishing their competitiveness. The issue of whether invasive plants may be more susceptible to impact from hurricanes has been discussed in the literature (Willis et al. 1999 as reported in Lieurance 2007). The second outcome is that hurricanes may facilitate the spread of the Australian pine by providing newly disturbed habitats to invade, by increasing available light, or by disseminating the wind-dispersed seeds. From another study, the invasive *Acacia auriculifomris* in southern Florida rapidly recovered from foliar damage sustained during a hurricane, and thus it may have a competitive advantage over native species and may have actually benefited from this natural disturbance event (Lieurance 2007). The question of whether tropical cyclones foster or hinder Australian pine populations in the Bahamas is uncertain. An initial step toward determining the impact of hurricanes would be to examine the amount of damage that occurred to Australian pine populations following a specific storm event.

This current study investigates the impact of a Category 3 hurricane (Hurricane Frances, 2004) on populations of Australian pine on San Salvador Island, The Bahamas. The specific objectives of this research are to investigate the spatial variability of hurricane damage with regards to the hurricane track, to examine the relationship between type of damage and individual size, and to monitor changes in population data before and after landfall. Little background data exists regarding the hurricane survivability of Australian pines, especially within the Bahamas. This study is an initial attempt to catalog the amount of damage, the types of damage, and the short-term impacts of a hurricane on Australian pine populations. The results presented here may provide insight into the general levels of Australian pine population resiliency to hurricane damage. Moreover, results from this research may be of value to Bahamian and Caribbean resource managers, such as the Bahamas Trust, that are charged with the tasks of controlling and eliminating this problematic and invasive species on similar small islands.

AUSTRALIAN PINE IN THE BAHAMAS. The Australian pine is believed to have several negative effects on the native Bahamian flora and fauna (Hammerton 2001). The invasive species forms thick, monospecific stands that shade and aggressively compete for resources with the native vegetation (Elfers 1988, Hammerton 2001, Swearingen 2008). Additionally, the needle leaves are thought to be allelopathic, the thick leaf litter is thought to restrict establishment of native plants, the vegetative structure provides little food or nesting sites for native bird species, and Australian pine stands have very low insect diversity (Elfers 1988, Hammerton 2001, Patil et al. 2002, Swearingen 2008). Additionally, Sealey (2006) purports that the shallow root system of this plant is not effective in retaining sediment during storm events and will topple easily during high winds. Thus the Australian pine may provide little protection to stop beach erosion, and it may actually undermine the stability of the beach (Sealey 2006).

HURRICANES AND TROPICAL FOREST. Few studies of the relationship between hurricanes and Australian pines in the Bahamas exist. There are several studies that have investigated hurricane damage to trees within tropical forests. Hurricane damage to tropical forests is highly variable and the extent of damage often depends on multiple factors, such as differences in tree species, topographic variations, and variability in local wind direction and speed (Lugo et al. 1983, Boucher et al. 1990, Bellingham 1991, Tanner et al. 1991, Zimmerman et al. 1996, Boose et al. 1994, Ostertag et al. 2003). These differences, in addition to the absence of on-site meteorological data, present challenges to developing generalities about hurricanes as a natural disturbance agent and to comparing studies across multiple regions (Tanner et al. 1991). Local peak wind gusts, for example, were described as being one of the more important factors contributing to tropical rainforest damage following Hurricane Hugo, (Category 3, Boose et al. 1994). In other cases, topographic position seems to be the most important factor governing the extent of hurricane damage. Trees on ridges were more likely to have been damaged by Hurricane Georges (Category 2, 1998, NOAA 2008) than trees along valley floors (Ostertag et al. 2003). Similarly, topographic position was an important factor explaining mortality of trees in Jamaica from Hurricane Gilbert (Category 3, Bellingham 1991). These studies illustrate the complex nature of the interaction between hurricanes and tropical forests.

