Hurricane disturbance and the regeneration of *Lysiloma latisiliquum* (Fabaceae): a tropical tree in south Florida

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Abstract

Large-scale catastrophic disturbances such as hurricanes may be critical events for the regeneration of late secondary canopy tree species. The impact of Hurricane Andrew, a severe Category 4 hurricane, on the tropical tree *Lysiloma latisiliquum* was examined in three south Florida subtropical forests along a gradient of hurricane disturbance (high, moderate, none). The population closest to the northern eye wall of the hurricane had the highest mortality and most severe structural damage while the population near the southern eye wall of the hurricane experienced less mortality and damage. Posthurricane reproduction was least in the disturbed sites while the undisturbed site had extensive reproduction in both 1993 and 1994. Average seed production was low due to seed predation by a bruchid beetle but some populations experienced spatial and temporal escape from this seed predator. Germination from a dormant seed bank occurred only at the most severely disturbed site in 1992. Seed germination was associated with both tip-up pits and high understory light levels. In experimental trials, fluctuating heat treatments for 5 days increased seed germination. Severe hurricane disturbance is believed to have triggered germination from a dormant seed bank through strong diurnal soil temperature fluctuations resulting from extensive canopy removal. In south Florida, the temporal and spatial dynamics of both hurricane and fire disturbance are predicted jointly to influence the population dynamics of this canopy tree species. © 1997 Elsevier Science B.V.

Keywords: Disturbance; Hurricane; *Lysiloma latisiliquum*; Seed germination; Tip-up pit

1. Introduction

Hurricanes are common disturbances to both tropical and temperate forests worldwide (Pielke, 1990). The role of hurricanes in influencing forest structure, composition, and dynamics has recently received quantitative ecological analysis in the neotropics (Bellingham, 1991; Walker, 1991; Brokaw and Walker, 1991; Whigham et al., 1991; Yih et al., 1991; Horvitz et al., 1995) and paleotropics (Unwin et al., 1988; Shimizu, 1994; Herwitz and Young, 1994; Elmqvist et al., 1994). While these studies emphasize mortality, damage, and recovery of community structure, hurricane effects on particular plant species have rarely been examined due to the lack of preexisting ecological data (but see You and Petty, 1991; Boucher et al., 1994). Responses of tropical tree species to hurricane disturbance include resprouting of standing adults (Yih et al., 1991; Basset, 1993; Bellingham et al., 1994), recruitment of seedling and saplings of primary forest species (You and Petty, 1991; Yih et al., 1991), and germination of a dormant seed bank (Ferguson et al., 1995; Horvitz et al., 1995). For late secondary species that
require large-scale disturbance for either seed germination or seedling recruitment, hurricanes may be critical events in population dynamics.

Subtropical hardwood forests in south Florida are subject to hurricanes at average intervals of 8.5 years (Chen and Gerber, 1990), the highest frequency in the continental US. In addition to hurricane disturbance, subtropical hardwood forests in south Florida are usually embedded in a dominant habitat of Slash Pine (*Pinus elliottii* var. *densa*) rockland and are subject to frequent fires that burn through the pinelands (Snyder et al., 1990). Forest fires maintain the subtropical forest/pineland boundaries (Loope and Urban, 1980; Loope and Dunevitz, 1981), with surface fires usually burning only the edge of the subtropical forests due to the higher humidity and moist organic layer present within the hardwood forests. In drought years, however, severe fires infrequently enter and burn some forests as ground fires (Robertson, 1953; Loope and Urban, 1980; Loope and Dunevitz, 1981). Although most subtropical forest tree species are killed by intense ground fires, some species respond positively to fire disturbance through seedling recruitment. The large canopy tree *Lysiloma latissilium* (L.) Bentham recruits new seedlings in the burned edge of forests after low-intensity surface fires and throughout the forest after severe ground fires (Slater and Platt, 1995). Because fire effects are usually spatially patchy, a mosaic of new *Lysiloma* seedlings and surviving adults persist in the ecotonal areas surrounding the hardwood forests (J.B. Pascarella, personal observation, 1992).

