Palm Stem Shape Correlates with Hurricane Tolerance, in a Manner Consistent with Natural Selection

M. PATRICK GRIFFITH

ERICKA WITCHER

LARRY NOBLICK

AND

CHAD HUSBY

Montgomery Botanical Center
11901 Old Cutler Road
Miami, FL 33156
patrick@montgomerybotanical.org

Palms have been characterized as tolerant of high winds, but that may be a simplified view. The effects of hurricanes on palm collections at Montgomery Botanical Center offered the opportunity to investigate aspects of natural selection for wind tolerance. A major finding is that wind tolerance is correlated with geography – Caribbean palms are more resistant than South American palms. This finding prompted further investigation of palm habit – basic morphology – in relation to wind resistance. Here, we present data on basic stem shape (height and diameter), root habit characters and their relationship to wind tolerance, using examples from *Coccothrinax* and *Syagrus*. We find that stem shape correlates with hurricane tolerance in *Syagrus*, but not in *Coccothrinax*; this is consistent with natural selection of Caribbean palms for high winds.

Growing palms is a rewarding pursuit most days. Even so, from time to time, pests, accidents, or lightning can bring disappointment or even heartache. Probably the worst palm tragedies come from cyclones, severe tropical windstorms, which are called hurricanes in the Atlantic. This journal reported on one such disaster 20 years ago (Klein 1992).

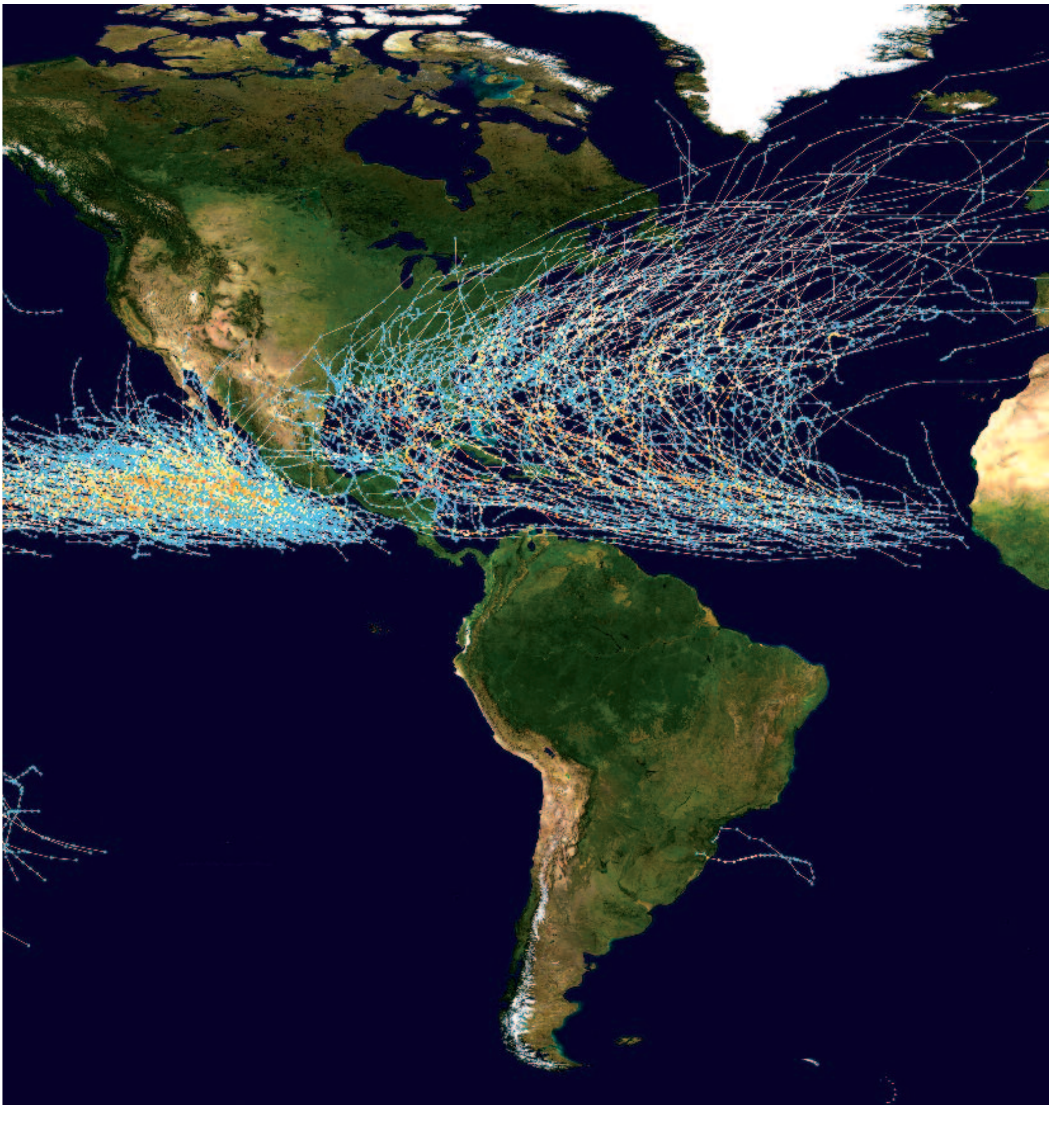
Even that report highlighted one potential benefit of such bad days. Klein (1992) noted the potential for scientific study on the plants lost to Hurricane Andrew – calling them "grist for the scientific mill." Fisher et al. (1996) made use of that 'windfall' to gain an understanding of ventricose palm trunk anatomy, using cultivated *Acrocomia*. Dowe (2009) similarly studied how wild

