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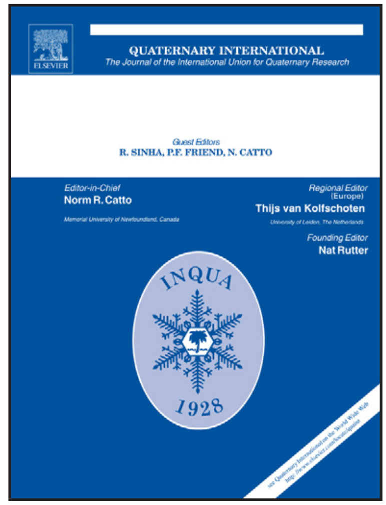

Paleoecological record of hurricane disturbance and forest regeneration in Nicaragua

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Title: **PALEOECOLOGICAL RECORD OF HURRICANE DISTURBANCE AND FOREST REGENERATION IN NICARAGUA**

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ABSTRACT

Studying infrequent phenomena (e.g. hurricanes) and slow processes (e.g. forest regeneration) greatly challenges the ecological techniques of real-time studies. By combining the two relatively new approaches of paleotempestology and fine-resolution palynology, this study provides insight into the impacts of hurricanes and the post-hurricane regeneration of forests. I analyzed a 5 m sediment core from a swamp lagoon on the Caribbean Coast of Nicaragua that covered the entire 8,000 yr history of the swamp (Urquhart 1997). X-rays revealed a sand layer dating to c. 3300 BP of the type deposited by hurricanes. Pollen analyses showed this sand layer was followed by major changes in vegetation and fires. This pattern is identical to the wake of Hurricane Joan, which struck the area in 1988 and left 90,000 hectares of damaged swamp forest that burned shortly after. After the prehistoric hurricane, forest vegetation did not return until 500 years later, due to repeated burning. This parallel event of the past illustrates a possible course for modern forest regeneration. As a counterpart to direct ecological analysis, fine-resolution paleoecological study can provide great insight for the study of rare events and slow processes.

Key Words: Disturbance, fire, forest, hurricane, Nicaragua, paleoecology, pioneer, pollen, regeneration, swamp, tropics.

Key Phrases: Paleoecological forest regeneration; Severe hurricane struck Nicaragua 3300 y before present, Disturbance 3300 y before present parallels present hurricane and fires; Long time span coverage with paleoecological techniques; Forest returned 500 y after prehistoric hurricane; First study of forest regeneration with paleoecological analysis;

INTRODUCTION

Difficulties exist in studying rare events and slow processes through real-time ecological studies. Hurricane damage to tropical and subtropical coastal ecosystems is regular phenomenon (Liu and Fearn 1993, 2000, Boucher 1990), but infrequent in ecological time. The result is a series of sites that have been studied (Puerto Rico, South Carolina, Nicaragua, and Florida), but for only a single disturbance event (Hurricanes Hugo, Hugo, Joan, and Andrew, respectively), resulting in a conclusions of unknown generality and applicability. Additionally, forest regeneration after severe damage requires decades to centuries, far beyond the time scale of most ecological studies.

Paleoecological studies provide the opportunity to survey long periods for rare events and slow ecological processes can be addressed. Past studies have outlined sediment layers generated by prehistoric hurricanes (Liu and Fern 1993, 1997, Davis et al. 1989), but have not analyzed the impacts of the hurricanes on vegetation. Fine resolution palynology is a suitable method to analyze vegetation changes associated with past hurricanes (Sturludottir and Turner 1985, Green et al. 1988).

In October 1988, Hurricane Joan, a class 4 hurricane on a scale of 1 to 5, struck the Caribbean Coast of Nicaragua near the town of Bluefields. With winds up to 290 km/h, it severely damaged 500,000 ha of tropical forest, including 100,000 ha of swamp forests (Boucher et al. 1990). In the dry season following the hurricane, swamp forests burned widely as a result of downed vegetation and human agricultural fires. During the decade that has passed since the hurricane, terrestrial ferns have dominated the vegetation, which shows few signs of forest regeneration. The hurricane disturbance and subsequent fires greatly altered the ecosystem, which now may require decades or centuries to regenerate to its forested state.

Boucher (1992) estimated that hurricanes affect the Caribbean Coast of Nicaragua with a periodicity of about 100 years. The likelihood of a previous hurricane and the slow regeneration of the damaged swamps prompted me to conduct a paleoecological study to search for evidence of past hurricanes. To identify and study past hurricanes, I analyzed a 5.0 m sediment core from Laguna Negra, Nicaragua. I found one sediment layers (292-296) ascribable to prehistoric hurricanes (Liu and Fearn 1993, 1997, 2000; Liu et al. 1994). Analyses that include a fine resolution paleoecological dissection of one of these layers are presented below.

In this study, I addressed several questions attempting to relate the hurricane disturbance of 1988 to past events: (1) Have there been major hurricanes in this area in the past? (2) How frequent are major hurricanes in this area? (3) Was fire damage associated with past hurricane disturbance? (4) What species colonized after the hurricane and/or fire disturbance? (5) How much time was necessary for forest regeneration?

REGIONAL SETTING

Laguna Negra (Black Lagoon) is a small blackwater lagoon located inland from the Caribbean Coast of Nicaragua at 12° 02’ 42.05” N, 83° 55’ 39.22” W (Figure 1). It is approximately 150 m x 60 m, with a maximum depth of 6.8 m and average depth of ~5m. Caño Negro, or Blackwater Creek, flows into and out of the lagoon. However, it has approximately no net current and is much shallower than the lagoon. Above Laguna Negra, Caño Negro is about 3 m wide and 1 m deep. It probably continues only a few hundred meters above the lagoon. At its exit from Laguna Negra, Caño Negro is approximately 6 m across and 2 m deep. It deepens to a depth of 10 m for most of its length and a width of up to 60 m.

Laguna Negra is located 17 km from the open Caribbean Sea and 13 km from Bluefields Bay, a large saltwater bay surrounding the town of Bluefields. It is located only 4 km from Rio Escondido, a large river that rose 5 m during Hurricane Joan in 1988. Laguna Negra and Caño Negro have a significant response to tides. While the Caribbean tides are minimal, visible tidal changes were observed 17 river km upstream from the mouth of Caño Negro (Urquhart, unpublished data). During the dry season, the water of Caño Negro becomes brackish. Red mangroves (*Rhizophora mangle* L.) grow along the river banks to within five river km of Laguna Negra.