The longest ecological study of a south Florida subtropical forest has been the analysis of forest structure and dynamics at Castellow Hammock in Goulds, FL (Phillips, 1940; Alexander, 1967; Molnar, 1990; Mack, 1992). This forest, which was originally surrounded by pineland on all sides, is now largely isolated by agricultural development except a thin strip of pineland on the north and west sides (Molnar, 1990). At this site that did not experience fire or hurricane disturbance from 1940 to 1989, *Lysiloma* exhibited characteristics typical of a pioneer tree species. *Lysiloma* was the primary hammock tree species that invaded the adjacent pineland once fire was excluded (1940–1967) and initiated a succession toward subtropical hardwood forest (Alexander, 1967; Molnar, 1990). Within the boundaries of the original hardwood forest, however, *Lysiloma* declined in density, frequency, basal area, dominance, and importance value. By 1989, the population structure of *Lysiloma* in the mature forest at Castellow consisted only of very large senescing adults (Molnar, 1990; Mack, 1992; J.B. Pascarella, personal observation, 1992). Within the forest, these trees were the primary cause of treefall gaps (mean size = 0.05 ha) (Molnar, 1990). However, within these same gaps, very few *Lysiloma* seedlings were found (Molnar, 1990).

Due to the agricultural and suburban development surrounding Castellow forest, the ecotonal fire-maintained edge that is an important habitat for *Lysiloma* had been eliminated by 1989. Based on the life-history data, the long-term probability of persistence of *Lysiloma* within undisturbed subtropical forest in south Florida was low under the fire-exclusion regimes typical of urban forest preserves found outside Everglades National Park. Both Molnar (1990) and Mack (1992), however, suggested that hurricane disturbance may play an important role in determining the long-term coexistence of canopy tree species in south Florida hardwood forests.

The passage of Hurricane Andrew on August 24, 1992 offered the opportunity to compare the impact of hurricane disturbance on *Lysiloma* populations at Castellow Hammock and two other sites. Hurricane Andrew was a strong but compact Category 4 hurricane with sustained winds greater than 242 km h⁻¹ and gusts of 282 km h⁻¹ near its center (Mayfield et al., 1994). Three main questions were addressed: (1) Did this disturbance encourage regeneration of senescent *Lysiloma* populations within mature forests that have not experienced recent hurricane or fire disturbance? (2) Did damage and regeneration differ along the gradient of hurricane disturbance? (3) Did hurricane disturbance provide a spatial or temporal escape from predispersal seed predation?

2. Methods

2.1. Study species

*Lysiloma latissilium* (= *L. bahamense* Bentham) is a mimosoid legume canopy tree (13–20 m
height, > 50 cm d.b.h.) in tropical and subtropical semievergreen and semideciduous forests of south Florida, the Bahamas, Cuba, and the Yucatán Peninsula (Long and Lakela, 1971; Elias, 1974; Tomlinson, 1980; CIQRO, 1982; Olmsted et al., 1983). Flowering occurs from March–August and seed dispersal is through wind dispersed indehiscent pods that ripen during the fall–winter months. Pods land on the forest floor, decay, and the seeds become incorporated into the seed bank (Thompson, 1980). No arils or elaisomes are present. Predispersal seed predation has been noted although levels of seed predation were not quantified (Tomlinson, 1980). Developing seeds are attacked in the summer months by a specialist bruchid beetle, *Merobruchus lysiloma* Kingsolver, which feeds only on *Lysiloma latisiliquum* and the related West Indian species *Lysiloma sabicu* Bentham (J. Kingsolver, personal communication, 1993).

2.2. Study sites

Subtropical hardwood forests in south Florida are found on small localized outcrops of limestone and contain primarily tropical tree and shrub species of wide distribution throughout moist to dry limestone forest areas of the Caribbean (Tomlinson, 1980; Smith and Vankat, 1992). I studied two forests on the mainland (Castellow Hammock in Goulds, FL (CAS) and Mosier Hammock in Everglades National Park (MOS)) and one forest in the upper Florida Keys (John Pennekamp State Park on Key Largo, FL (JPS)). All populations occur between 80° and 81°W and 25° and 26°N. Castellow Hammock consists of 55 acres of inland hammock and pineland at SW 223 St. and SW 162 Ave. and is managed as a natural area by Metro-Dade Parks. Study plots were located in the inside of the forest with plots in both historical hammock and successional hammock from pineland. Mosier Hammock is in the Long Pine Key campground area in Everglades National Park. Study plots were east and west of the nature trail. John Pennekamp State Park is found at mile marker 102.5 along U.S. 1 in Key Largo, FL. Study plots were within the mature undisturbed forest near the end of the hammock nature trail.