Archontophoenix palms are affected by major cyclones in the Southern Hemisphere. This work with palms fits into a context of other new findings that come from hurricanes (e.g. Horvitz & Koop 2001, Holt 2006).

At Montgomery, Hurricane Wilma in 2005 offered an opportunity to learn about palms and how they tolerate very high winds. These studies found that Caribbean palm species have evolved greater tolerance for high winds than South American palms (Griffith et al. 2008). This was fairly straightforward; we had assembled palms from throughout the New World in one location, and after the hurricane, we simply counted how many were lost as a result. Since we knew where these garden palms were collected, and could make estimates of how they were related (based on Asmussen et al. 2006 and others), we could compare hurricane tolerance with biogeography and phylogeny.

Our opinion was that palms offer an excellent model system to investigate evolution of hurricane tolerance (Griffith et al. 2008) because the single growing point on many palm species meant that severe wind damage

1. Extent of cyclone geography in the New World (Public domain image adapted from US National Oceanic and Atmospheric Administration data). This composite of all cyclone tracks from 1985-2005 demonstrates the near-discrete boundaries of the 'hurricane-prone' Caribbean and 'hurricane-free' South America, at more or less 10 degrees north latitude. *Coccothrinax* is native to the hurricane-prone area, and *Syagrus* is native to the hurricane-free area (with one exception).



would be a strong force of natural selection; if the single trunk fails, that palm will not reproduce again. The other fact that made this study possible is the near-binary geographic distribution of hurricanes in the Western Hemisphere (Fig. 1).What these conditions allowed was a technical insight on natural selection in this group. In the strict sense, natural selection works to reduce variation in a given trait. We found that South American palms were quite variable with regard to surviving high winds, but Caribbean palms were uniformly resistant, demonstrating natural selection through frequent hurricanes. The hurricane tolerance of Caribbean palms was also shown to be correlated with geography alone, and independent of phylogeny (Griffith et al. 2008).

When that insight – that Caribbean palms evolved to survive high winds – comes up in conversation, it prompts a natural question: "how?" Our study simply discovered the correlation of biogeography and hurricane tolerance. We included some basic comparisons (e.g. *Pseudophoenix*, *Coccothrinax* and *Syagrus*) to show that there appears to be no correlation with palmate vs. pinnate leaves, crownshaft vs. no crownshaft habit, or swollen vs. cylindrical trunks.

A Hypothesis

This paper continues the study of palms and hurricanes, by presenting a more detailed comparison of *Coccothrinax* and *Syagrus*, looking at data on very basic stem allometry and its relationship to mortality from hurricane damage. It is clear that for equal amounts of wind load, such as from a hurricane, and equal stem diameter and mechanical properties, a taller palm will have greater risk of mechanical failure (i.e. death), due to increased leverage. Thus, stem morphology may show patterns consistent with natural selection to resist high winds. Here, we explore this hypothesis – stem shape correlates to hurricane tolerance – using palms from hurricane-prone and hurricane-free areas.