The vegetation around Laguna Negra was until recently a mature swamp forest, composed of species such as *Symphonia globulifera* L. f. (Clusiaceae), *Carapa guianensis* Aubl. (Meliaceae), *Pterocarpus officinalis* Jacq. (Fabaceae), and *Raphia taedigera* Mart. (Arecaceae).

In 1988, the passage of Hurricane Joan set off a devastating series of changes to the swamps around Bluefields, Nicaragua (Vandermeer et al. 1990). While hurricane winds severely damaged the trees of the swamp, fires during the dry season of 1989–just three months after the hurricane–killed almost all of the trees in the forest. The resulting landscape was colonized by pioneering herbaceous species that appear to be retarding regeneration. The most abundant pioneer is the fern, *Blechnum serrulatum* Rich., accompanied by grasses (Poaceae), sedges (Cyperaceae), and cattails (*Typha* sp.). Immediately surrounding the lagoon, a 10-20 m thick strip of forest has survived, with the above-mentioned forest species and *Annona glabra* L. (Annonaceae), *Cassipourea elliptica* Poit. (Rhizophoraceae), *Pachira aquatica* Aubl. (Bombacaceae), and *Acoelorraphe wrightii* Becc. (Arecaceae).

A very diverse tropical moist forest occurs within 5 km of Laguna Negra (Vandermeer et al. 1995). While notoriously poor dispersers of large quantities of pollen, trees from the moist forest could influence the pollen spectrum in sediments. Wind-pollinated species, such as *Podocarpus guatemalensis* Standl., are likely dispersed from the moist forest. Savannas of *Pinus caribaea* var. *hondurensis* Morelet grow on ancient beaches approximately 20 km northeast of Laguna Negra. Because of trade winds (E-NE), the prolific pollen of *Pinus* is expected at low levels in the pollen record.

MATERIALS AND METHODS

In October 1995, I obtained two 5 m sediment cores from the deepest part of Laguna Negra, using a modified Livingstone sampler with a locking piston (Colinvaux et al., 1999). The cores were capped for transport. Before opening, the cores were X-rayed to check for variation in sediment density. I opened them with a side cutting saw made specifically for opening core tubes. After opening, I described the sediments using a Munsell Color Chart and made visual descriptions of the stratigraphy. The analyses in this paper are from the first of the two cores–the *Laguna Negra IA* core, which spans the entire 8,000 yr history of the coastal swamp (Urquhart, 1997).

I concentrated pollen from 0.5 cm^3 subsamples according to standard palynological methods (Faegri et al. 1989). To each subsample, I added single commercial *Lycopodium* tablet (~12,500 spores) per sample as exotic markers for pollen concentration calculation. I counted the samples to at least 350 grains. Roubik and Moreno (1990) and the pollen reference collection at the Smithsonian Tropical Research Institute aided in the identification of pollen. Pollen concentrations were calculated by the following formula:

$$\text{grains/cm}^3 = \frac{(2\ \text{samples/cm}^3)\bullet(12{,}500\ \text{spores per sample})\bullet(\#\ \text{pollen grains counted})}{(\#\ \textit{Lycopodium}\ \text{spores counted})}$$

I prepared a pollen diagram using Tilia and Tilia Graph (Grimm 1990). Using the CONNISS (Grimm 1987) subroutine of Tilia program, I analyzed the data for stratigraphic grouping and produced a dendrogram, used for delimiting pollen zones based on changes in similarity clusters.

Microscopic charcoal particles were divided into two categories (5-30 µm, > 30 µm) and tallied. In the pollen diagram these two categories are merged, and the total counts are presented. Macroscopic charcoal particles were observed in some samples when they were passed through a 250 µm screen.

I did Loss on Ignition (LOI) measures for 1 cm^3 samples from a majority of the depths used for pollen concentration. The samples were dried at 200° C and weighed (dry weight) and then combusted at 550° C and weighed again. Percent mass lost on ignition (LOI) was calculated by the following formula:

$$\text{LOI} = (\text{dry weight} - \text{combusted weight}) / \text{dry weight}$$

From the combusted samples, I measured Carbonate concentration by using 0.5 N HCl to evolve carbonate from the samples after LOI burning (Carver 1971). The remaining material was dried at 200° C and weighed. Percent Carbonate was calculated by the following:

Carbonate = (Dry Weight after HCl) * (1-LOI)

After X-ray and palynological analyses indicated zones of interest, I extracted five sediment samples for AMS (Accelerator Mass Spectrometry) dating. The samples from 310, 300, 295, 290, and 278 cm established the chronology for the region around the sand layer at 292-296 cm depth. Two macroscopic wood fragments, from 25 cm and 466 cm depth, were measured similarly to establish the time span of the core. The samples were prepared using a series of acid and base washes specified by the Center for AMS at Lawrence Livermore National Laboratory (CAMS-LLNL) and transported to CAMS-LLNL, where I assisted directly in the remainder of the preparation and dating process. The $\delta^{14}C$ fractions were measured in the LLNL accelerator. To calibrate the $\delta^{14}C$ fractions in calculating radiocarbon ages, several samples were measured for $^{13}C/^{12}C$ ratios. For samples where I did not directly measure the $^{13}C/^{12}C$ ratio, I averaged the values for like samples and used this to calculate radiocarbon ages. Calibration of radiocarbon dates followed Stuiver et al. (1998). A single bulk sediment sample, 255-250 cm, dated by Beta Analytic also fell in the range of depths analyzed in this paper and is reported here. All dates reported in this paper are ^{14}C years BP.

RESULTS

Stratigraphy and Chronology.–The age recorded for 466 cm depth defines the span of the core, 8020 ± 60 ^{14}C years (Table 1). A wood fragment from 25 cm depth yielded a modern radiocarbon age, demonstrating that the core spanned from c. 8,000 yrs to present.