Hurricane Andrew passed over the southern portion of Dade County, FL on August 24, 1992 (Mayfield et al., 1994). JPS was well south of the path of Hurricane Andrew, MOS was south of the southern eyewall (Armentano et al., 1995), and CAS was within the northern eyewall (Horvitz et al., 1995). Five 5×10-m plots had been established before Hurricane Andrew at CAS in June 1992 and were established after Hurricane Andrew at MOS in December 1992 and JPS in December 1993.

2.3. Damage and mortality

JPS did not suffer structural damage to the forest (R. Skinner, personal communication, 1993) while CAS and MOS were surveyed in December 1992 to estimate mortality and damage. Damage from Hurricane Andrew was placed into the following classes: trees tipped over with the bole on the ground and roots ripped out of the soil, top snapped, tree upright but loss of major limbs, tree upright but minor limb loss, tree bent over (> 15° orientation but less than < 60°), and no damage (tree upright, minor limbs present). The compass orientation of tipped-up boles and the areas of the tip-up pit were recorded. Light availability in the understory was estimated using hemispherical canopy photographs in a separate study (Pascarella, 1995).

2.4. Seedling recruitment

In December 1992 at CAS, I selected the first six tipped-up trees alongside the nature trail, measured their d.b.h., and recorded the number of *Lysiloma* seedlings and measured their heights in two 1×1-m plots in each of two areas: the tip-up pit and along the bole. In December 1993, seedlings were counted at all sites and the location of seedlings was classified into tip-up pit or level ground. The surface area of the tip-up pits was calculated as the surface area of a circle. Seedling height was measured for all seedlings in the plots. A random subsample of 25 individuals was marked in December 1993 and followed until December 1995 for survival and growth. At all sites, reproductive activity of adult trees in the study plots was surveyed in December 1993 and 1994 by counting the number of adult trees with seed pods. Seed rain into the soil was estimated using ten randomly placed 1×1-m quadrats in each plot in December 1994. The number of seed pods was
recorded. Fifty randomly selected seed pods from the forest floor were opened and the number of seeds/pod and bruchid beetle activity determined in December 1993 and 1994.

2.5. Experimental seed germination

To examine seed germination behavior under different light conditions, ten seeds (ten replicates per treatment) were placed inside wire mesh cages to protect against postdispersal seed predation in June 1993 at CAS in both shaded (treefall crowns with abundant vine cover) and sunny (treefall pit areas) and monitored monthly for seed germination for 1 year. To examine the influence of soil temperature fluctuations on germination, ten seeds (15 replicates per treatment) were placed in potting soil, moistened, and heated for 10 h daily at 66°C for 5 days while control seeds were moistened but not heated. Pots were then placed in an outdoor irrigated shadehouse and germination monitored at the end of 2 months.

3. Results

3.1. Damage and mortality

Mortality of adult *Lysiloma* trees differed significantly among study sites. Eighty percent of the adults died at CAS while only 17% died at MOS and none died at JPS (Table 1). Mortality at CAS and MOS was associated with the most severe damage type of tip-ups or top snapping. None of the lightly damaged trees at MOS Hammock died and all were vigorously resprouting by December 1993.

The distribution of damage type also differed significantly between sites (Table 1). CAS had the most severe damage while MOS suffered light damage. No damage was noted at JPS (Fig. 1(A)). At CAS, most trees tipped over or the main trunk snapped (Fig. 1(B)), while at MOS most trees snapped or suffered major branch loss but remained upright. The type of damage suffered may have been influenced by the size of adult *Lysiloma* trees. All trees at CAS were greater than 40 cm d.b.h. while trees at MOS were mostly less than 10 cm d.b.h.