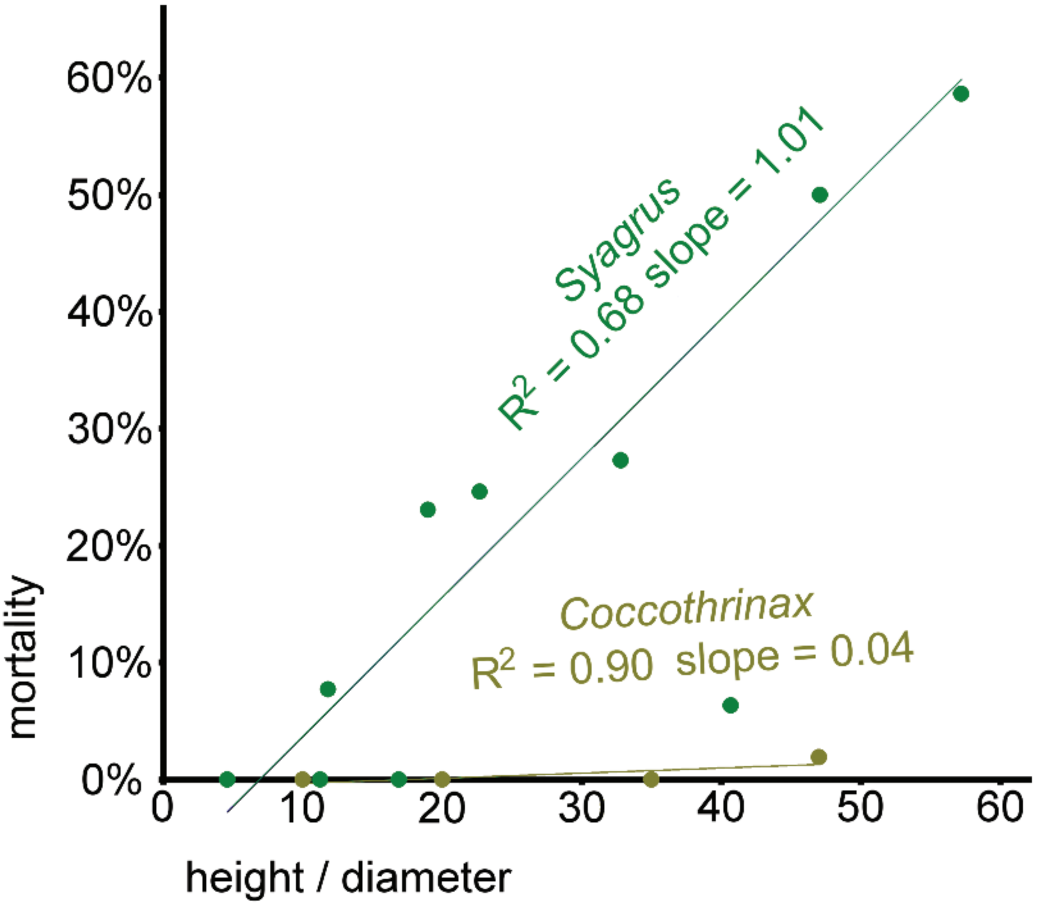
Methods

Palms studied: This study used collections of *Coccothrinax* and *Syagrus* at Montgomery Botanical Center. Specimens examined are detailed in Table 1. We chose to focus on these two genera for the following reasons: (1) adequate sample sizes of palms available, (2) availability of many species with single, self-supporting trunk habit (excluding rattans, branching, and clumping palms), and (3) the

Table 1. Species and number of plants examined, percent mortality, height / diameter ratio, and root diameter (in cm). Percent mortality data are from Griffith et al. (2008).

