

Cyclone Tolerance in New World Arecaceae: Biogeographic Variation and Abiotic Natural Selection

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- **Background and Aims** Consistent abiotic factors can affect directional selection; cyclones are abiotic phenomena with near-discrete geographic limits. The current study investigates selective pressure of cyclones on plants at the species level, testing for possible natural selection.
- **Methods** New World Arecaceae (palms) are used as a model system, as plants with monopodial, unbranched arborescent form are most directly affected by the selective pressure of wind load. Living specimens of known provenance grown at a common site were affected by the same cyclone. Data on percentage mortality were compiled and analysed in biogeographic and phylogenetic contexts.
- **Key Results** Palms of cyclone-prone provenance exhibited a much lower (one order of magnitude) range in cyclone tolerance, and significantly lower ($P < 0.001$) mean percentage mortality than collections from cyclone-free areas. Palms of cyclone-free provenance had much greater variation in tolerance, and significantly greater mean percentage mortality. A test for serial independence recovered no significant phylogenetic autocorrelation of percentage mortality.
- **Conclusions** Variation in cyclone tolerance in New World Arecaceae correlates with biogeography, and is not confounded with phylogeny. These results suggest natural selection of cyclone tolerance in cyclone-prone areas.

Key words: Abiotic selection, Arecaceae, biogeography, cyclone, hurricane, phylogenetic independence.

INTRODUCTION

The role of abiotic natural selection has been considered since Darwin's era. Darwin thought abiotic environmental factors to be generally too random to provide directionality to selection (Niklas, 1992). Studies of selection can advance a leading role for biotic factors (Allmon and Ross, 1990), or abiotic factors (Totland, 2001). Over long time scales, consistent abiotic factors can affect directional selection on plants (Caruso *et al.*, 2003).

Consideration of plant evolution in an abiotic context of high winds is increasingly relevant. Tropical cyclones have increased in frequency and intensity since 1970, and the trend is expected to continue (Emmanuel, 2005). High winds have a demonstrated influence on vegetation (Coutts and Grace, 1994). Relationships among high winds and canopy dynamics, seedling recruitment and stand demographics have been demonstrated throughout tropical, subtropical and temperate regions (Gresham *et al.*, 1991; Zimmermann *et al.*, 1994; Asner and Goldstein, 1997; Hirsh and Marler, 1997; Quine and Bell, 1998). Cyclones can directly influence vegetation, forest structure, canopy height, community composition, structural adaptations and evolutionary patterns (Webb, 1958; Hopkins, 1990; Clarke and Kerrigan, 2000; Grove *et al.*, 2000; Horvitz and Koop, 2001; de Gouvenain and Silander 2003).

Palms (Arecaceae) offer an apt model system for investigating evolution of tolerance to mechanical stress via wind. Many palm species have rigidly determined unbranched

monopodial stem architecture, derived entirely from primary growth (Tomlinson, 2006). Damage from wind load has a potentially more direct selective effect on individual plants with unbranched monopodial architecture than on branched plants. Mature palms also have an easily quantified, limited number of leaves, facilitating estimations of surface area, and enabling accurate estimations of potential wind load (Sterken, 2007). In terms of general biomechanical study of palms, a robust canon exists (Tomlinson, 1962; Rich, 1987; Isnard *et al.*, 2005; among others). Palms are described as mechanically efficient (Tomlinson, 2006) and well-adapted to wind stress (Lippincott, 1995; Fetcher *et al.*, 2000), and palms are sometimes observed as prominent surviving plant groups following high wind events (Loope *et al.*, 1994; Vandermeer, 1994; Ostertag *et al.*, 2005).

Intrinsic biotic factors may have a primary influence in cyclone tolerance in some Arecaceae (J. L. Dowe, unpubl. res.). Studies of primary axis anatomy, lignification and stress suggest that the palm trunk is adapted to distribute high load stress efficiently through flexibility (Tomlinson, 1990; Huang *et al.*, 2002; Kuo-Huang *et al.*, 2004). Palm stem and leaf mechanical properties have both been considered in the context of adaptive value for high wind environments (Rich, 1986; Tomlinson, 1990; Niklas, 1999). Knowledge about broad patterns of high wind tolerance in Arecaceae can inform and guide further studies in these areas.

Large-scale unplanned disturbances such as cyclones illuminate natural systems in ways that controlled experimentation may not (Holt, 2006; Schoener and Spiller,

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2006; cf. Cooper-Ellis *et al.*, 1999). Live plant collections affected by an unplanned natural disturbance offer potentially broader insights (Klein, 1992; Fisher *et al.*, 1996; Dosmann, 2006). Taxonomically and biogeographically, broad plant collections may offer insight into natural selection via pressure from catastrophic wind events in the context of biogeography and phylogeny. The current study investigates the effects of a cyclone on a taxonomically and geographically diverse collection of palms growing in a single location.

MATERIALS AND METHODS

Plants studied

Arecaceae specimens at Montgomery Botanical Center (Coral Gables, FL, USA; 25°39'N, 80°16'W) were used in the current study. Specimens were obtained and cultivated through ongoing *ex situ* conservation collection development operations. The study group was circumscribed to include only *Arecaceae* specimens: (a) from the New World; (b) of mature age; (c) with adequate numbers (>10 individuals per taxon) represented; and (d) with solitary, self-supporting, arborescent axes (excluding other palm habits such as clumping palms with multiple axes and lianas). Taxa studied and respective sample sizes are detailed in Table 1.