The X-rays of the sediment cores revealed a 4 cm thick layer of sand at 292-296 cm depth (Figure 2). Liu and Fearn (1993, 1997) ascribed such bands in coastal swamps to hurricane surges. The band had a distinct fining-upward nature (denser below and finer above), similar to those deposited by some hurricanes (Davis et al. 1989). The denser material at the base of the layer is indicative of a high-energy event, such as a tsunami or hurricane. In the Caribbean region, hurricanes are frequent and there is no record from other areas of a major Holocene tsunami in the Caribbean. The sand layer defined the location for palynological analysis of the prehistoric hurricane event.

Loss on Ignition and Percent Carbonate values discriminate the band of denser sediments seen in X-rays. Loss on Ignition was only 29.0% for the sand layer at 295 cm depth compared to 50.0-63.8% for other samples in the 250 cm – 310 cm range. Percent Carbonate was only 10.2% at 295 cm and ranged from 17.7-24.2% for the other samples. For comparison, clays from 490 cm depth (base of core) were 22.8% carbonate.

The chronology of this period is based on five AMS 14 C dates and one conventional (beta counter) date. The dates span from 3830 BP to 2820 BP (Table 1, Figure 3). Because of the rapid sedimentation at the hurricane band, I calculated two separate regressions for deposition times, before the hurricane and after the hurricane. The two dates prior to the sand layer give a deposition time of 20 y/cm. Isolating the dates after the influx, the dates align with a slope of ~15 y/cm of sedimentation. These are comparable to deposition times in accumulating peats of the swamp (Urquhart, 1999).

The age of 3340 ± 50 for 295 cm depth (bottom of sand layer) is indistinguishable from the age of 3360 ± 60 y for 290 cm (top of sand layer). The five centimeters of sediments accumulated in this span arrived very rapidly, furthering the suggestion of a storm surge from a hurricane rapidly depositing the sand layer.

In 1988, Hurricane Joan pushed a storm surge to the town of El Rama, located 55 km upstream from Blueifelds located on the Rio Escondido (J. Vandermeer, Personal Communication). The Rio Escondido runs within 4 km of Laguna Negra to the northwest, and the storm surge of Hurricane Joan in the river could have spilled over into Laguna Negra. Possibly due to methodological failures resulting in no stable mud-water interface to analyze, there was no signal of Hurricane Joan observed in the sediments. The mud-water interface mixed around in the coring tube, producing a homogenized upper 20 cm of the sediments. Additionally, the type of sediments Hurricane Joan would have produced differs greatly from prehistoric and is not ideal for detection. The modern sediments of the nearshore Caribbean and Bluefields Bay, from which a sand layer would originate, have become very silty due to agricultural expansion (P. Christie and J. Ryan, pers. comm.). The silty sediments would not leave as clear a signal as sand, further contributing to why there were no observable features in the Xrays of the mud-water interface.

Following the tradition of naming hurricanes, the prehistoric hurricane presented here are named Hurricane Elisenda (3340 ± 50 y BP) after a young girl living near Laguna Negra in the forests damaged by Hurricane Joan.

Notes on Pollen Types.–Spores of the fern, *Blechnum serrulatum*, are monolete and psilate like many other fern spores, but the perrine is distinct in having gemmae. Fern spore perrines are not always resistant to acetolysis (Punt et al. 1994), and many of the *B. serrulatum* spores may have lost their identifying perrines. All fern spores in the appropriate size range (30-40 mm) with gemmae were assigned to *B. serrulatum*, the remainder being noted simply as monolete fern spores. This may be an underestimate of *B. serrulatum* abundance.

Unlike most tropical pollen spectra, I found little Moraceae/Urticales pollen in the sediments. Typically, researchers divide the Urticales into different morphotypes depending on pore number, identifying only a few genera: *Cecropia, Ficus,* and *Trema* (Rodgers and Horn 1996). However, because of low numbers of Urticales, I lumped all but *Cecropia* and *Trema* into a single category. Only one *Ficus* grain appeared in the pollen counts.

Pollen Zones.–The CONNISS dendrogram provided the framework for dividing the pollen diagrams (Figures 4 and 5) into zones. The transitions between zones are based on stratigraphic changes in similarity of pollen assemblages.

<u>Pollen Zone 1. Pre-disturbance</u>. In the pre-disturbance zone, the vegetation was forest, including *Campnosperma* and *Alchornea* (Figures 4 and 5).

<u>Pollen Zone 2. Hurricane Elisenda.</u> This zone is isolated in the pollen diagram because a sand layer occurs in the sediments at this depth. The sand layer is 4 cm thick, ranging from 296-292 cm depth. Loss on ignition values dropped from 63% at 296.5 to 29% at 295 and 37% at 292.5. Above 292.5, LOI values were around 50%. This sand layer is coarse sand of the type brought in by a tidal surge, either from a tsunami or a hurricane. Because of the resulting changes in vegetation and fires that occurred after

this event, this sand deposit is interpreted as the result of a storm surge after a hurricane. Liu and Fearn (1993) found similar sand layers in coastal ponds in Alabama correlating to hurricanes.

Pollen Zone 3. Fire Period 1. Duration ~ 200 years. This zone has the presence of charcoal and high abundance of disturbance taxa pollen, e.g. Cyperaceae, Gramineae, and *Typha*. There is also an increase in abundance of *Blechnum serrulatum* fern spores. This fern is the same fern that is currently dominant in the fire-damaged swamps around Bluefields. While fires and graminoids may suggest a drought, the persistence of *Podocarpus* pollen argues against this. Furthermore, *Blechnum serrulatum* is only found in very moist environments. Some microscopic charcoal is found in the pollen preparations, and macroscopic charcoal was present in the samples at 288 cm and 285cm.

Pollen Zone 4. Regeneration Period 1. Duration ~75 years. In this zone, the pollen spectrum begins to change to reflect a forested vegetation. Both *Campnosperma* and *Alchornea* increase. Microscopic charcoal fragments decrease, and macroscopic fragments were not present. This period represents a regenerating swamp forest in the absence of fires.