Species	n[1]	% mortality	Mean H / D	Mean root diameter (cm)
Coccothrinax argentata	13/7	0.00%	7.8±3.4	0.175±0.05
Coccothrinax barbadensis	106/10	1.90%	58.2±26.2	0.367±0.05
Coccothrinax scoparia	34/5	0.00%	23.7±3.3	0.3±0.1
Coccothrinax spissa	27/6	0.00%	10.3±0.8	0.2±0.1
Syagrus amara	13/5	0.00%	16.9±4.3	0.85±0.1
Syagrus botryophora	29/8	58.60%	57.2±6.0	0.325±0.08
Syagrus coronata	33/27	0.00%	4.6±5.5	$0.767 \pm 1.4 \times 10^{-16}$
Syagrus kellyana	11/17	0.00%	11.2±5.2	0.55±0.15
Syagrus oleracea	13/8	27.30%	32.8±5.5	0.475±0.2
Syagrus orinocensis	17/8	23.10%	19±5.3	0.65±0.1
Syagrus romanzoffiana	61/34	24.60%	22.7±6.7	0.367±0.11
Syagrus sancona	2/1	50.00%	47.1	0.45±0.13
Syagrus vermicularis	16/14	6.30%	41±11.6	0.425±0.05
Syagrus × costae	13/12	7.70%	11.8±2.54	0.7±0

[1] First n is for mortality data, second n is for morphology data.



2. Percent mortality as a function of height / diameter for each species in the study (Table 1). Green points are *Syagrus*, and tan points are *Coccothrinax*. Taller and thinner *Coccothrinax* are almost imperceptibly more likely to fail (slope = 1/25), while *Syagrus* failure is correlated with trunk shape (slope = 1/1).

geographic distribution of these two groups. *Coccothrinax* is essentially a Caribbean Basin genus (Henderson et al. 1995), and *Syagrus* is essentially a South American genus (Noblick et al. in press) — with one important exception, *Syagrus amara*. Finally, it was decided that the plants needed to be 10 years old or older, to exclude plants not yet mature enough.

Wind event: Specimens were examined for the effects of Hurricane Wilma, which crossed the study site on 24 October 2005. Wind speeds of up to 49–55 m/sec (95–105 knots) were recorded near the study site (Pasch et al. 2006).

Data collection: Data on plants killed as a result of the hurricane were compiled in the weeks after the wind event (as in Griffith et al. 2008). For this study, we also gathered measurements of height and diameter on living specimens of the study species at Montgomery. Height was determined by measuring from the ground at the base of the plant to the point where the petiole of the lowest green leaf crossed the vertical line of the trunk, this being the only consistently obtainable standard for height on these palms due to the presence of adherent leaf bases. On smaller palms (1–2 m), a retractable 10 m steel tape measure was used. On larger palms (2–5 m), an extendable fiberglass measuring pole was used, with the hook placed on the base of the lowest green petiole. On the tallest palms (≥ 5 m), a hypsometer was used, sighting from the point where the lowest green leaf attached to the trunk, and to the ground at the base of the plant. Three measurements were taken with the hypsometer and the average recorded. Diameter was measured at 1 m from ground level along the trunk for greater efficiency and consistency in the field, rather than at the traditional "DBH" of 4.5 feet. A 50 cm caliper was placed on top of the meter stick to measure the diameter of the trunk. When diameter exceeded 50cm, a measuring tape was used.

3 (left). *Syagrus amara* (MBC 96165*C) collected from Guadeloupe in 1996. This Caribbean species, in an otherwise South American genus, is exceptionally wind resistant. Note the prominent basal trunk swelling (see also Figure 6). 4 (right). An exceptionally tall (6.9 m to crown, 21 cm diameter) *Coccothrinax spissa,* MBC 60814*A. This individual (H/D = 32.8) is known as the Florida State Champion of its species. The seed was collected in 1960 in the Dominican Republic. At Montgomery, it has survived decades of high winds and several major hurricanes.

Preliminary survey of primary root diameters was also performed on a random subset of the palms studied.

Analysis: Height and Diameter were both standardized to m, and then divided to give the H/D ratio (Height divided by diameter), to provide a standard, dimensionless comparative measure of how stout each palm is relative to its height. H/D was averaged to give a mean H/D value for each species. Root diameters were also averaged for each species. The metrics were graphed against % mortality data (Griffith et al. 2008) using Excel (Microsoft Corporation 2010), and simple linear least-squares regressions and R^2 values were calculated.

Results

Percent mortality for each species is compared to its H/D ratio in Table 1. Percent mortality varied from no loss (e.g. *Coccothrinax argentata*) to nearly 60% (*Syagrus botryophora*). Figure 2 plots these points, and shows an immediately obvious difference between the two genera studied. Linear regression on these data gives R^2 values of 0.37 for the total data, 0.68 for *Syagrus* taken alone and 0.90 for *Coccothrinax* taken alone, further establishing that the genera have divergent trends. The regression slopes for each genus were 1.01 for *Syagrus* and 0.04 for *Coccothrinax*. A test of the coefficient of an interaction term in a multiple regression model for the complete data shows that the difference in these regression slopes is statistically significant ($p = 0.0212$), and each regression is significant (*Coccothrinax*, $p=0.0463$; *Syagrus,* $p = 0.0032$).