At CAS, *Lysiloma* tip-ups (n = 6) were to the southwest (67%) or southeast (33%) showing that some trees fell over during the entry while others fell during the exit of the hurricane. Tipped up trees created pits that averaged 8.42 m² in area and were 20 to 60 cm in depth. After the hurricane, tip-up pits consisted of exposed limestone rocks with pockets of soil and were completely clear of vegetation (Fig. 1(C)). Pit area was significantly positively correlated with the d.b.h. of the fallen tree (Pearson correlation. P < 0.01, r² = 0.70, n = 6). The site closest to the northern eye wall of the hurricane (CAS) had the highest posthurricane light levels, the site south of the southern eye wall (MOS) intermediate light levels, and the site distant from the hurricane (JPS) the lowest light levels (Pascarella, 1995). The most damaged site (CAS) had light levels two times higher than the lightly damaged site (MOS) and six times higher than the undamaged site (JPS) (Pascarella, 1995).

Table 1
Mortality and damage of *L. latifolium* populations. The percentage of individuals damaged and the percent of individuals dying from this damage are in parenthesis. Mortality was significantly different between sites (P < 0.05. χ² = 11.71, d.f. = 2) as was damage class (P < 0.05. χ² = 11.71, d.f. = 2)

<table>
<thead>
<tr>
<th>Site and sample size</th>
<th>CAS (10)</th>
<th>MOS (18)</th>
<th>JPS (2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>D.b.h. ± 1 SE (cm)</td>
<td>40.62 ± 3.61</td>
<td>11.29 ± 1.37</td>
<td>50.5 ± 2.5</td>
</tr>
<tr>
<td>Mortality (%)</td>
<td>80</td>
<td>17</td>
<td>0</td>
</tr>
<tr>
<td>Tip-up (%)</td>
<td>80 (100)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Top snapped (%)</td>
<td>20 (0)</td>
<td>39 (100)</td>
<td>0</td>
</tr>
<tr>
<td>Major branch loss (%)</td>
<td>0</td>
<td>39 (0)</td>
<td>0</td>
</tr>
<tr>
<td>Minor branch loss (%)</td>
<td>0</td>
<td>17 (0)</td>
<td>0</td>
</tr>
<tr>
<td>Bent over (%)</td>
<td>0</td>
<td>6 (0)</td>
<td>0</td>
</tr>
<tr>
<td>No damage (%)</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
</tbody>
</table>
3.2. Seedling recruitment

Two months after the hurricane, in October 1992, a Lysiloma seedling cohort germinated at CAS (Fig. 1(D)). Seedlings at CAS were more common in tip-up pits than along the bole in tipped-up Lysiloma trees alongside the nature trail (\( \bar{x} \) pit seedlings \( \pm 1 \) SD = 26.83 \( \pm 22.99 \) vs \( \bar{x} \) bole seedlings \( \pm 1 \) SD = 1.5 \( \pm 1.12 \), \( P < 0.05 \), \( t = -2.68 \), d.f. = 5.1). Mean seedling height \( \pm 1 \) SE in October 1992 was 34.3 \( \pm 2.3 \) cm \((n = 161\) seedlings). Within the plots, the surface area covered by the tip-up pits at CAS was 67.5 \( m^2 \) or 27% total area. By December 1993, 287 Lysiloma seedlings were present at CAS with 60% seedlings found in the tip-up pits and the remaining 40% in a large treefall gap in Plot 5. No seedlings emerged at MOS or JPS in any year. Mean seedling height \( \pm 1 \) SE by December 1993 was 125 \( \pm 12.4 \) cm \((n = 25)\), December 1994 was 175 \( \pm 18.9 \) cm \((n = 25)\), and 230 \( \pm 35.4 \) cm by December 1995 \((n = 23)\). Mean d.b.h. by December 1995 was 3.5 \( \pm 0.8 \) cm and seedling survival was 92%.