Wind event

The study plants were investigated for the effects of Hurricane Wilma, a cyclonic storm which affected the collections on 24 October 2005. Wind speeds of up to 95–105

knots (175.9–194.5 k.p.h.) were recorded as the cyclone crossed the study site (Pasch *et al.*, 2006).

Data collection

Data related to each plant's condition and mortality were compiled during the period 25 October to 10 November 2005. Data on numbers of plants killed by Hurricane Wilma were extracted from these records, as well as from collections census data from before the wind event (Table 1).

Analysis

Percentage mortality resulting from the wind event was calculated for each taxon using the compiled data. Resulting percentage mortality for each taxon was investigated in two contexts: (1) biogeographic patterns; and (2) phylogenetic dependence.

Biogeographic analysis. The geographic limits of Atlantic cyclone activity were determined via a review of meteorological data from 1851 to 2006 (NOAA, 2007; described by Jarvinen *et al.*, 1984). These data were used to circumscribe cyclone-influenced and cyclone-free geographic regions. Provenance data for the taxa studied were mapped and compared with the known geographic limits of Atlantic cyclones. Percentage mortality by taxon was plotted against latitude of provenance. Via comparison of the geographic limits of cyclone activity and provenance data, taxa were divided into cyclone-prone and cyclone-free groups. Average percentage mortality for taxa from cyclone-prone and cyclone-free taxa was calculated. Tests for significance were performed on the two subgroups via the binomial test (Hollander and Wolfe, 1999), using the overall average

TABLE 1. Collections, provenance and mortality data for the current study

Taxon	Latitude	Longitude	<i>n</i> Sampled	<i>n</i> Killed	Voucher specimen
<i>Acrocomia aculeata</i> Lodd. ex Mart.	-1.58	-48.75	43	7	Noblick 5019, FTG
<i>Attalea phalerata</i> Mart. ex Spreng.	-1.58	-48.75	27	0	Noblick 5018, FTG
<i>Attalea pindobassu</i> Bondar	-11.78	-40.74	13	0	Noblick 4600, FTG
<i>Butia capitata</i> Becc.	-14.76	-46.35	12	0	Noblick 5090, FTG
<i>Butia eriospatha</i> Becc.	-26.58	-53.83	11	1	Noblick 4878, FTG
<i>Coccothrinax argentata</i> (Jacq.) L. H. Bailey	24.67	-81.37	13	0	Noblick 5076, FTG
<i>Coccothrinax barbadensis</i> Becc.	16.28	-61.45	106	2	Hahn 7651, NY
<i>Coccothrinax scoparia</i> Becc.	18.12	-71.62	34	0	Hahn 7751, NY
<i>Coccothrinax spissa</i> L. H. Bailey	18.33	-70.37	27	0	Hahn 7710, NY
<i>Gaussia attenuata</i> Becc.	18.45	-66.94	18	0	Proctor s.n., NY
<i>Pseudophoenix vinifera</i> (Mart.) Becc.	18.48	-70.71	37	0	Noblick 5459, FTG
<i>Roystonea oleracea</i> O. F. Cook	16.32	-61.78	41	3	Hahn 7646, NY
<i>Roystonea regia</i> O. F. Cook	26.02	-81.4	146	0	Noblick 5250, FTG
<i>Sabal minor</i> (Jacq.) Persoon	27.82	-81.8	20	0	Noblick 5452, FTG
<i>Sabal palmetto</i> Hort.	30.48	-81.5	204	2	Noblick 5444, FTG
<i>Syagrus amara</i> Mart.	16.2	-61.65	13	0	Hahn 7649, NY
<i>Syagrus botryophora</i> Mart.	-15.85	-38.9	29	17	Noblick 5002, FTG
<i>Syagrus cearensis</i> Noblick	-7.38	-34.96	42	1	Noblick 5132, FTG
<i>Syagrus × costae</i> Glassman	-8.88	-36.5	13	1	Noblick 4980, FTG
<i>Syagrus oleracea</i> (Mart.) Becc.	-14.51	-46.36	11	3	Noblick 5084, FTG
<i>Syagrus orinocensis</i> (Spruce) Burret	5.67	-67.67	13	3	Noblick 4946, FTG
<i>Syagrus picrophylla</i> Barb.Rodr.	-16.92	-41.48	17	0	Noblick 5156, FTG
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	-25.65	-54.47	61	15	Noblick 5112, FTG
<i>Syagrus vermicularis</i> Noblick	-5.03	-47.02	16	1	Noblick 4974, FTG
<i>Thrinax radiata</i> Mart.	24.7	-81.03	124	5	Noblick 5081, FTG

proportion of mortality for the whole dataset (ignoring provenance) as the null hypothesis for group comparison.

Phylogenetic independence analysis. In the absence of a complete cohesive molecular phylogeny for all Arecaceae, a diagram of putative relationships was constructed using available information. Relationships among the taxa studied were compiled via a review of available work (Nauman and Sanders, 1991; Gunn, 2004; Asmussen *et al.*, 2006; A. W. Meerow, USDA-ARS, USA, unpubl. res.; L. R. Noblick, unpubl. res.). To evaluate potential autocorrelation of percentage mortality via synapomorphic derivation of cyclone tolerance, the percentage mortality for each taxon was mapped onto this estimation of relationships, and a randomization test version of von Neumann's test (von Neumann *et al.*, 1941) for serial independence (Abouheif, 1999) was performed on these data given the *a priori* phylogeny. The test for serial independence compared the distribution of mortality data on the *a priori* putative phylogeny against 1000 random re-distributions of mortality data on the phylogeny, as implemented by Phylogenetic Independence v2.0 (Reeve and Abouheif,

2003). This test for serial independence was repeated ten times to evaluate the consistency of the results obtained.