HURRICANE FRANCES' TRACK ACROSS SAN SALVADOR ISLAND. The Australian pine damage results from this study are examined within the context of relative location of each study site to the hurricane eye-wall. Therefore a meteorological review of Hurricane Frances as it tracked across San Salvador Island is warranted. On the afternoon of September 2, 2004 Hurricane Frances made landfall on San Salvador Island at 13:00 EST (Fig. 1). The National Weather Service (Beven 2004) stated that by 14:00 EST, Hurricane Frances was moving west–northwest at 21 km h^{-1}, had sustained winds of 233 km h^{-1}, hurricane-force winds extending 129 km from the center, and an estimated storm surge between 1.8 to 4.3 m near the eye wall. Local observations recorded by the weather station at the Gerace Research Centre (GRC) 14:00 EST showed that all of the sustained winds greater than 30 km h^{-1} were from the north and northeast directions. By 20:00 EST, seven hours after the initial landfall, the leading edge of the eye wall moved over and away from San Salvador Island. The estimated sustained winds were

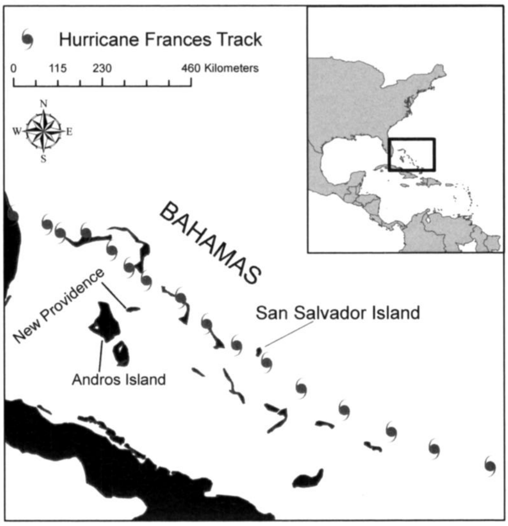

FIG. 1. Track of Hurricane Frances across The Bahamas, September 1–September 6, 2004. Hurricane symbols were plotted from coordinates on the National Hurricane Center website (Beven 2004, NOAA 2008). Note: the size of the hurricane symbol does not represent the actual size of the storm. Base map data were adapted from ESRI Data.

193 km h^{-1} on the northeast quadrant of the storm, and at the trailing edge of the eye wall on the southeast quadrant, winds were estimated to be 162 km h^{-1} (Beven 2004).

A tropical weather summary from the National Hurricane Center stated that Hurricane Frances was a Category 3 hurricane as it passed over San Salvador Island (Beven 2004). The director of the GRC reported that the field station, located on the north coast of the island, was under the eye (clear, calm conditions) for only 15 min whereas residents in Cockburn Town, located on the central western coast, were in the eye for at least 45 min (pers. comm., Vince Vogeli, Director of GRC). The northern portion of the island would have been affected by the eye wall (location of the most intense winds and rain) for a longer duration than the central or southern portion of the island. Parnell et al. (2004) reported that the southern end of the island had a 3.75 to 5.0 m storm surge that extended inland for 100 m and that the southwest coastline had a storm surge of 2.65 m that extended up to 10 m inland. No storm surge data exist for the other regions of the island.

Hurricane Frances was the last major hurricane to make landfall on San Salvador

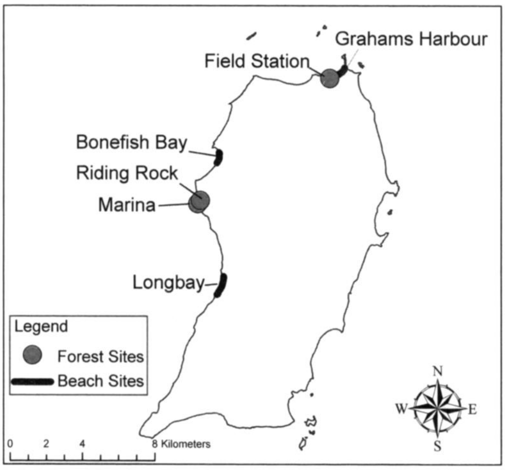

FIG. 2. Forest and beach Australian pine study sites on San Salvador Island, The Bahamas. The base map of San Salvador Island is from Robinson and Davis (1999).