Light level was more strongly correlated with number of seedlings in the open (\( r^2 = 0.86 \), \( P = \).
Table 2
Reproduction and seed predation

<table>
<thead>
<tr>
<th>Site</th>
<th>Year</th>
<th>% Reproductive (no. trees)</th>
<th>Pod density (m⁻¹)</th>
<th>% Pods attacked (no. pods)</th>
<th>Seeds per pod ± 1 SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Prehurricane and undisturbed sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>UMAMI a</td>
<td>1991</td>
<td>100 (14)</td>
<td>10.5</td>
<td>98</td>
<td>1.44 ± 0.05 (50)</td>
</tr>
<tr>
<td>JPS</td>
<td>1993</td>
<td>100 (2)</td>
<td>15.3</td>
<td>100</td>
<td>0.18 ± 0.07 (50)</td>
</tr>
<tr>
<td>JPS</td>
<td>1994</td>
<td>100 (2)</td>
<td>18.1</td>
<td>100</td>
<td>0.00 ± 0.00 (50)</td>
</tr>
<tr>
<td><strong>Disturbed posthurricane sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>MOS forest</td>
<td>1993</td>
<td>0 (15)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>MOS edge</td>
<td>1993</td>
<td>100 (10)</td>
<td>13.5</td>
<td>40</td>
<td>5.98 ± 0.52 (50)</td>
</tr>
<tr>
<td>MOS forest</td>
<td>1994</td>
<td>13 (15)</td>
<td>0.7</td>
<td>100</td>
<td>0.00 ± 0.00 (50)</td>
</tr>
<tr>
<td>CAS</td>
<td>1993</td>
<td>0 (2)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>CAS</td>
<td>1994</td>
<td>0 (2)</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

*a Population at the University of Miami Microbiome, Coral Gables, FL.
- data not available.

0.06, n = 5) than with number of seedlings in tip-up pits (r² = 0.27, P = 0.67, n = 5). No significant correlation was found between mean light level/plot and number of tip-up pits/plot (r² = 0.15, P = 0.81, n = 5) suggesting that pit formation does not guarantee high light levels immediately above a pit during a hurricane as other trees may fall over the pit.

Hurricane Andrew removed the entire 1992 maturing seed crop at CAS and MOS. In 1993, the adult trees at JPS reproduced (Table 2). Although seed pods were abundant on the shaded soil layer, most were empty. Only 14% of the pods contained seeds and evidence of seed predation by the bruchid beetle, *Merobruchus lysilotomae*, was present on most pods with frass and larva exit holes in pods. At both MOS and CAS, surviving adult trees within mature forest did not flower in 1993. However, some small adults outside the forest study plots in the pineland/hardwood forest ecotone flowered in 1993 at MOS. Mean number seeds/pod of these individuals was the highest observed at any site. In 1994, all sampled adults at JPS were reproductive but high levels of seed predation again limited seed production. All sampled pods were attacked by bruchids and only one seed was produced. At MOS, a few adults in the forest plots reproduced but few seed pods were produced. Seed production was also limited by high incidences of bruchid beetle predation with all sampled pods attacked by bruchids and only one seed produced. No individuals at CAS reproduced in 1994.

3.3. Experimental seed germination

None of the caged seeds placed in CAS in June 1993 in either shade or sun germinated within the year observation period. Most placed seeds were still present by June 1994 and had not been removed by postdispersal seed predators. In the shadehouse, the heat treatment had a significant effect as heat treated seeds had 35 times greater germination than unheated control seeds (\( \bar{x} \) seed germination heat treatment pots ± 1 SE = 34.7 ± 3.2% vs \( \bar{x} \) seed germination control pots ± 1 SE = 1.3 ± 0.91%, \( P < 0.0001 \). Mann–Whitney \( U = 225 \), \( n = 30 \), data arcsin transformed).

4. Discussion

4.1. Damage, mortality, and understory light availability

The impact of hurricane disturbance on *Lysilotoma* varied depending on both the intensity of hurricane disturbance and adult size. Mortality and damage were greatest at the site that experienced the highest wind speeds, while most adults were not killed and suffered less damage at the site that experienced lower wind speeds. However, this pattern may be related to size.