Pollen Zone 5. Fire Period 2. Duration ~75 years. A fire, evidenced by increased charcoal, damages the regenerating forest, reducing the pollen of *Campnosperma* and *Alchornea*. *Gramineae* pollen increases sharply, as do fern spores. The sample from 268 cm had a significant amount of macroscopic charcoal before pollen concentration, as well as microscopic charcoal in the concentrated pollen mixture.

Pollen Zone 6. Regeneration Period 2. Duration ~90 years. In this zone, forest elements increase. *Campnosperma panamensis, Cordia alliodora, Ilex*, and *Alchornea* pollen all increase. Cyperaceae, Gramineae, and *Typha* pollen and fern spores all decrease. This is the regeneration of a swamp forest. Six pollen counts, spaced at 1cm (~ 15 years), define the regeneration.

Pollen Zone 7. Swamp Forest. In this zone, tree pollen is common again. *Campnosperma* pollen achieves the levels it will maintain for several centuries. *Alchornea, Ilex, Myrica*, and *Cordia* are present at substantial levels. Disturbance taxa are reduced to their background levels (always present because they are wind dispersed and travel from other ecosystems too). The loss of *Blechnum serrulatum* spores indicates its replacement in the swamp by a woody forest. This zone begins 400-500 years after the initial hurricane disturbance.

DISCUSSION

Hurricane Elisenda, c. 3300 BP.–The pollen diagram illustrates the effect of both hurricane and fires on the Laguna Negra ecosystem. The combination of hurricane and fires also occurred when Hurricane Joan struck the Caribbean Coast of Nicaragua in 1988 (Table 2). In the following dry season, fires swept through the damaged forest. Hurricane winds have both direct and indirect effects on forest trees. Directly, the trees are stripped of their leaves and their branches or trunks broken. Indirectly, a large amount of downed woody debris and vegetation are left by the hurricane, providing fuel for fires that further damage the trees. The extreme result of this was observed in the 1989 fires that burned 90,000 of 100,000 ha of hurricane-damaged swamp forest in Nicaragua (Brooks and Vandermeer, unpublished data).

Fires in wet tropical ecosystems are often associated with droughts (Uhl and

Kauffman 1990, Horn and Sanford 1992), but several features of the pollen diagram suggest that the fires were not generated by a long period of drought (decades to centuries). *Podocarpus* pollen remained constant throughout the diagram. *Podocarpus* is a slow growing tree that requires a wet lowland *terra firme* forest (Liu and Colinvaux 1985), and its continued presence demonstrates the existence of a wet forest nearby. *Blechnum serrulatum*, the fern that colonized the post-disturbance swamps, is a wet area specialist as well (McCullough et al. 1956).

Regeneration periods 1 and 2 could be a single period without a true fire zone separating them, but several data refute this. The simultaneous increase of forest elements *Campnosperma* and *Alchornea* at 272 cm depth suggest a true forest development, rather than a statistical artifact. The sediments at 268 cm–the layer that defined Fire 2–were the only sediments in the entire core with visible amounts of macroscopic charcoal dust. Clark (1988) determined that larger charcoal particles are a more significant indication of fire, whereas microscopic charcoal is dispersed over long distances and redeposited and thus may not signify a local fire disturbance. The abundance of macroscopic charcoal suggests a distinct fire from those in Fire Period 1. Fire 2 produces significant changes in the vegetation different than would be expected in a continually regenerating forest. *Campnosperma* and *Alchornea* pollen both drop. The spike of Gramineae pollen and an increase in *Blechnum serrulatum* spores at 265 cm depth clearly illustrate a post-disturbance swamp.

Regeneration period 2 is separated from other pollen zones by the CONISS dendrogram. During this regeneration event, counts spaced approximately 15 years apart indicate a gradual increase in *Campnosperma*, along with increases in *Ilex* and

Alchornea. *Blechnum*, Gramineae, and Cyperaceae decrease to stable levels.

A regenerated forest appears in Pollen Zone 7, approximately 400-500 years after Hurricane Elisenda. The period of regeneration is extremely long, partly because it was set back repeatedly by fires. The length of regeneration is especially important to managers wishing to restore the forests affected by Hurricane Joan. The similarities between Hurricane Elisenda and Hurricane Joan (Table 2)–in each case fires swept through the damaged landscape and pioneering vegetation colonized–suggest that regeneration from Hurricane Joan could take an extremely long time. Repeated fires are the greatest danger for the regenerating forests near Bluefields, and evidence of their susceptibility to fire was demonstrated by the La Union fire of 1995, which burned ~30 hectares of the damaged swamps.

Prehistoric Hurricanes.– Identifying prehistoric hurricanes is possible through the analysis of sediment composition in coastal areas (Liu and Fearn 1993, 2000). Determining the frequency hurricane damage to the Laguna Negra swamp was one of the objectives of this study. Although Boucher (1992) estimated that hurricanes impact the Caribbean Coast of Nicaragua approximately every century, not all of these hurricanes would have the same effect on the forest. Liu and Fearn (1993, 2000) were able to estimate the frequency of severe hurricanes (Category 4 or 5) along the Louisiana Coast by observing sand layers in Lake Shelby, located less than 1 km from the Gulf of Mexico. However, since Laguna Negra is 15 km inland, only extremely severe hurricanes would leave an impression in the sediments. Hurricane Joan (Class 4) was unobservable in the sediments, although this may have been the result of methodological failures.

Because Laguna Negra is situated farther inland than many of the other sites where hurricane prehistory has been studied, the origin of sand layers in it is open to other interpretations, including slope wash, soil erosion, drought, or flooding. Slope wash and soil erosion are unlikely explanations because Laguna Negra is isolated in an enormous coastal plain, with 30-50 km separating it from the nearest significant slopes. The percent carbonate for the sand layer (10.2% at 295 cm depth) was markedly different from the values in the remainder of the core (17.7-24.2%), including the value for erosional clays deposited at the base of the core (22.8%; Urquhart 1997). Flooding from Rio Escondido, located 10 km to the north, is possible but even during Hurricane Mitch (1996), the intense rains did not produce flooding from Rio Escondido into this region (Urquhart, unpublished data). Similarly, sediments deposited from Rio Escondido flooding would likely have been similar to those at the base of the core—weathered clays with similar carbonate content, not the distinctly low carbonate of the sand layer. The persistence of wet forest element *Podocarpus* pollen in low density throughout the pollen diagram (Figure 4) refute the possibility of long-term drought generating the sand layers.