RESULTS

Taxa and percentage mortality

The average sample size per taxon for the taxa studied was 44, and ranged from 11 to 204. The percentage mortality for each taxon is presented in Figs 1 and 2. Values for percentage mortality per taxon ranged from 0.00% to 58.62%, with average percentage mortality per taxon of 7.58%, and overall percentage mortality for the entire study of 5.59%. The mortality rates do not correlate with the sample size per taxon (Table 1).

Circumscription of cyclone geography

Table 2 presents an overview of Atlantic cyclone data by decade from 1851 to 2006. A total of 1363 Atlantic cyclones are recorded for the period. All cyclone tracks occurred at least partially north of 10°N, 97.87% of

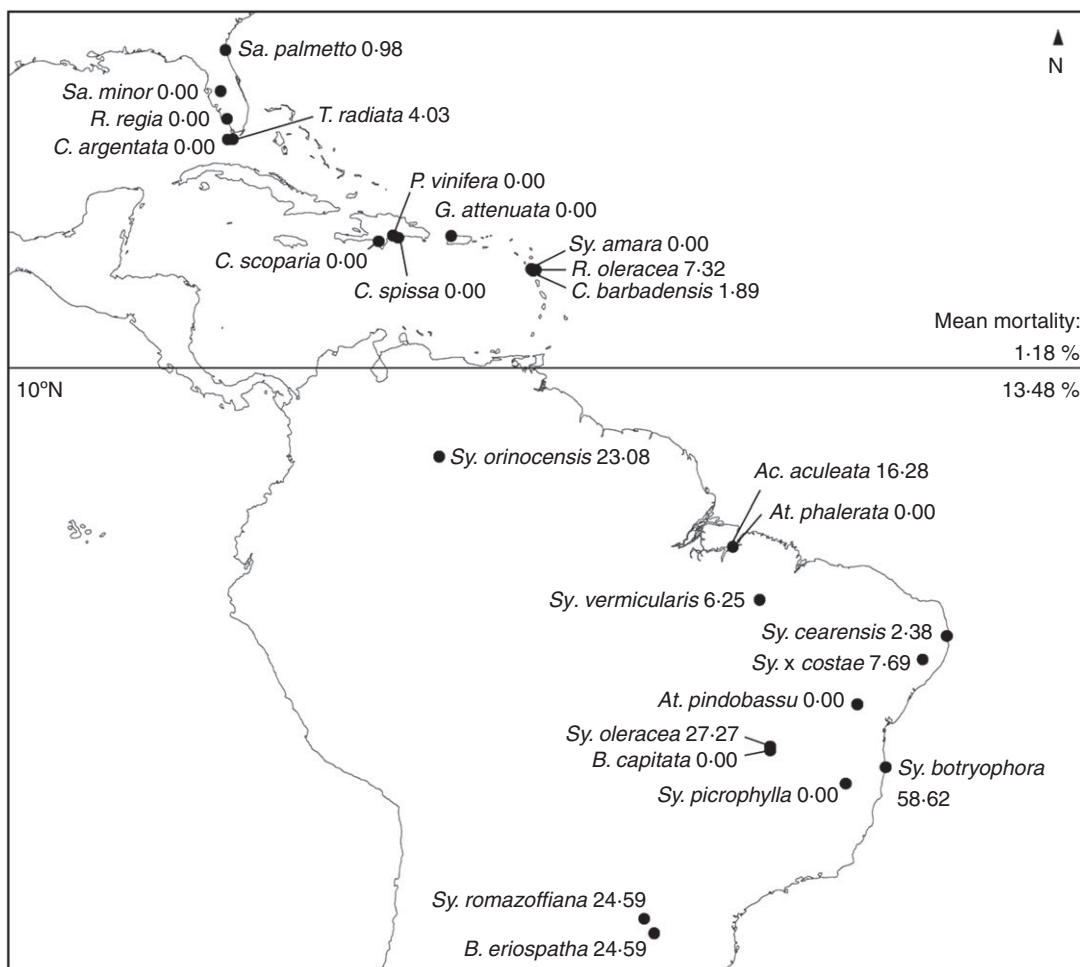


FIG. 1. Provenance of specimens studied relative to the occurrence of cyclones. Numbers after each taxon are the percentage mortality of the taxon following Hurricane Wilma in 2005 (calculated from Table 1). Taxa from south of 10°N latitude (see Table 2) had mean observed percentage mortality over ten times greater than those northward ($P < 0.001$).

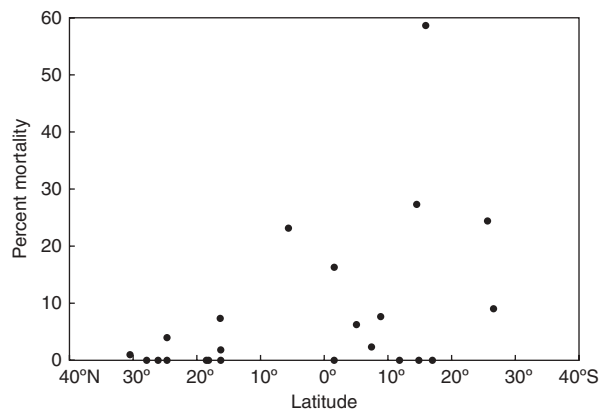


FIG. 2. Latitude of provenance versus percentage mortality of taxa studied. Specimens native to cyclone-prone latitudes (north of 10°N) have significantly lower ($P < 0.001$) observed percentage mortalities following Hurricane Wilma.