Island since 2004. Since then, two tropical depressions have hit the island, both occurring in the summer of 2007. No severe tropical weather has been reported for San Salvador between Hurricane Frances 2004 and December 2007, the period in which field surveys of the Australian pines were completed for this study (NOAA CSC, 2008).

Materials and Methods. STUDY AREA. San Salvador Island (24° N, 74° W) is a small island within the Commonwealth of The Bahamas, and it is located in the central-eastern region of the island archipelago (Fig. 1). The island is approximately 11 km wide east to west and 19 km long north to south, with a total surface area of 95 km² (GRC 2008, Fig. 2). The geology of the island is described as a complex system of eolianite limestones that were deposited during the middle to late Quaternary Period (Carew and Mylroie 1995).

The climate on San Salvador represents a transition between the subtropical-temperate climate of the northern Bahamas and the semiarid tropical climate of the southern Bahamas. Typically summer temperatures range from 22 to 32 °C and winter temperatures range from 17 to 27 °C (Shaklee 1994). The island receives approximately 100 cm of rainfall per year, but the rainfall pattern is highly seasonal with a pronounced wet season (June–October) and dry season (November–May). During the late summer and early fall, tropical cyclones are possible and occur on average about once every three years (Shaklee 1994). The last major hurricane to hit San Salvador Island before Frances was Hurricane Floyd (Category 4) in 1999 (Gamble et al. 2000).

STUDY DESIGN. The research design for this study consisted of recording the amount and type of damage to Australian pines from Hurricane Frances four months and 16 months after landfall. Hurricane damage was assessed within two different sample populations. The first sample population included larger trees (most individuals greater than 300 cm height) located within forest stands. The second sample population included smaller trees (most individuals less than 300 cm height) and seedlings (individuals less than 100 cm high) located within sandy beach environments. These two environments were chosen for study because they denote two separate Australian pine population types prevalent on San Salvador (Rodgers 2005). The forest population represents older individuals within populations that may have been established for a longer duration. The forest Australian pines were also more inland and at higher elevations (> 5 m elevation). The beach populations represented smaller (seedlings and saplings) individuals within more recently established populations.

Three Australian pine forest study sites were established in January 2004 for another study (Rodgers 2005) and were used again in this work (Fig. 2). The first is located near the GRC on the northern coast approximately 20 m from the shore and is referred to as the "Field Station" site (Fig. 2). The second site is located at the Riding Rock marina on the central western coast (Fig. 2). Trees in this study site occur on dredge spoil and are located only a few meters from shore. This site is referred to as the "Marina" stand. The third site is located approximately 35 m east of the Riding Rock Inn Marina on flat ground within shallow, sandy soils (Fig. 2). This study site is referred to as "Riding Rock".

The field sampling methodology was adapted from Peet et al. (1998). Within each of the three forest study sites, 50 m transects were laid out along the longest axis of the stand. Five 10 × 10 m sample plots were established on alternating sides of the 50 m transect. The Riding Rock site only had space for four study plots. The fifth plot was located 50 m north of the initial transect starting point. Within each plot, the total number of individual trees was counted and the diameter of each tree was measured at approximately 20 cm from the surface. Diameter measurements were taken at this height because many of the sampled Australian pines were bifurcated above the 20 cm level.

During the January 2005 field season, four months after hurricane landfall, the three forest sites were revisited and the number of trees and the tree diameters measured along previously established 50 m transects. Field measurements occurred several months after landfall and there is no direct evidence linking the damage reported in this study to Hurricane Frances. However, the absence of significant tropical cyclones making landfall or other major storm events in this vicinity from September 2004 to January 2006 (NOAA CSC 2008) strongly suggests that the observed vegetation damage was associated with Hurricane Frances.