Hurricane Elisenda, 3340 ± 50 y BP, was either a very severe or very unique hurricane. It produced significant changes in the vegetation and a very thick sand layer in the sediments, suggesting that its landfall had both strong winds and a large tidal surge. The date of Elisenda (3340 ± 50 y BP) corresponds well with the inception of hurricane impacts on the Gulf Coast of Alabama (3240 ± 80) and Florida (3310 ± 80 BP) (Liu and Fearn 1993). Liu and Fearn (1993, 2000) suggest an episode of abrupt environmental change at this time, causing changes in hurricane tracks or possibly the onset of Caribbean hurricanes. Hurricane Elisenda correlates well with this, and the pervasive layer of sand throughout the Caribbean/Gulf of Mexico at this time may signal a great period of tropical storms.

Although Laguna Negra could not provide the most complete record of hurricane damage for its region, it provided the opportunity to study both the occurrence of prehistoric hurricanes and their effects on vegetation. The analysis of the impact of Hurricane Elisenda sheds great light on the reciprocal event in modern times, Hurricane Joan. While direct studies of regeneration could take decades or centuries, the paleoecological comparison of Hurricane Elisenda suggests that fire after hurricanes is one of the most important factors in retarding regeneration. The current importance of the swamp forest resource to local people has generated interest in how long regeneration after Hurricane Joan will take. If the goal is the regeneration of a forested ecosystem, control of anthropogenic fires must be included as principal management techniques during the regeneration period. Suppression of natural fires may further contribute to forest regeneration, but the natural history of Neotropical swamps is so poorly known that the role of natural fire in the ecosystem is unknown. Nonetheless, human activity in the area is very significant and reduction of agricultural fires will avoid the setbacks in regeneration observed in the analysis of Hurricane Elisenda.

Paleoecological reconstruction of hurricane disturbance at 3300 BP shows a similar pattern to the modern hurricane's effects: 1) fires followed the hurricane and 2) pioneering vegetation, including the swamp fern *Blechnum serrulatum*, became abundant. Beyond the initial damage, forest regeneration after the prehistoric hurricane was slowed by repeated fires. Forest returned approximately 500 years after the initial damage. This study represents the first analysis of forest regeneration or secondary succession patterns using paleoecological methods. This technique is of great importance for the study of slow processes and infrequent events, because it allows the coverage of the long historical record.

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Table 1. Samples and radiocarbon dates for samples from the Laguna Negra 1A core.

Sample Number	Depth	Material	Dating Method	$\delta^{13}C$	^{14}C Age (^{13}C adjusted)	Calendar years BP
CAMS 32695	310	sediment	AMS	-31.8*	3830 ± 70	4510-4300
CAMS 32212	300	sediment	AMS	-32.57	3630 ± 60	4090-3890
CAMS 32211	295	sediment	AMS	-31.95	3340 ± 50	3680-3490
CAMS 32694	290	sediment	AMS	-31.8*	3360 ± 60	3720-3500
CAMS 32219	278	sediment	AMS	-30.88	3200 ± 60	3470-3360
Beta-88796	250-255	sediment	conventional	-30.1	2820 ± 90	3020-2800
CAMS 32208	25	wood	AMS	-27.9	>modern	>modern
CAMS 32217	466	wood	AMS	-27.0	8020 ± 60	8960-8620

***** $\delta^{13}C$ value averaged from measured values other sediment samples.

Table 2. Chronology of and similarities and differences between the prehistoric Hurricane Elisenda (3350 BP) and modern Hurricane Joan (1988 AD).

	Hurricane Elisenda 3350 BP	Hurricane Joan 1988 AD
Stage 1	Hurricane with storm surge (296-292 cm)	Hurricane with storm surge
Stage 2	Fires (290-278 cm)	Fires (1989)
Stage 3	Post fire vegetation with high density of *Blechnum* ferns (290-275 cm)	Post fire vegetation dominated by *Blechnum* ferns (1990-present)
Stage 4	a. Repeated fires (268 cm) b. *Raphia* palms absent	a. Small repeated fires (1995, 1998, 2004) b. *Raphia* palms may aid regeneration
Stage 5	Forest regeneration after 500 years	Unknown time to regeneration

Figure 1. Map of the Laguna Negra area on the Caribbean Coast of Nicaragua. Stippled areas are present swamp vegetation.

Figure 2. X-radiograph of Laguna Negra 1A core, *c.* 305-275 cm depth, illustrating sand layer between 296 cm and 292 cm, with select radiocarbon dates and loss on ignition values (LOI).

Figure 3. Chronlogy, loss on ignition, and carbonate values for 250-310 cm depth in the Laguna Negra 1a core. Sand layer deposited by hurricane illustrated by band, with gradient indicating the density of sediments (darker=higher). Radiocarbon dates in ^{14}C Y BP ± 1σ.

Figure 4. Fine-resolution pollen percentage diagram for Laguna Negra, Nicaragua with chronological scale. The diagram represents only the section from 250 cm – 310 cm depth from a 5 m core.

Figure 5. Fine-resolution pollen and stratigraphy summary diagram for Laguna Negra, Nicaragua with chronological scale. The diagram represents only the section from 250 cm – 310 cm depth from a 5 m core.