Horvitz et al. (1995) found that the highest mortality of all tree species (stems > 2 cm d.b.h.) was at
the CAS forest (67%), while a lightly damaged forest north of the eye wall that had similar posthurricane light levels to MOS suffered the least tree mortality (32%). Both Horvitz et al. (1995) and Koptur et al., personal communication (1995) found that large trees suffered disproportionately more damage than small trees. Ross et al. (1995), working in hardwood forests in north Key Largo damaged by Hurricane Andrew, also found that large trees suffered the most damage with many snapped and tipped up. Hardwood forests within Everglades National Park (similar in location to MOS) had high levels of damage but low mortality. Damage patterns differed in these forests in that small trees suffered more mortality than larger trees due to trunk snapping and burial by canopy debris (Slater et al., 1995). As Lysiloma can grow to be one of the largest canopy trees in these forests, it is particularly susceptible to being damaged by strong hurricane winds (Molnar, 1990; Ross et al., 1995).

Posthurricane light levels at the most severely disturbed site were much higher than in large canopy gaps from tropical rain forest areas (Dirzo et al., 1992). By 1995, light levels were decreasing rapidly in the understory but were still relatively high in the mid to upper canopy of the disturbed forests (Horvitz et al., 1995).

4.2. Adult reproduction and seed predation

In normal years, adult reproduction is high but most seeds are lost to seed predation by the bruchid beetle Merobruchus lysilomae and total seed rain can be very low in spite of hundreds of pods produced by adult trees. Hurricane disturbance caused a limited cessation of reproduction for at least 2 years after Hurricane Andrew at the severely disturbed site while reproduction ceased for 1 year and was minimal the second year at the lightly disturbed site. In contrast, reproductive adults were noted in both years at the undisturbed site.

Hurricane disturbance allowed limited temporal escape from M. lysilomae at the lightly disturbed site as evidenced by the higher seed production in 1993. Temporal escape was limited to the first year after disturbance as seed predation levels were very high in 1994. At this site, beetle populations may have been maintained by the availability of the small adults within the fire-maintained forest edge that flowered in 1993. Resource availability (i.e. flowering adults of Lysiloma) for M. lysilomae should be strongly linked to the fire-regime and the population structure of Lysiloma as forests in managed natural areas such as Everglades National Park that experience frequent surface fires at their edges usually have small adults in the ecotone area that may resume flowering the year after a hurricane. In CAS, the lack of a pine/hammock ecotone due to urbanization and fire suppression, the even-aged adult population structure resulting from a previous disturbance, and the severe mortality and damage to adults may limit recolonization of this site by M. lysilomae until the seedlings reach reproductive maturity and/or surviving adults begin to reproduce. Because these conditions have not occurred for 2 years within CAS, it is unknown whether the population of M. lysilomae at CAS was extirpated. A population of a flower-galling moth, Periploca sp. (Cosmopterigidae), that feeds on flowering adults of a native forest shrub, Ardisia escallonioides (Myrsinaceae), was extirpated for 2 years following Hurricane Andrew at CAS in spite of abundant flowering in 1993 and 1994. This moth eventually recolonized the site in the fall of 1994 through apparent immigration from nearby forests (J.B. Pascarella, unpublished data). Studies of insect response to hurricane disturbance in Puerto Rico found that many insects were absent immediately after the hurricane but then showed population outbreaks the following year (Torres, 1992).

4.3. Interaction of fire and hurricane disturbance

Limited seed germination of Lysiloma was noted following Hurricane Andrew only in tip-up pits within damaged forests in Everglades National Park (Slater and Platt, 1995; Armentano et al., 1995). Tip-up pits were uncommon in forests in Everglades National Park (Armentano et al., 1995; Slater et al., 1995). Slater and Platt (1995) have suggested that fire is the primary evolutionary and ecological factor regulating germination of this and other pioneer species in south Florida and that hurricane disturbance is not enough to sustain viable populations of this species. However, several lines of evidence suggest that hurricanes can maintain populations of L. latisiliquum: (1) the study sites of Slater and Platt (1995) were in the southern eye wall of the hurricane.
that suffered less severe damage than sites in the northern eye wall (compare estimates of mortality and damage in Horvitz et al., 1995 with Slater et al., 1995). The lack of tip-up pits and seed germination of *L. latisiliquum* in forests in Everglades National Park studied by Slater and Platt (1995) is similar to the observations at the forest MOS in Everglades National Park in this study that also lacked tip-ups and germination. (2) At the severely disturbed site in this study, seed germination was not limited to tip-up pits but was also found in other areas of high light availability such as very large gaps. Even within tip-up pits, germination of the seed bank was strongly correlated with the local light environment. Tip-up pits that were heavily shaded by fallen trees and vines had no seed germination while heavy seed germination was noted in tip-up pits that were highly insolated. In large gaps, however, seed germination occurred without physical soil disturbance. In severely damaged forests, tip-up pits can cover > 25% surface area but seed germination can also occur within large gaps extending the potential signal area for seed germination. (3) There may have been limited seed availability in the dormant seed bank in some Everglades National Park forests due to extensive postfire germination (1989) of the seed bank and the limited time (3 years) for adults to replenish the seed bank. (4) *L. latisiliquum* occurs in habitats where non-anthropogenic fire is a less frequent natural disturbance than hurricane disturbance.