Trees at the forest sites were categorized into one of three mutually exclusive damage types following the studies of Putz and Sharitz (1991) and Greenberg and McNab (1998). The "uprooted" damage class indicated trees that were tipped over prostrate with roots exposed. The "snapped" damage class indicated damage where the main (largest) stem was snapped or broken off but the lower portion of the tree was intact and rooted. "Broken limbs" was a damage type in which the main stem was intact but one or more large limbs were broken off. "Discolored" indicated damage where the foliage in the upper portion (the top ⅓ to ½) was brown while the lower foliage was green. "Browned" was a damage type where by the majority of foliage was brown. These last two damage types were applied only to individuals that were not snapped, uprooted, or had broken limbs. Thus an individual could only be classified within one damage type. If an individual tree appeared to be uninjured, having none of the signs described above, it was categorized as "undamaged." The average tree diameter and the number of individuals were also re-measured in January 2006, sixteen months after landfall. Changes in average size and number of individuals during the three-year study period were calculated. Analysis of variance (ANOVA) was used to test for significant differences in diameter among the different field seasons for each of the three forest study sites.

The three beach sample populations were located on the western coast of San Salvador Island (Fig. 2). They were established during the January 2005 field season, after Hurricane Frances. The Long Bay study site is located towards the south-central west coast. The Bonefish Bay site is located on the northern west coast. The Grahams Harbor site is located on the northern coast approximately 30 m shoreward of the Field Station study site. At each of the three beach sites, approximately 1 km transects were set parallel to shore. The lengths of the transects were as follows: Long Bay = 1.3 km, Bonefish Bay = 0.92 km, and Grahams Harbor = 1.2 km. Transect lengths were not consistent among the three sites due to the variability in length of the beaches. The total number of Australian pines along each transect as counted within the area spanning from the shoreline to the landward boundary of the beach. The landward boundary of the beach included either the front of a secondary wooded dune or a road. In most cases the landward boundary was within seven m of the beach transect. Additionally, the height of each Australian pine encountered was measured along the beach transects. Height was measured in place of diameter because the majority of individuals encountered were seedlings and smaller saplings with very little appreciable variation in stem diameter. Besides height measurements, the damage type of each individual was also noted. During the January 2006 field season, 16 months after landfall, the beach study sites were revisited and the number and height of Australian pines were measured along the same transects.

Results. Damage Within the Forest Sites. The Field Station forest site had the greatest tree damage. At this location 82 of 273 total trees (30%) showed evidence of being damaged in January 2005 (Table 1). Seventy two percent of all damaged trees were in the snapped category, making this the most abundant damage type. There were 15 trees uprooted (5.5%) and eight trees with broken limbs (2.9%). At the Marina site, only five of 231 trees showed signs of damage (2.1%). The Riding Rock also had very minimal damage where only 10 of 247 trees (4.0%) showed signs of being injured. Most of the damaged trees at this site were in the broken limb category.

The average diameter of the forest study sites significantly increased for each of the

Table 1. Number of Australian pines (% in parentheses) within each damage category for each of the three forest sites.

Forest site	Total	Uprooted	Snapped	Broken limbs	Discolored	Browned
Field Station	273	15 (5.5)	59 (21.6)	8 (2.9)	0	0
Marina	236	1 (0.4)	1 (0.4)	0	2 (0.8)	1 (0.4)
Riding Rock	257	0	1 (0.3)	8 (3.1)	1 (0.3)	0

field seasons ($P < 0.01$). Yet, the trees at the Field Station had the lowest percent increase in average diameter from January 2004 to January 2005 (17.5%; Fig. 3). In contrast the Marina site had the largest percent increase in average diameter during this time period (51%) followed by the Riding Rock site (28.9%). The percent increase in average diameter from January 2005 to January 2006 for the Field Station (7.1%) and Marina (11.7%) sites was much less than the diameter increases from the year before. Contrastingly, the Riding Rock site had a larger increase in average diameter from January 2005 to January 2006 (30.3%) than the year before. Overall the Field Station site exhibited the lowest percent increase in diameter over the course of the study period (2004 to 2006; 28%). This increase was less than a third of the increase in average diameter for the Marina and Riding Rock sites during the same time frame (> 66%; Fig. 3).