TABLE 2. Frequency and location of Atlantic cyclone activity, 1851–2006

Period	No. of cyclones	No. of cyclones active south of 10°N*	Southern maximum
1851–1860	60	0	12.0°N
1861–1870	76	1	9.5°N
1871–1880	75	1	8.5°N
1881–1890	82	1	9.9°N
1891–1900	84	2	8.7°N
1901–1910	79	3	7.7°N
1911–1920	54	0	10.3°N
1921–1930	56	1	9.5°N
1931–1940	104	1	8.8°N
1941–1950	98	0	10.2°N
1951–1960	98	0	10.1°N
1961–1970	98	3	8.0°N
1971–1980	96	0	10.0°N
1981–1990	96	6	7.2°N
1991–2000	111	6	8.3°N
2001–2006	96	4	8.9°N

Data adapted from NOAA (2007).

* In all but one case, cyclones active south of 10°N also tracked north of that line. The only recorded cyclone occurring entirely south of 10°N, in the south Atlantic, occurred in 2004 (Pezza and Simmonds, 2005).

Atlantic cyclone activity occurred entirely north of 10°N latitude, and all Atlantic cyclone activity over this period occurred north of 7°N latitude, with only one exception. For the purposes of this study, the effective cyclone-prone region of the geographic area of interest was determined to have a south boundary of 10°N latitude (Fig. 1).

Biogeography

Figure 1 presents provenance of the taxa included in the current study. Based on the determination of cyclone-prone geographic areas, the taxa were divided into those from cyclone-prone regions north of 10°N latitude, and taxa with provenance south of 10°N latitude which fall into the region determined as cyclone-free. Specimens from the cyclone-prone region are all of Antillean or peninsular

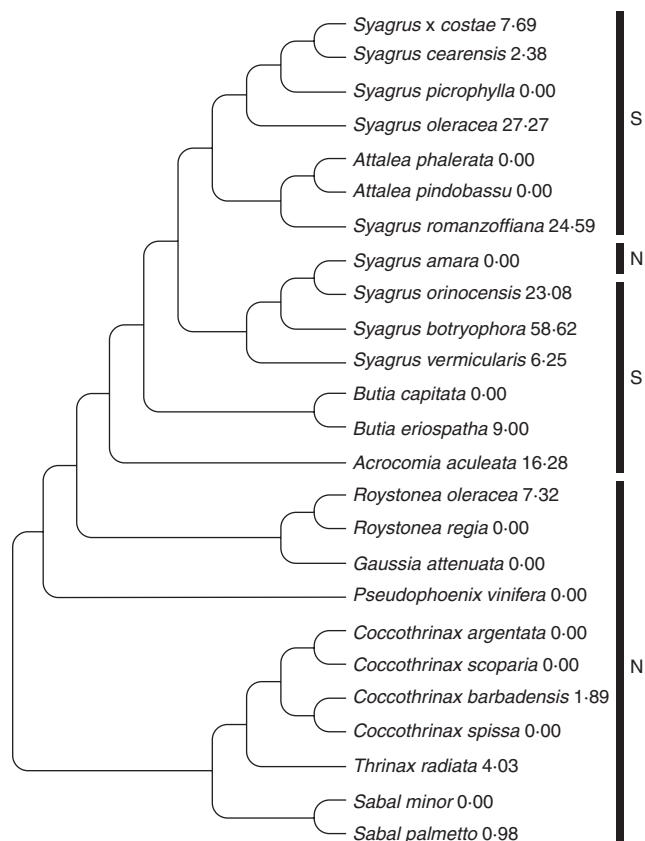


FIG. 3. Putative relationships among the taxa studied, for testing autocorrelation. Diagram adapted from known phylogenetic information (Nauman and Sanders, 1991; Gunn, 2004; Asmussen *et al.*, 2006; A. W. Meerow, USDA-ARS, USA, unpubl. res.; L. R. Noblick, unpubl. res.). Numbers after taxa are percentage mortality data. Bars to the right indicate the biogeographic group: N = north of 10°N latitude; S = south of 10°N latitude.

Floridian provenance, and specimens from the cyclone-free region are exclusively of South American provenance, and each of these two groups occurs over a wide geographic area.

Percentage mortality data differed significantly based on latitude (Fig. 2). Much higher variation of percentage mortality occurred in the taxa from south of 10°N. The range of mortality values per taxon was 0.00–7.32% in the cyclone-prone area, and 0.00–58.62% in the cyclone-free area. The mean percentage mortality per taxon for the cyclone-free area was 13.48%, and 1.18% for the cyclone-prone area. Mean percentage mortality of each group differed significantly from that of the overall data set according to the results of the binomial test ($P < 0.001$ in both cases).

Phylogenetic independence

Hypothesized relationships among the taxa studied are detailed in Fig. 3. The putative phylogeny broadly aligns with the biogeography of the collections studied, with a monophyletic clade of taxa from the cyclone-free area ('S,' Fig. 3.) circumscribing *Acrocomia*, *Attalea*, *Butia* and *Syagrus* (with the notable exception of *S. amara*).

Viewing the percentage mortality data as mapped onto the putative phylogeny suggests differential distribution

TABLE 3. Test for serial independence

Replication	Observed mean <i>C</i> -statistic	<i>P</i> -value
1	20.54	0.189
2	20.59	0.167
3	20.58	0.164
4	20.57	0.184
5	20.57	0.202
6	20.57	0.155
7	20.61	0.159
8	20.57	0.139
9	20.59	0.156
10	20.57	0.173
Average	20.5747	0.1688

of cyclone tolerance. The randomization test for serial independence of the percentage mortality data, given the relationships in Fig. 3, found no evidence of significant phylogenetic autocorrelation (Table 3 and Fig. 4). The average *C*-statistic for the ten runs was 20.5747, and the average *P*-value was 0.1688. This result rejects the hypothesis of synapomorphy as an influence on cyclone tolerance.