Considering the hypothesis

Thus, our hypothesis – palms show patterns of hurricane mortality that correspond with stem

5. *Syagrus botryophora* collections at MBC the day after Hurricane Wilma (October 25, 2005). These were grown from seed collected in 1994, in Bahia, Brazil, and were thus 11 years old in this photo. These are relatively tall and thin *Syagrus* (Average H/D = 57.2). See also Figure 7.

shape – is confirmed for *Syagrus*, and rejected for *Coccothrinax*. *Coccothrinax* is invariably windproof in this analysis, regardless of its trunk shape. Although the regression slope for *Coccothrinax* was significantly greater than 0, the magnitude is so small (4%) as to be effectively negligible, and certainly far lower than for *Syagrus,* which as a genus has an essentially 1:1 relationship between H/D and % mortality.

Since *Coccothrinax* is mainly distributed in the Caribbean Basin, we expect it has been selected for high winds, due to the ongoing presence of hurricanes there over millennia (Griffith et al. 2008). The very low range of % mortality (0–1.9%), regardless of stem shape, is consistent with natural selection for hurricane tolerance. On the other hand, *Syagrus* shows much greater variation (0–58.6% mortality) in its tolerance for high winds. As a South American genus, *Syagrus* has evolved in a hurricane-free environment, and thus continues to possess variation in wind tolerance, as this trait has not been under the same selective forces as Caribbean palms.

One exceptional *Syagrus* is *S. amara* (Fig. 3), the only *Syagrus* not native to South America, but found in the Lesser Antilles. Since these islands are exposed to hurricanes, we expect reduced mortality in *S. amara*, consistent with natural selection. We see exactly that; *S. amara* showed no mortality, despite H/D of 16.9. The only other *Syagrus* with no mortality are *S. kellyana* and *S. coronata*, which have the lowest and second-lowest H/D in the group.

At the other end of this trend is *S. botryophora* (Fig. 5), native to the Atlantic Coastal Forest of Brazil (Lorenzi et al. 2010). Montgomery lost well over half of its collection of *S. botryophora* to storms in 2005, and it has the highest H/D of the group, at 57.2. *Syagrus botryophora* evolved in a hurricane-free environment, and this tall, thin, fast-growing palm saw exceptional damage. Thus, the ability of *Syagrus* to survive high winds appears related to stem dimensions, where these palm trunks function as levers; with longer trunks, a given wind load can exert greater force at ground level, thus requiring greater trunk strength, perhaps obtained through greater diameter (cf. Sterken 2008).

Is there a 'hurricane habit' for palms?

So, although trunk shape can help explain hurricane mortality in *Syagrus*, it does little to explain how *Coccothrinax* tolerates high winds. *Coccothrinax* shows much variation in trunk


6 (left). *Syagrus amara* (MBC 20030597*A); see also Figure 3. Roots of this species are exceptionally robust within the genus, with diameter often reaching over 1cm. 7 (right). *Syagrus botryophora* (MBC 941217*F); see also Figure 4. Roots of *S. botryophora* are much thinner (Table 1) compared to *S. amara* (Figure 6).

shape, from very stout palms (e.g. *C. spissa*, Fig. 4), to very tall, slender plants (e.g. *C. barbadensis*), yet all are consistently windproof. So we return to that previous question of "how?"

Future investigations of trunk anatomy (cf. Fisher et al. 1996; Tomlinson 2006) could offer insight on how palms become windproof. One approach to this stem anatomy research would be to compare *Syagrus amara* to other *Syagrus* species. Another potential approach would be to quantify and survey the often swollen trunk bases of these palms. *Syagrus amara* collections at Montgomery show prominent basal swellings (Fig. 3). Since other Caribbean palms are quite divergent in habit and shape, perhaps a heretofore unexamined aspect such as root habit may influence wind tolerance. The above-mentioned basal trunk swellings in *S. amara* may enable greater numbers of roots. Individual roots may also play a role; initial survey shows that within *Syagrus*, *S. amara* has exceptionally robust root diameter (Fig. 6), while *S. botryophora* has very slender roots (Fig. 7). Preliminary survey of these primary root diameters shows some correlation between increasing root diameter and decreased wind mortality in *Syagrus* (slope = -0.81, R^2 = 0.47; data from Table 1). So, perhaps further examination of root morphology and structure will reveal a key adaptation for palms in high wind environments.