Tree damage within the forest sites was related to size class. Damage by size results are presented for only the Field Station because this was the only site that had significant damage. The damage types observed in this study were greater in the mid- and large-size classes (Table 2). Examining size classes with the largest number of individuals (≥ 25 individual trees), it was apparent that the 7–8 cm, 9–10 cm, and 11–12 cm classes had the greatest number of damaged trees. The 9–10 cm and 11–12 cm classes in particular had over 50% damaged trees. The 3–4 cm and 5–6 cm size classes each had approximately 15% damaged trees. The smallest size classes (≤ 1 cm) had no damaged trees and the larger size classes (≥ 13 cm diameter) all had damaged trees. Snapped trees occurred within all size classes except for the < 1 cm diameter class (Table 2). The mid-size categories (7 cm–12 cm) seemed to be especially prone to being snapped. All large tree size classes (≥ 13 cm diameter) had snapped individuals. The broken limb damage category was infrequent, occurring within only the 2 cm–12 cm diameter size range. Uprooted Australian pines were present in most small- and mid-size classes, but they were absent from the < 1 cm and infrequent in the 13 cm or larger size classes. Only one of the nine trees greater than or equal to 17 cm was uprooted (Table 2). However it should be noted that several larger Australian pines outside the study plots were observed to be toppled. One tree in particular (> 40 cm diameter) located on the island's southeastern shore was completely uprooted. Interestingly the leaves of this fallen tree were still green in January 2006 and it showed signs of sprouting and new growth.

DAMAGE AND POPULATION CHANGES WITHIN THE BEACH SITES. The Long Bay site had a substantial number of damaged Australian pines (34.9%), but the Grahams Harbor and Bonefish Bay sites had minimal damage; 5.5% and 2.1% respectively (Table 3). Most of the damaged individuals at the Long Bay site were either in the "browned" category (21.7%) or the "discolored" category (12.2%; Table 3). In examining the damage by height class for the Long Bay site (Fig. 4), it was evident that all Australian pines in the "browned" size category were less than or equal to 90 cm high. Damaged individuals in the "discolored" category ranged from 30 cm to 240 cm high, but the most frequent "discolored" size class was from 120 cm to 150 cm (Fig. 4). This

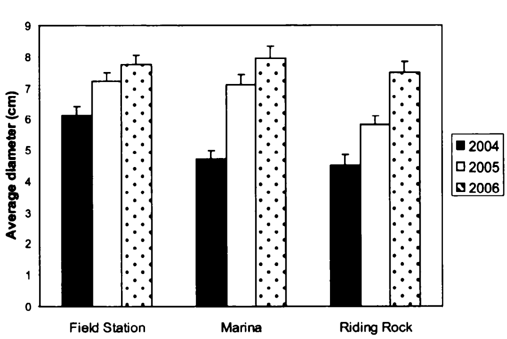

FIG. 3. Average Australian pine diameter among the three forest sites for the January 2004, January 2005, and January 2006 field seasons.

Table 2. Number of damaged trees by diameter size class for the Field Station study site (% in parentheses), January 2005. Diameter measurements were rounded to the nearest cm. The percent damaged is indicated in parentheses for size classes with 25 or more individuals.

Size Class (cm)	Trees total	Snapped (%)	Uprooted (%)	Broken limbs (%)
0–1	4	0 (0.0)	0 (0.0)	0 (0.0)
1–2	60	2 (3.3)	1 (1.7)	1 (1.7)
3–4	51	5 (9.8)	3 (5.9)	0 (0.0)
5–6	37	3 (8.1)	2 (5.4)	2 (5.4)
7–8	43	13 (30.2)	3 (7.0)	2 (4.7)
9–10	34	13 (38.2)	2 (5.9)	2 (5.9)
11–12	25	10 (40.0)	2 (8.0)	1 (4)
13–14	5	5	0	0
15–16	5	5	1	0
17–18	3	2	0	0
19–20	2	2	0	0
21–22	2	1	1	0
23–24	1	1	0	0
25+	1	1	0	0