DISCUSSION

Abiotic condition

The observed geographic limits of Atlantic cyclone activity (Table 2 and Fig. 1) create essentially discrete conditions which approximate a formal experiment with a test group and control group, albeit on very large geographic and temporal scales.

From 1851 to 2006, an average of nearly eight cyclones per year has occurred north of 10°N latitude, and a small percentage of these have tracked south of this parallel. Only one cyclone, Cyclone Catarina (2004), has occurred entirely south of 10°N latitude, between 25°S and 31°S latitude (Pezza and Simmonds, 2005). More accurate cyclone positional records correspond with the advent of aerial monitoring in 1944 (Neumann *et al.*, 1999): for the period 1944–2006, 667 cyclones were recorded, 97.15% of these occurred entirely north of 10°N latitude, and the southern maximum did not extend beyond 7°N latitude, with the exception of Cyclone Catarina.

Recent work has measured Caribbean cyclone activity in the 19th and 20th centuries (Miller *et al.*, 2006; Nyberg *et al.*, 2007), written records exist of Caribbean cyclone activity in the 16th century (Ludlum, 1963), and the sedimentary record shows evidence of cyclones in the Caribbean for at least 5000 years (Donnelly and Woodruff, 2007). Assuming that wind shear forces in the Atlantic have been present in more or less the same form during the Holocene, the regular presence of cyclones in the Caribbean and their absence in South America are conditions that likely existed on a time scale of at least that length. This creates two very different long-term adaptive regimes, one with frequent and regular cyclones as a possible selective pressure, and one without. Relative to the long-lived perennial habit of the plants studied, the frequency and history of the differential abiotic condition is temporally consistent, and therefore expected to affect directional selection (Levins, 1968; Reboud and Bell, 1997).

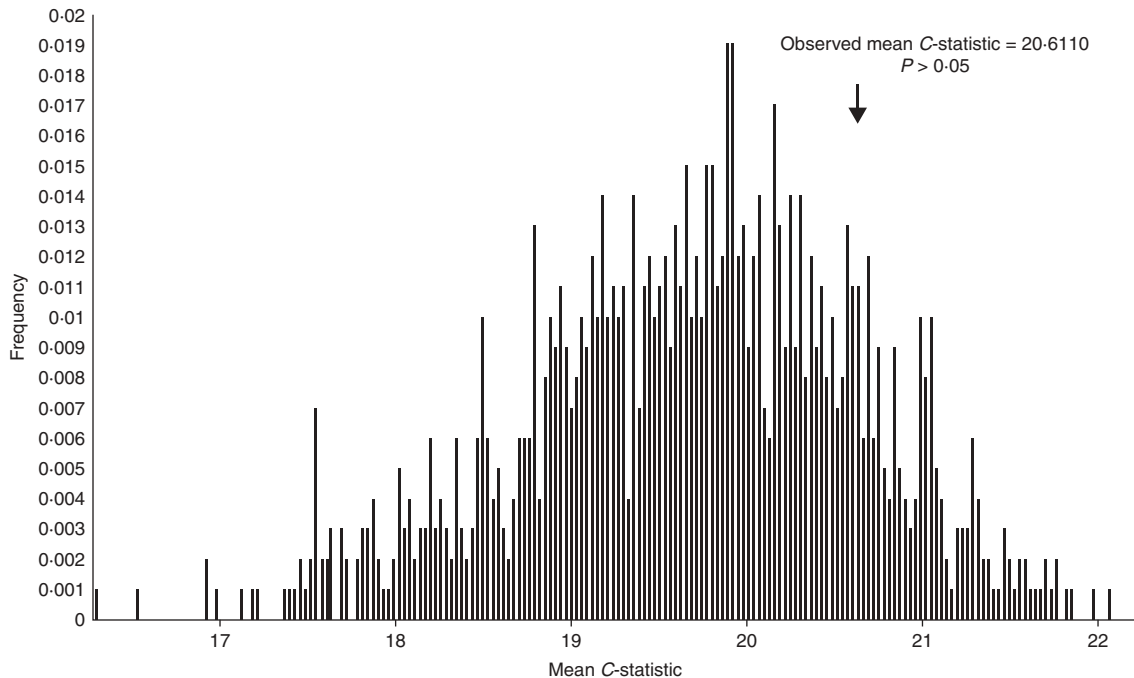


FIG. 4. Phylogenetic independence of cyclone mortality: representative randomization test for serial independence of cyclone mortality data, given the hypothesized phylogeny (Fig. 3). The observed mean *C*-statistic for the given series (20.6110) does not fall far to the right of the distribution of mean *C*-statistics for these 1000 randomized replicates ($P = 0.1590$). Cyclone tolerance is not confounded with phylogeny; lack of evidence of phylogenetic autocorrelation for cyclone tolerance leaves open the possibility of selection for higher cyclone tolerance dependent on geographic distribution.

Model system

As noted in the Introduction, palm collections provide a suitable model system for investigating potential selective pressure from high winds. The intersection of the differential abiotic condition (frequent regular high winds over many generations) with a particularly vulnerable habit (unbranched monopodial arborescence) presents an opportunity to investigate empirical patterns of natural selection in response to this abiotic selective pressure.