Fig. 1

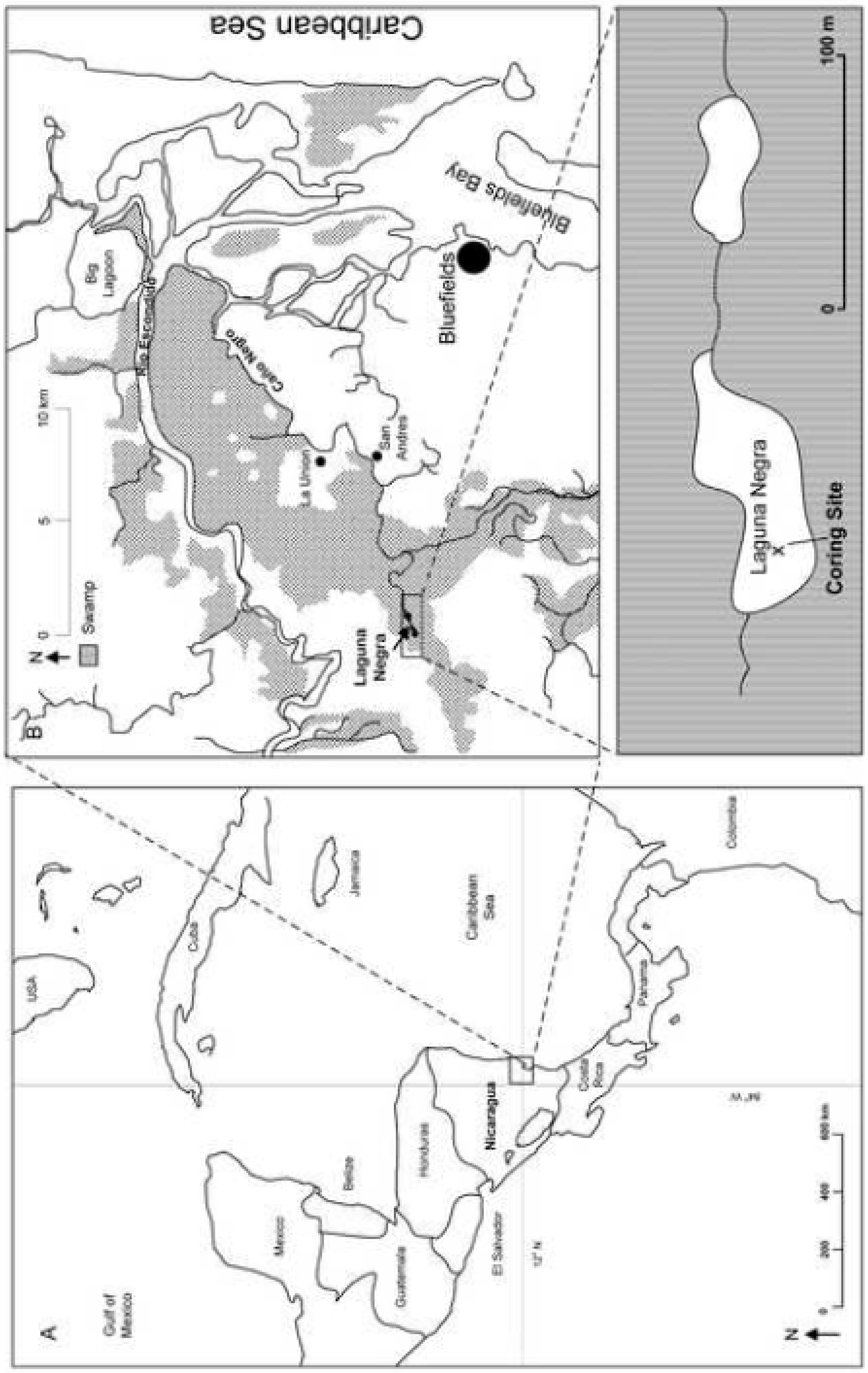

A
B
Caribbean Sea
Bluefields Bay
Bluefields
Big Lagoon
Rio Escondido
San Andres
La Union
Laguna Negra
Swamp
Laguna Negra
Coring Site
100 m
Gulf of Mexico
Mexico
Belize
Guatemala
Honduras
El Salvador
Nicaragua
Costa Rica
Panama
Colombia
Cuba
Jamaica
USA
Caribbean Sea

Fig. 2

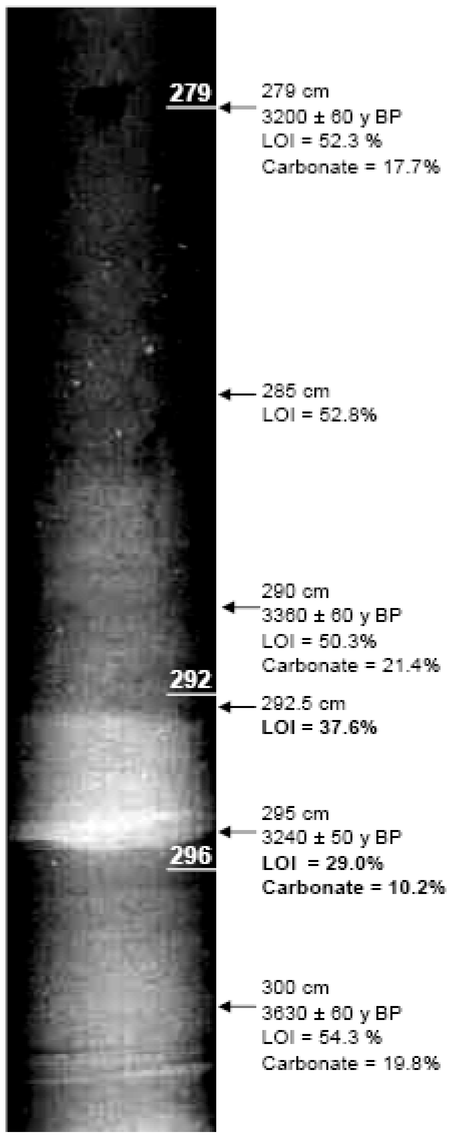

279
279 cm
3200 ± 60 y BP
LOI = 52.3 %
Carbonate = 17.7%
285 cm
LOI = 52.8%
290 cm
3360 ± 60 y BP
LOI = 50.3%
Carbonate = 21.4%
292
292.5 cm
LOI = 37.6%
295 cm
3240 ± 50 y BP
296
LOI = 29.0%
Carbonate = 10.2%
300 cm
3630 ± 60 y BP
LOI = 54.3 %
Carbonate = 19.8%