height class had both a large number of individuals (23) and a high proportion of damaged individuals in the "discolored" damage category (34%). Few individuals in the Long Bay beach site were greater than 210 cm (11 trees) and of these there were only four "discolored" individuals. In January 2006, the Long Bay site exhibited a 31.5% population decrease from the year before (Fig. 5). The other two beach sites, in contrast, experienced population increases, 6% at Bonefish Bay and 7% at Grahams Harbor.

Discussion. SPATIAL VARIABILITY OF HURRICANE DAMAGE. The right-front quadrant of a hurricane typically has the strongest wind speeds and the most extensive hurricane damage due to the constructive forces of the overall storm movement with the angular momentum of the storm (Riel 1979, Stull 2000). The northwestward track of Hurricane Frances would have positioned the right-front quadrant towards the northern end of San Salvador Island, within the vicinity of the Field Station study site. Evidence for stronger winds in the north comes from at least two sources, the NWS and island residents. Hence, northern areas experienced stronger winds for a longer duration. The Field Station had the greatest number of damaged trees and experienced the slowest growth and population increase after landfall. In contrast the other two forest study sites that were located similar distances south of the eye-wall were virtually undamaged. These spatial damage patterns add another dimension to previous studies regarding the variability of tropical forest damage from hurricanes (Boose et al. 1994, Ostertag et al. 2003). In the case of Australian pines in the Bahamas, it is suggested that the location relative to the eye wall may be of

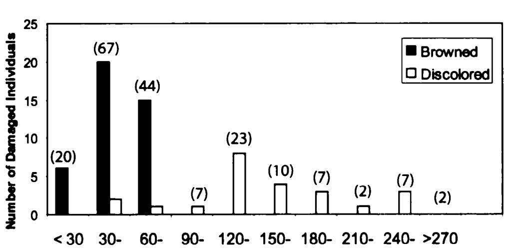

FIG. 4. Australian pine damage type by height size class for the Long Bay site. Black bars represent trees that were browned (all foliage was brown) and white bars represent trees that were discolored (top ⅓ to ½ of the foliage was brown).

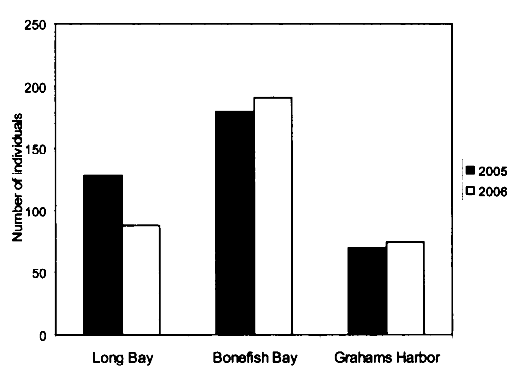

FIG. 5. Number of Australian pines for each beach site location during the January 2005 (four months after Hurricane Frances) and during the January 2006 (16 months after Hurricane Frances) field seasons.

Table 3. Number of Australian pines (% in parentheses) within each damage category for each of the three beach sites.

Beach Site	Total	Uprooted	Snapped	Broken limbs	Discolored	Browned
Grahams Harbor	72	1 (1.4)	1 (1.4)	1 (1.4)	1 (1.4)	0
Bonefish Bay	190	0	3 (1.6)	0	0	1 (0.5)
Long Bay	189	0	2 (1.0)	0	23 (12.2)	41 (21.7)

greater importance in determining the extent of hurricane damage.

The Grahams Harbor beach site was adjacent to the Field Station forest site, but it received almost no significant damage. Because the storm tracked in a northwestward direction across the island, this northern beach study site may have been sheltered from the seaward-blowing hurricane winds by the fore dunes. The Long Bay site further south would have experienced landward-blowing winds due to the counter-clockwise rotation around the storm's center of low pressure. Ultimately this may have generated a more extensive storm surge at this beach site (2.7 m storm surge reported near Long Bay by Parnell et al. 2005).