A potential challenge in the current study may be the degree to which potentially confounding variables affect the analysis. For the current study, the specimens were not planted in exacting identical conditions in specific anticipation of a cyclone. Rather, curatorial practice made the collections useful for research unanticipated at accession (Dosmann, 2006). Edaphic, topographical and other factors associated with the siting of individual plants may introduce systematic variation into the model system, potentially obscuring effects of the environmental factor of interest. Previous studies demonstrate that topography and protectedness of specific sites can influence cyclone damage (Bellingham, 1991; Brokhaw and Gear, 1991; Frangi and Lugo, 1991), but the relationship to mortality is not consistent (Putz and Shanz, 1991). The effect of variation in site conditions, even between widely separated and topographically variable sites, may be less influential than intrinsic biotic factors with regard to cyclone tolerance in palms (J. L. Dowe, unpubl. res.). Total elevation difference at the study site is <6 m, and the specimens are more or less uniformly exposed. Potential effects of microsite variation throughout the collections are mitigated by the sample sizes and breadth of locations of individual specimens throughout the landsite.

Testing the hypothesis

Insights gleaned from unplanned disasters (Klein, 1992; Holt, 2006; Schoener and Spiller, 2006) can be more rigorous if hypotheses are carefully stated, model systems are defined, and records are available. The central question of this study addresses whether cyclones exert a selective effect on plants. The null hypothesis is that there is no difference in cyclone tolerance between palms of cyclone-prone and cyclone-free provenance. The null hypothesis is rejected with a high degree of statistical confidence ($P < 0.001$; Figs 1 and 2). Therefore, it is possible that the frequent and regular occurrence of cyclones has exerted a selective pressure towards increased wind tolerance in Caribbean *Arecaceae*.

The effective boundary of Atlantic cyclone geography (10°N latitude) bisects the natural distributions of two of the taxa included in this study, *Acrocomia aculeata* and *Roystonea oleracea*. *Acrocomia aculeata* is widespread through the Caribbean basin, from Cuba and Mexico southward throughout Paraguay and into southern Brazil (Henderson *et al.*, 1995); *Roystonea oleracea* is found throughout the Lesser Antilles, to Trinidad, westward through Venezuela, and into Colombia (Henderson *et al.*, 1995). Estimating the centre of origin for these two taxa

is beyond the scope of the current study, but it is worth noting that the centre of diversity for *Roystonea* is the Caribbean basin, while the other *Acrocomia* species (*A. hassleri*) occurs in Paraguay and southern Brazil (Henderson *et al.*, 1995). Reanalysis of the percentage mortality data excluding these two taxa may offer a more discrete estimation of the differences between the two geographic groups: with *A. aculeata* and *R. oleracea* excluded, the overall mean percentage mortality changes from 7.58% to 7.21%, the mean percentage mortality per taxon for the cyclone-prone group falls by half, from 1.18% to 0.63%, while the mean percentage mortality per taxon of the cyclone-free group changes slightly, from 13.48% to 13.25%. The differences between the groups remain significant ($P < 0.001$). Whether *R. oleracea* is included or excluded, the range of observed percentage mortality (either 0.00–7.32% or 0.00–4.03%) for the Caribbean group remains below the average mean percentage mortality for the entire study (either 7.58% or 7.21%). Geographically dependent differences in mortality between the groups are well supported.

Phylogenetic considerations

Having rejected the null hypothesis that the geographic groups display no difference in cyclone tolerance, the potential confounding effect of shared ancestry must be considered, as biogeography and phylogeny appear correlated (Fig. 3). The results of the randomization test for serial independence (Table 3 and Fig. 4) show no significant evidence that the observed percentage mortality data is phylogenetically autocorrelated (i.e. the result of shared ancestry). This suggests that the observed variation by biogeography is not confounded by phylogenetic factors.

As above, reanalysis of the data with exclusion of *Acrocomia aculeata* and *Roystonea oleracea* could be advisable, as exclusion of these two species divides the study organisms into very discrete groups based on the 10°N latitude line. Excluding these two taxa and re-running the test for serial independence, the null hypothesis (that the percentage mortality data are not phylogenetically autocorrelated) is still not rejected ($P = 0.320$).

Wind as a selective pressure

Based on the significant differences in cyclone tolerance based on geography observed in the model system (Figs 1 and 2), along with the lack of autocorrelation in the hypothesized phylogeny (Table 3 and Fig. 4), empirical evidence from the current study suggests that frequent and regular high wind events exert a selective pressure towards increased tolerance. Ultimate cause of mortality in all cases was damage from high winds, but proximate causes showed some variation. Major causes of death were stem failure just below the primary meristem (crown), stem failure in mid-stem, and uprooting and subsequent desiccation. Anecdotal observations of variation in leaf shedding, petiole and stem flexibility, and root depth may suggest specific adaptive mechanisms for cyclone tolerance. Thorough analysis of morphological, anatomical or edaphic

characters associated with cyclone tolerance is outside the scope of the current study, but these types of observations can provide a starting point for further investigation.

The Caribbean palm taxa included in this study possess a wide range of stem, leaf and crown morphologies but, as a group, these taxa have little variation in and low observed percentage mortality, i.e. greater cyclone tolerance. *Pseudophoenix* and *Coccothrinax* provide two examples of widely different morphology, showing pinnate versus palmate leaves, crownshaft versus no crownshaft habit, and very different stem heights, stem diameters and stem allometry, yet these genera are basically identical with regard to cyclone tolerance. In the South American taxa studied, much greater variation in cyclone tolerance is observed.