Differences in mode of failure can also be considered (Griffith et al. 2008). For example, Fig. 5 shows *Syagrus botryophora* specimens that are either uprooted or broken at mid-trunk.

Table 2. Relative proximate cause of mortality of *Syagrus* at MBC due to hurricanes.

Cause	Percentage of losses
Unspecified mechanical damage	40%
Uprooted/toppled	36%
Trunk snapped	20%
Crushed by falling debris	4%

Mechanical failure of the crown was also observed. Review of all *Syagrus* lost to storm damage at Montgomery shows no clear majority of failure mode (Table 2). Further investigation of failure mode as compared to morphology will certainly provide additional insight.

Everyone involved with this palm collection hopes for no further hurricanes. However, given current knowledge in the biology of wind tolerance in palms, the next storm will present further opportunity for research.

Acknowledgments

We thank: Charles Bauduy, Laurie Danielson, Xavier Gratacos, Sandra Rigotti-Santos, Randy Russ, Arantza Strader and John Watson for caring for the palms and stewarding the data used here, and an anonymous reviewer for helpful suggestions.

LITERATURE CITED

ASMUSSEN, C.B., J. DRANSFIELD, V. DEICKMANN, A. S. BARFOD, J.-C. PINTAUD AND W.J. BAKER. 2006. A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny. Botanical Journal of the Linnaean Society 151: 15–38.

DOWE, J.L. 2009. A preliminary note on the impact of Cyclone Larry on populations of *Archontophoenix alexandrae* (Arecaceae), north Queensland, Australia. Palms & Cycads 102: 4–8.

FISHER, J.B., J.N. BURCH AND L.R. NOBLICK. 1996. Stem structure of the Cuban Belly Palm (*Gastrococcus crispa*). Principes 40: 125–128.

GRIFFITH, M.P., L.R. NOBLICK, J.L. DOWE, C.E. HUSBY,AND M. CALONJE. 2008. Cyclone tolerance in New World Arecaceae: biogeographic variation and abiotic natural selection. Annals of Botany 102: 591–598.

HENDERSON, A., G. GALEANO,AND R. BERNAL. 1995. Field guide to the palms of the Americas. Princeton University Press, Princeton, NJ.

HOLT, R.D. 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.

HORVITZ, C.C. AND A. KOOP. 2001. Removal of non-native vines and post-hurricane recruitment in tropical hardwood forests of Florida. Biotropica 33: 268–281.

KLEIN, W.M. 1992. Fairchild Tropical Garden hit by Hurricane Andrew. Principes 36: 225–227.

NOBLICK, L.R., W.J. HAHN, AND M.P. GRIFFITH. In press. Structural cladistic study of Cocoseae, subtribe Attaleinae (Arecaceae): Evaluating taxonomic limits in Attaleinae and the neotropical genus *Syagrus*. Brittonia.

PASCH, R.J., E.S. BLAKE, H.D. COBB III AND D.P. ROBERTS. 2006. Tropical cyclone report: Hurricane Wilma, 15–25 October 2005. Miami: National Oceanic and Atmospheric Administration.

STERKEN, P. 2008. The elastic stability of palms. Plant Science Bulletin 54: 153–154.

TOMLINSON, P.B. 2006. The uniqueness of palms. Botanical Journal of the Linnaean Society 151: 5–14.

The Bequest of Richard Douglas

Richard Douglas took great pride in developing his garden and donating his time to the Northern California local chapter of the Palm Society and served as IPS President during 1983 and 1984. Richard's generosity extended far beyond family, friends and acquaintances and was truly reflective of his love for palms. Richard left wonderful memories with all of us, but more than that, left us with a gift of life. The IPS has been given a generous bequest of $15,000 from his estate trust. We gratefully acknowledge this bequest to the IPS' endowment fund, which supports research and education.

LELAND LAI
President, IPS