Fig. 3

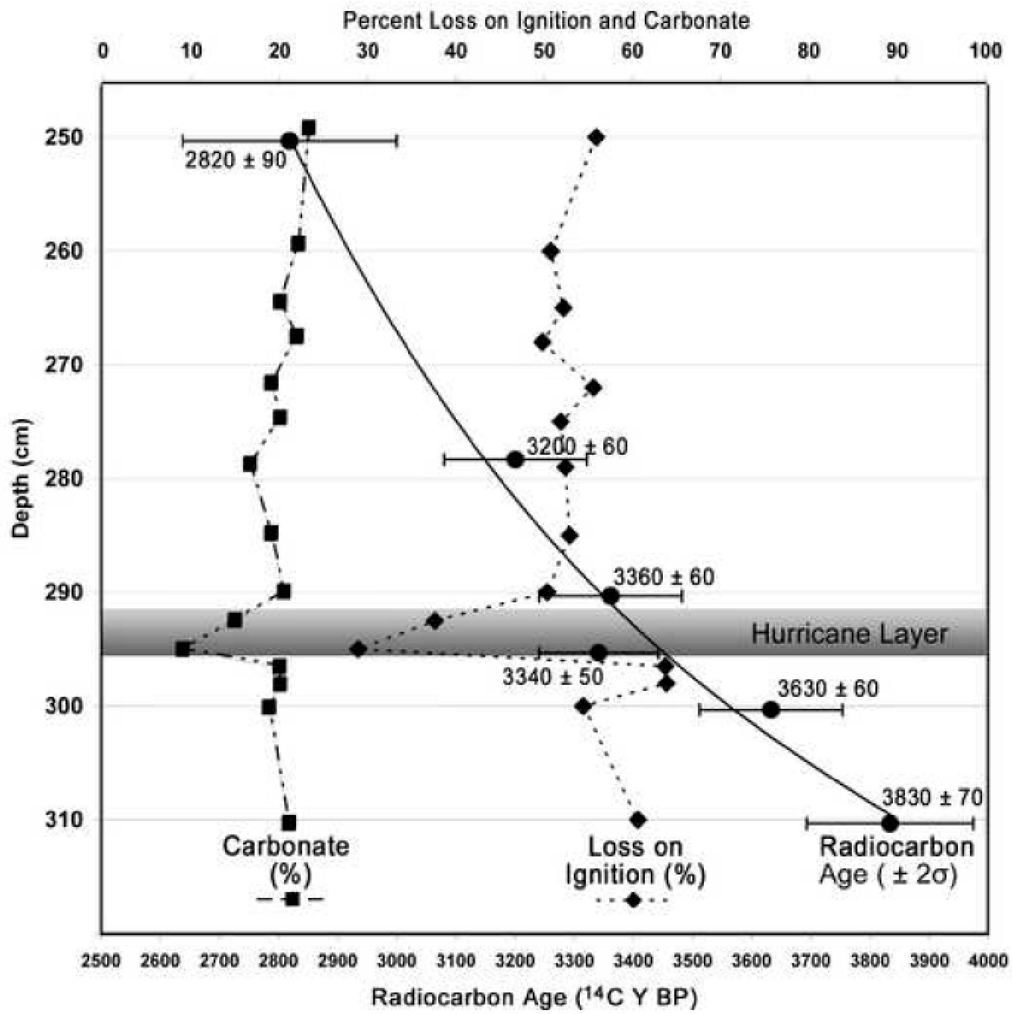
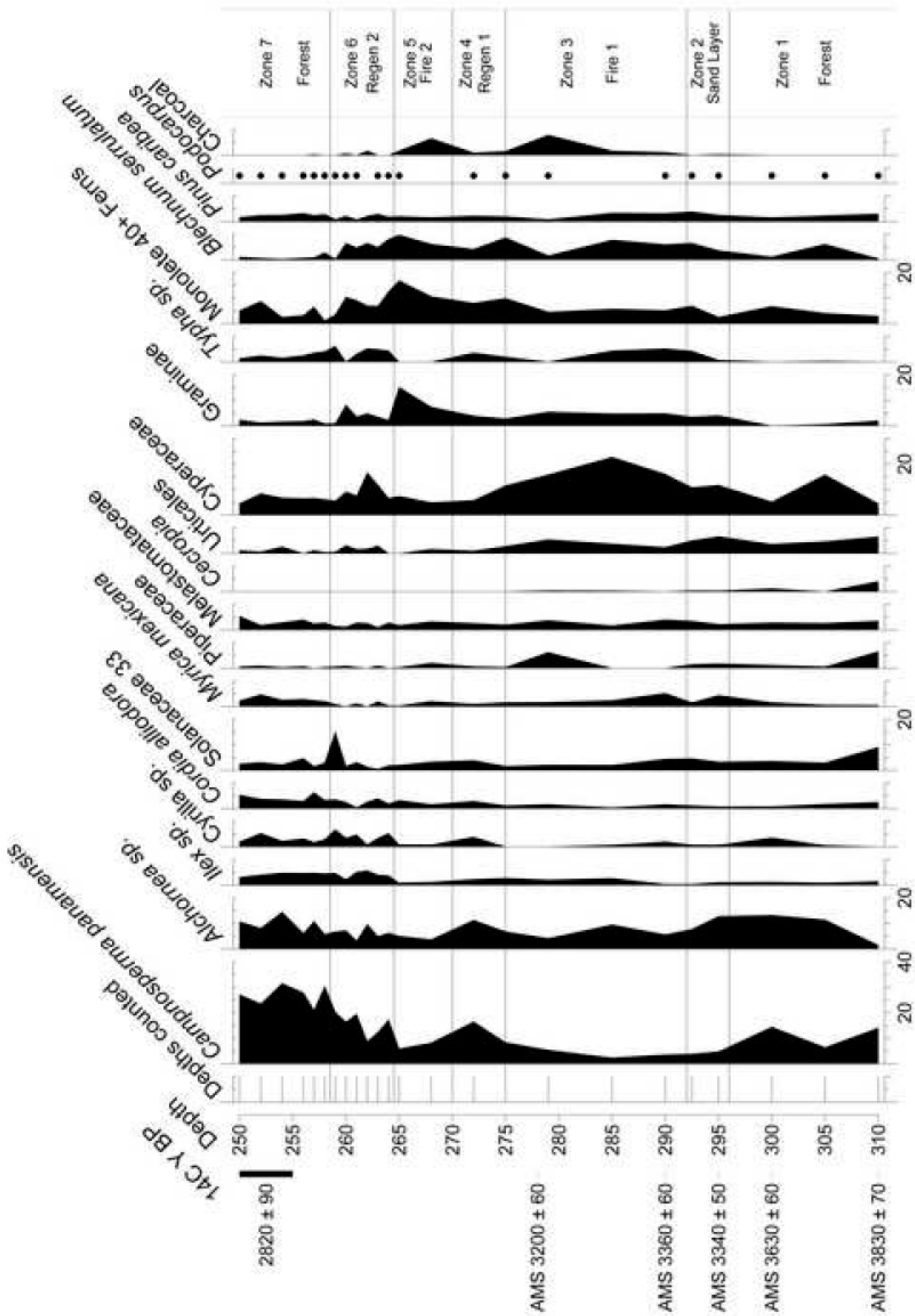
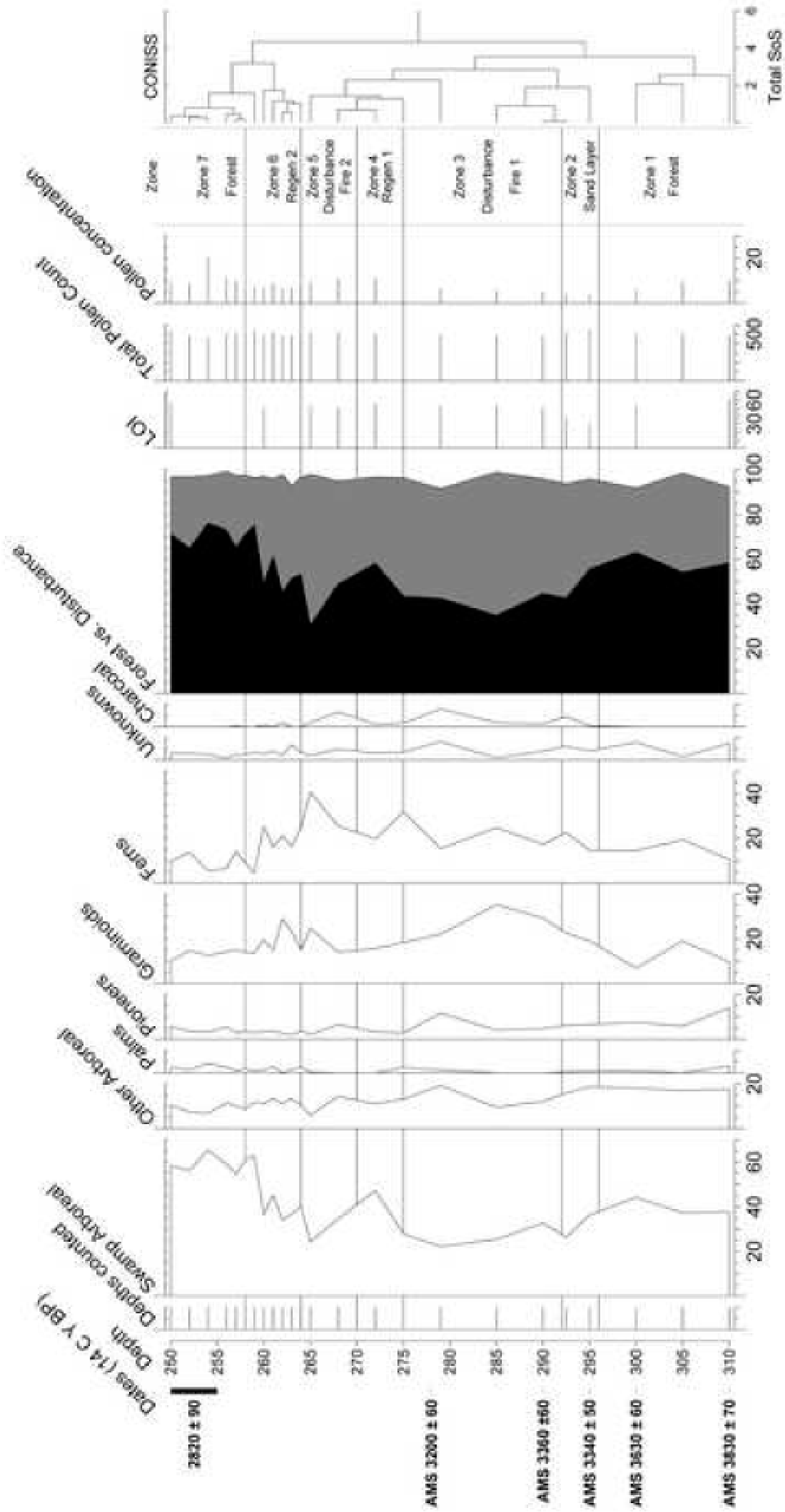