Coccothrinax and *Syagrus* are two genera with diverse stem allometry. Among *Coccothrinax*, very little variation in percentage mortality is observed, whereas in *Syagrus*, percentage mortality data appear to correlate with stem height to diameter ratio (M. P. Griffith, unpubl. res.).

Broader applications

The Arecaceae are pantropical and very widely distributed in the subtropics (Uhl and Dransfield, 1987). The current study utilizes New World Arecaceae of a certain habit, but the hypotheses tested here can be more broadly examined using collections from other areas. One report (Jones, 2006) suggests that cyclone tolerance may vary in African palms (*Hyphaene*, *Borassus*).

In the context of observed increasing frequency and intensity of cyclones (Emmanuel, 2005), a model system to investigate long-term natural selection in vegetation will be of use. The current study presents evidence that long-lived perennial vegetation can adapt to the selective pressure of frequent high winds at the species level, and provides a starting point for more specific investigation of allometric adaptation.

Elucidating the mechanism or mechanisms of cyclone tolerance in palms will be of interest. Further examination for morphological or anatomical adaptations will be of use. Results here can inform studies of specific adaptive mechanisms of cyclone tolerance, and provide a framework for other investigations into adaptation to wind stress.

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LITERATURE CITED

Abouheif E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evolutionary Ecology Research* **1**: 895–899.

- Allmon WD, Ross RM, eds. 1990.** *Causes of evolution: a paleontological perspective*. Chicago, IL: University of Chicago Press.
- Asmussen CB, Dransfield J, Deickmann V, Barfod AS, Pintaud J-C, Baker WJ. 2006.** A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny. *Botanical Journal of the Linnean Society* **151**: 15–38.
- Asner GP, Goldstein G. 1997.** Correlating stem biomechanical properties of Hawaiian canopy trees with hurricane wind damage. *Biotropica* **29**: 145–150.
- Bellingham PJ. 1991.** Landforms influence patterns of hurricane damage: evidence from Jamaican montane forests. *Biotropica* **23**: 427–439.
- Brokxaw NVL, Grear JS. 1991.** Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* **23**: 386–392.
- Caruso CM, Peterson SB, Ridley CE. 2003.** Natural selection on floral traits of *Lobelia* (Lobeliaceae): spatial and temporal variation. *American Journal of Botany* **90**: 1333–1340.
- Clarke PJ, Kerrigan RA. 2000.** Do forest gaps influence the population structure and species composition of mangrove stands in northern Australia. *Biotropica* **32**: 642–652.
- Cooper-Ellis S, Foster DR, Carlton G, Lezberg A. 1999.** Forest response to catastrophic wind disturbance: results from an experimental hurricane. *Ecology* **80**: 2683–2696.
- Coutts MP, Grace J, eds. 1994.** *Wind and trees*. Cambridge: Cambridge University Press.
- Donnelly JP, Woodruff JD. 2007.** Intense hurricane activity over the past 5,000 years controlled by El Niño and the West African monsoon. *Nature* **447**: 465–468.
- Dosmann MS. 2006.** Research in the garden: averting the collections crisis. *Botanical Review* **72**: 207–234.
- Emmanuel KA. 2005.** Increasing destructiveness of cyclones over the past 30 years. *Nature* **436**: 686–688.
- Fetcher N, Cordero RA, Voltzow J. 2000.** Lack of ecotypic differentiation: plant responses to elevation, population origin, and wind in the Luquillo Mountains, Puerto Rico. *Biotropica* **32**: 225–234.
- Fisher JB, Burch JN, Noblick LR. 1996.** Stem structure of the Cuban Belly Palm (*Gastrococcus crispus*). *Principes* **40**: 125–128.
- Frangi JL, Lugo AE. 1991.** Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* **23**: 324–335.
- de Gouvenain RC, Silander Jr JA. 2003.** Do tropical storm regimes influence the structure of tropical lowland rain forests. *Biotropica* **35**: 166–180.
- Gresham CA, Williams TM, Lipscomb DJ. 1991.** Hurricane Hugo wind damage to southeastern U.S. coastal forest tree species. *Biotropica* **23**: 420–426.
- Grove SJ, Turton SM, Siegenthaler DT. 2000.** Mosaics of canopy openness induced by tropical cyclones in lowland rain forest with contrasting management histories in northeastern Australia. *Journal of Tropical Ecology* **16**: 883–894.
- Gunn BF. 2004.** The phylogeny of the Cocoeae (Arecaceae) with emphasis on *Cocos nucifera*. *Annals of the Missouri Botanical Garden* **91**: 505–522.
- Hirsh H, Marler T. 1997.** Damage and recovery of *Cycas micronesica* after Typhoon Paka. *Biotropica* **34**: 598–602.
- Henderson A, Galeano G, Bernal R. 1995.** *Field guide to the palms of the Americas*. Princeton, NJ: Princeton University Press.
- Hollander M, Wolfe DA. 1999.** *Nonparametric statistical methods*, 2nd edn. New York, NY: Wiley-Interscience.
- Holt RD. 2006.** Making a virtue out of a necessity: hurricanes and the resilience of community organization. *Proceedings of the National Academy of Sciences of the USA* **103**: 2005–2006.
- Hopkins MS. 1990.** Disturbance – the forest transformer. In: Webb LJ, Kikkawa J, eds. *Australian tropical rainforests: science – values – meaning*. East Melbourne: CSIRO, 40–52.
- Horvitz CC, Koop A. 2001.** Removal of non-native vines and post-hurricane recruitment in tropical hardwood forests of Florida. *Biotropica* **33**: 268–281.
- Huang YS, Chen SS, Lin TP, Chen YS. 2002.** Growth strain in coconut palm trees. *Tree Physiology* **22**: 261–266.
- Isnard S, Speck T, Rowe NP. 2005.** Biomechanics and development of the climbing habit in two species of the South American palm genus *Desmoncus* (Arecaceae). *American Journal of Botany* **92**: 1444–1456.