HURRICANE DAMAGE AND SIZE CLASS. In the tropics, the relationship between tree size and hurricane damage is not clear. Lugo et al. (1983) reported that uprooted trees were more common for larger individuals and snapped stems were more likely in smaller trees. Bellingham (1991), however, found no relationship between tree diameter and hurricane damage. With regards to Australian pine in the Bahamas, there does appear to be a relationship between the damage and size class. The larger individuals ($\geq$ 7 cm diameter) in the inland forest sites were susceptible to being snapped and uprooted whereas smaller individuals (< 7 cm diameter) were largely undamaged.

The relationship between hurricane damage and size was also apparent for the beach individuals. The "browned" damage category may be the most harmful of all damage types for the beach individuals. Yet, this damage type only occurred within the smallest height classes ($\leq$ 90 cm). These results suggest that the larger beach individuals, and thus those that are seed-bearing, have a higher survival probability. Furthermore, during successive years without a direct land-falling hurricane, there may be sufficient time for the smaller seedlings to mature into the larger size classes and reduce their susceptibility to hurricane damage.

OVERALL CONSEQUENCES OF HURRICANE FRANCES TO AUSTRALIAN PINE POPULATIONS. Previous studies of hurricane induced tree mortality in the Caribbean indicate a wide range in mortality rates (Tanner et al. 1991). For example, Hurricane Joan in Nicaragua (Category 4, 1988) resulted in 80% of trees being felled while Hurricane Gilbert in Jamaica damaged only 14% of trees (Boucher et al. 1990, Tanner et al. 1991, Bellingham 1991). By comparison, damage to Australian pine populations on San Salvador Island was on the lower end of this damage continuum. Less than 13% of forest individuals and only 16.4% of beach individuals surveyed showed signs of hurricane damage. Therefore, it is apparent that Hurricane Frances had only a minor effect on Australian pine populations, especially when placed in context of the other published reports.

In regards to recovery of the Australian pine on San Salvador the most common damage type in the forest study (the "snapped" category) was not fatal. Australian pine has the ability to grow rapidly (Hammerton 2001) and based on the growth habits of this species it is likely that snapped individuals will be able to regenerate. The importance of stem regeneration to hurricane survivability, especially for angiosperm trees, has been demonstrated (Boucher et al. 1990). Moreover, even the most damaged forest study site, the Field Station, still had positive growth during subsequent years after Hurricane Frances. Therefore the damage that occurred within the forest sites may be of only limited significance in controlling the Australian pine population on San Salvador Island.

Within the beach sites, many of damaged individuals were discolored, and this damage type was probably not fatal. Only the smaller trees may have been directly killed (browned), and this group represented only a small fraction of the overall beach population. Moreover, because only the Long Bay site experienced a reduction from 2005 to 2006, it is evident that any long-term impact on population size may be local in scope. Additionally, the infrequency with which hurricanes make landfall on San Salvador Island, the high survivability of existing populations, and the prolific seed productivity (Hammerton 2001) suggest that it is unlikely that Hurricane Frances had a significant negative impact on the beach Australian pine populations. A hurricane of larger magnitude, one that stalls for a longer duration, or more frequently land falling storms may be required to cause significant population declines.

Conclusion. The long-term negative effect of Hurricane Frances on San Salvador's Australian pine population is suggested to be minor, yet more research is needed. It is still not clear, for example, how fast injured individuals will recover or if they may die later on. It is not clear whether the discolored or browned individuals at the Long Bay study site will result in reduced growth or decreased germination of seeds. It is also uncertain whether the hurricane may have actually facilitated an increase in Australian pine populations by dispersing seeds into new environments and from creating newly disturbed ground to colonize. Continued monitoring of San Salvador Australian pine populations is important to shed light on the long-term consequences of hurricanes on this invasive species in the Bahamas and other tropical locations.

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