Percent Loss on Ignition and Carbonate
0
10
20
30
40
50
60
70
80
90
100
Depth (cm)
250
260
270
280
290
300
310
2820 ± 90
3200 ± 60
3360 ± 60
Hurricane Layer
3340 ± 50
3630 ± 60
3830 ± 70
Carbonate (%)
Loss on Ignition (%)
Radiocarbon Age (± 2σ)
2500
2600
2700
2800
2900
3000
3100
3200
3300
3400
3500
3600
3700
3800
3900
4000
Radiocarbon Age (14C Y BP)

Fig. 4


Zone 7
Forest
Zone 6
Regen 2
Zone 5
Fire 2
Zone 4
Regen 1
Zone 3
Fire 1
Zone 2
Sand Layer
Zone 1
Forest
Charcoal
Podocarpus
Pinus caribea
Blechnum serrulatum
Monolete 40+ Ferns
Typha sp.
Graminae
Cyperaceae
Urticales
Cecropia
Melastomataceae
Piperaceae
Myrica mexicana
Solanaceae 33
Cordia alliodora
Cyrilla sp.
Ilex sp.
Alchornea sp.
Campnosperma panamensis
Depths counted
Depth
14C Y BP
2820 ± 90
AMS 3200 ± 60
AMS 3360 ± 60
AMS 3340 ± 50
AMS 3630 ± 60
AMS 3830 ± 70

528 Fig. 5



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