- Jarvinen BR, Neumann CJ, Davis MAS. 1984. A tropical cyclone data tape for the North Atlantic Basin, 1886–1983: contents, limitations, and uses. *NOAA Technical Memorandum NWS NHC* 22.
- Jones C. 2006. After the hurricanes of 2005. *Palms* 50: 57–59.
- Klein WMcK. 1992. Fairchild Tropical Garden hit by Hurricane Andrew. *Principes* 36: 225–227.
- Kuo-Huang LL, Huang YS, Chen SS, Huang YR. 2004. Growth stresses and related anatomical characteristics in coconut palm trees. *IAWA Journal* 25: 297–310.
- Levins R. 1968. *Evolution in changing environments*. Princeton, NJ: Princeton University Press.
- Lippincott C. 1995. Reintroduction of *Pseudophoenix sargentii* in the Florida Keys. *Principes* 39: 5–13.
- Loope L, Duever M, Herndon A, Snyder J, Jansen D. 1994. Hurricane impact on uplands and freshwater swamp forest. *Bioscience* 44: 238–246.
- Ludlum D. 1963. *Early American Hurricanes, 1492–1870*. Boston, MA: American Meteorological Society.
- Miller DL, Mora CI, Grissino-Mayer HD, Mock CJ, Uhle ME, Sharp Z. 2006. Tree-ring isotope records of tropical cyclone activity. *Proceedings of the National Academy of Sciences of the USA* 103: 14294–14297.
- Nauman CE, Sanders RW. 1991. Preliminary classificatory studies in *Coccothrinax* (Palmae: Coryphoideae). *Selbyana* 12: 91–101.
- Neumann CJ, Jarvinen BR, McAdie CJ, Hammer GR. 1999. Tropical cyclones of the North Atlantic Ocean 1871–1998. *Historical Climatology Series* 6.
- von Neumann JR, Kent H, Bellinson HR, Hart BI. 1941. The mean square successive difference. *Annals of Mathematical Statistics* 12: 153–162.
- Niklas KJ. 1992. *Plant biomechanics: an engineering approach to plant form and function*. Chicago, IL: University of Chicago Press.
- Niklas KJ. 1999. A mechanical perspective on foliage leaf form and function. *New Phytologist* 143: 19–31.
- NOAA. 2007. *Re-analysis project*. Atlantic Oceanographic and Meteorological Laboratory, Hurricane Research Division.
- Nyberg J, Malmgren BA, Winter A, Jury MR, Kilbourne KH, Quinn TM. 2007. Low Atlantic hurricane activity in the 1970s and 1980s compared to the past 270 years. *Nature* 447: 698–702.
- Ostertag R, Silver WL, Lugo AE. 2005. Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica* 37: 16–24.
- Pasch RJ, Blake ES, Cobb HDIII, Roberts DP. 2006. *Tropical cyclone report: Hurricane Wilma, 15–25 October 2005*. National Oceanic and Atmospheric Administration, Miami.
- Pezza AB, Simmonds I. 2005. The first South Atlantic hurricane: unprecedented blocking, low shear and climate change. *Geophysical Research Letters* 32: L15712.
- Putz FE, Shanz RR. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, U.S.A. *Canadian Journal of Forest Research* 21: 1765–1770.
- Quine CP, Bell PD. 1998. Monitoring of windthrow occurrence and progression in spruce forests in Britain. *Forestry* 71: 87–97.
- Reboud X, Bell G. 1997. Experimental evolution in *Chlamydomonas*. III. Evolution of specialist and generalist types in environments that vary in time and space. *Heredity* 78: 507–514.
- Reeve J, Abouheif E. 2003. *Phylogenetic independence*, Version 2.0. Department of Biology, McGill University.
- Rich PM. 1986. Mechanical architecture of arborescent rain forest palms. *Principes* 30: 117–131.
- Rich PM. 1987. Mechanical structure of the stem of arborescent palms. *Botanical Gazette* 148: 42–50.
- Schoener TW, Spiller DA. 2006. Nonsynchronous recovery of community characteristics in island spiders after a catastrophic hurricane. *Proceedings of the National Academy of Sciences of the USA* 103: 2220–2225.
- Sterken P. 2007. *The elastic stability of palms*. Brussels: Peter Sterken.
- Tomlinson PB. 1962. The leaf base in palms – its morphology and mechanical biology. *Journal of the Arnold Arboretum* 43: 23–45.
- Tomlinson PB. 1990. *The structural biology of palms*. Oxford: Oxford University Press.
- Tomlinson PB. 2006. The uniqueness of palms. *Botanical Journal of the Linnean Society* 151: 5–14.
- Totland O. 2001. Environment-dependent pollen limitation and selection on floral traits in an alpine species. *Ecology* 82: 2233–2244.
- Uhl NW, Dransfield J. 1987. *Genera Palmarum*. Lawrence, KS: Allen Press.
- Vandermeer J. 1994. Effects of Hurricane Joan on the palms of the Caribbean coast rainforest of Nicaragua. *Principes* 38: 182–189.
- Webb LJ. 1958. Cyclones as an ecological factor in tropical lowland rainforest, north Queensland. *Australian Journal of Botany* 6: 220–228.
- Zimmermann JK, Everham EMIII, Waide RB, Lodge DJ, Taylor CM, Brokaw NK. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* 82: 911–922.