In spite of abundant seed rain at the undisturbed site, seeds did not germinate under the closed canopy of this mature forest. Seeds persist in a dormant condition although quantitative data on seed longevity and dormancy in this species are lacking. Mimosoid genera either have soft, seeds that germinate immediately or hard seeds with dormancy (Corner, 1976; Nielson, 1992). *Lysiloma* (Tribe Ingeae) belongs to this later group whose seeds can have a very long dormancy and in which germination is often associated with seed coat scarification (Cavanagh, 1980; Auld, 1986; Dean et al., 1986). The field experiments on seed germination found no germination even in the tip-up pits 1 year posthurricane suggesting the environment of these pits had changed. Most pits were highly vegetated by the fall of 1993 by young *Lysiloma* seedlings and other pioneer species whose presence reduced soil insolation. Because heat increased germination in the shadehouse, this suggests that immediate posthurricane soil temperature increases were the proximal mechanism that broke seed dormancy. Increased soil temperatures during and after forest fires and land clearing that exposes a buried seed bank would also have a similar effect. Fluctuating soil temperatures have been documented as a trigger for seed germination for some tropical species, primarily legumes and pioneer trees (Quinlivan, 1966; Vasquez-Yanes and Orozco-Segovia, 1982, 1994; Nielson, 1992).

Although fire and hurricanes may act in a similar manner to trigger seed germination through soil temperature fluctuations, they differ in their effects on juveniles and adults. Fires usually kill seedlings, juveniles, and small adults with some larger adults surviving. Hurricanes act mostly on large adults with smaller adults suffering less damage and mortality. Both disturbances are also patchy and the effects on tree populations depend both on predisturbance population structure and intensity of disturbance. The frequency of fire versus hurricane disturbance may affect potential recruitment from a seed bank if seed banks become depleted following severe disturbance.

Pioneer species that recruit seeds from buried seed banks are often short-lived species such as *Trema micrantha*, *Solanum erianthum*, and *Carica papaya*, all species that germinated extensively in some south Florida forests damaged by Hurricane Andrew (Horvitz et al., 1995). While *L. latisiliquum* also uses buried seed banks, it is much larger, longer-lived (60–100 years), slower in growth, older at first reproduction, has abiotic seed dispersal, and dominates early to middle stages of forest regrowth. It is best described as a late-secondary species which requires large-scale disturbance for regeneration. The abundance of *L. latisiliquum* in some south Florida subtropical forests reflects the frequent natural disturbances of fires and hurricanes that impact these forests. For populations of *L. latisiliquum* in isolated forest preserves that no longer experience forest fires due to loss of adjacent pineland habitat, hurricanes may be critical for population persistence. Although hurricanes are common in the south Florida region, local populations of late secondary species such as *L. latisiliquum* may be susceptible to population extinctions due to stochasticity in hurricane size and strength.
In addition to natural disturbances, *L. latisiliquum* does well after anthropogenic disturbance and is an early pioneer into abandoned cleared land (CIQRO, 1982; Ross et al., 1995). Its response to disturbance and usefulness for wood products (Elias, 1974; CIQRO, 1982; Scurlock, 1987) suggests that this species should be investigated for productive management of secondary forests in its native range and similar climatic areas (Boucher et al., 1994). Data from forest areas in the Yucatán, Cuba, and the Bahamas that have different disturbance regimes and histories may help in determining the importance of large-scale disturbances such as fires and hurricanes as well as anthropogenic impacts on life-history traits and population dynamics of *L. latisiliquum*.

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